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### RESEARCH ARTICLE

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## Flow and scour constraints on uprooting of pioneer woody seedlings

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#### Key Points:

- Uprooting thresholds for pioneer woody seedlings are measured with pull tests
- Uprooting thresholds are influenced by water table-dependent root morphology
- Scour decreases the uprooting threshold and fundamentally influences uprooting

#### Supporting Information:

- Supporting Information S1
- Figure S1
- Figure S2
- Figure S3
- Data Set S1

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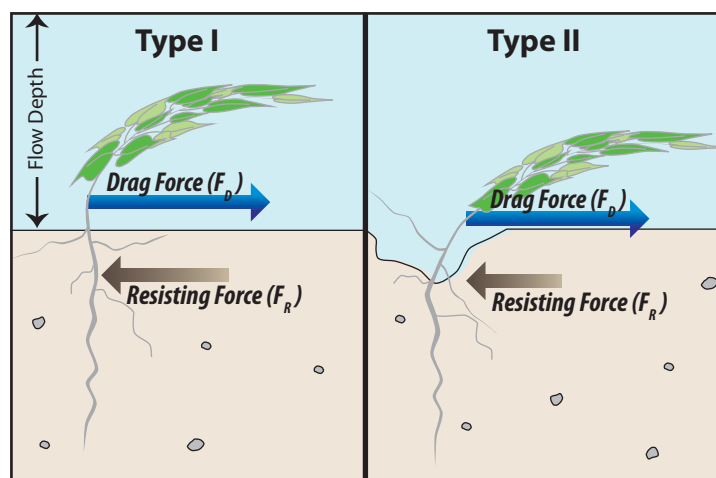
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**Abstract** Scour and uprooting during flood events is a major disturbance agent that affects plant mortality rates and subsequent vegetation composition and density, setting the trajectory of physical-biological interactions in rivers. During flood events, riparian plants may be uprooted if they are subjected to hydraulic drag forces greater than their resisting force. We measured the resisting force of woody seedlings established on river bars with in situ lateral pull tests that simulated flood flows with and without substrate scour. We quantified the influence of seedling size, species (*Populus* and *Tamarix*), water-table depth, and scour depth on resisting force. Seedling size and resisting force were positively related with scour depth and water-table depth—a proxy for root length—exerting strong and opposing controls on resisting force. *Populus* required less force to uproot than *Tamarix*, but displayed a greater increase in uprooting force with seedling size. Further, we found that calculated mean velocities required to uproot seedlings were greater than modeled flood velocities under most conditions. Only when plants were either shallowly rooted or subjected to substrate scour ( $\geq 0.3$  m) did the calculated velocities required for uprooting decrease to within the range of modeled flood velocities, indicating that drag forces alone are unlikely to uproot seedlings in the absence of extreme events or bar-scale sediment transport. Seedlings on river bars are most resilient to uprooting when they are large, deeply rooted, and unlikely to experience substrate scour, which has implications for ecogeomorphic evolution and river management.

### 1. Introduction

Woody riparian trees affect flow and sediment transport fields [Nepf, 2012; Yager and Schmeckle, 2013; Manners *et al.*, 2015] and as a result may have multiscale influences on river morphology [Tooth and Nanson, 2000; Gurnell and Petts, 2006; Curran and Hession, 2013]. Flume experiments on how vegetation affects flow and sediment transport have shown that plants generally steer and slow flow, which increases fine sediment deposition within vegetation patches [Zong and Nepf, 2010; Kui *et al.*, 2014]. These observations may explain how riparian vegetation alters river morphology over longer timescales, as pioneer riparian plants raise the elevation of bars on which they have recruited, ultimately building floodplains characterized by mature riparian forests [Bendix and Hupp, 2000; Osterkamp and Hupp, 2010]. The evolution of a channel in the presence of vegetation is therefore contingent on establishment of pioneer woody riparian seedlings on bars within active river channels, and subsequently either their survival or uprooting through flooding events that may inundate bars [Corenblit *et al.*, 2007]. This tipping point in the trajectory of river-vegetation interactions and ecosystem development—establishment and survival of pioneer riparian seedlings on river bars, versus uprooting before plants can instigate morphodynamic feedbacks—remains understudied despite its geomorphic and ecological implications [Edmaier *et al.*, 2011]. To address this gap in knowledge of ecogeomorphic feedbacks, in this study we quantify riparian seedling uprooting thresholds.

Ecologically, riparian trees act as “foundational” species that support other species and ecosystem functions [Ellison *et al.*, 2005]. However, riparian trees may cause adverse impacts. Vegetation may encroach in channels as a result of flow regulation or invasion of nonnative species, subsequently altering flood hydraulics, sediment transport, and channel morphology, decreasing stream conveyance capacity and increasing flood risk [Wu and He, 2009]. Such effects have been observed in many western U.S. rivers as a result of invasion of the nonnative woody shrub tamarisk (*Tamarix* spp.) within riparian zones [Allred and Schmidt, 1999; Merritt and Cooper, 2000; Swanson *et al.*, 2011; Manners *et al.*, 2014]. In response to ecological, flooding, and



**Figure 1.** Conceptual model of seedling uprooting, whereby river flow subjects a seedling to a drag force ( $F_D$ ) which, if it is greater than the resisting force of the roots and substrate ( $F_R$ ), uproots the seedling. Scour may reduce  $F_R$ , lowering  $F_D$  required to uproot a seedling [after Edmaier et al., 2011].

water-use concerns [Faanes and LeValley, 1993; Wu and He, 2009], management efforts have included manual removal, herbicide application [Shafroth et al., 2005; Pollen-Bankhead et al., 2009; Vincent et al., 2009], and flushing flows seeking to scour and uproot unwanted vegetation [Kondolf and Wilcock, 1996; Wilcock and Kondolf, 1996; Tena et al., 2013]. The success of these various management strategies has been mixed [Kondolf, 1998; Pollen-Bankhead et al., 2009], in part because the physical thresholds required to uproot seedlings are poorly understood.

Those uprooting thresholds depend on the balance between the flow forces acting on the vegetation during floods versus the forces stabilizing the plant. The force that vegetation experiences during flood flows can be parameterized as a drag force ( $F_D$ ):

$$F_D = \frac{1}{2} \rho C_D A_c U_c^2, \quad (1)$$

where  $\rho$  is density of water,  $C_D$  is drag coefficient,  $A_c$  is projected vertical frontal area, and  $U_c$  is approach velocity [Wu et al., 1999]. Vegetation may uproot during floods if the drag force ( $F_D$ ) exceeds the plant's resisting force ( $F_R$ ; Figure 1) [Gran and Paola, 2001; Coulthard, 2005; Edmaier et al., 2011, 2014].

Uprooting thresholds therefore depend not only on the flow strength but also on the factors controlling  $F_R$ , which we expect to include species-dependent and groundwater-dependent root morphology, and scour depth [Edmaier et al., 2011, 2014]. In noncohesive soils, such as those comprising river bars where riparian seedlings recruit,  $F_R$  increases with root length and number of roots [Bailey et al., 2002; Pollen-Bankhead and Simon, 2009; Schwarz et al., 2010; Edmaier et al., 2014]. Laboratory experiments with *Avena sativa* L. have found root length to be a primary factor controlling uprooting [Perona et al., 2012], although this has not been confirmed for woody riparian species. Root morphology, in turn, is strongly influenced by groundwater dynamics. Woody riparian species (e.g., *Populus* and *Salix*, of the Salicaceae family) typically grow lateral roots to soil depths that correspond to the upper limits of the water table during early growth of the plant, though taproots can extend farther [Amlin and Rood, 2002; Karrenberg et al., 2003; Stella and Battles, 2010; Rood et al., 2011; Pasquale et al., 2012]. A field experiment using *Salix* cuttings found root density to be greatest at a predictable, often occurring water table level [Pasquale et al., 2012]. Root length can also vary among species. For example, in the western U.S., *Tamarix* can achieve greater rooting depths than native trees under equivalent growing conditions [Stromberg, 2013]. Based on these findings, Pasquale et al. [2012] expected the depth to the greatest root density to influence uprooting susceptibility. Field tests of the resisting force of *Populus* trees found that bending and/or uprooting covaried with metrics of plant size [Stone et al., 2013; Peterson and Claassen, 2013].

Vegetation uprooting in noncohesive soils may occur by two distinct mechanisms (Figure 1) [Edmaier et al., 2011]. The first mechanism, Type I, occurs when the drag force acting on the plant ( $F_D$ ) exceeds its anchoring ability ( $F_R$ , in the absence of any scour), resulting in roots breaking or slipping out of the substrate. In Type II uprooting, scour around the base of the plant is required to reduce  $F_R$  before uprooting can occur. Scour-driven uprooting (Type II) can be further differentiated between scour induced by the presence of stems (which we will call Type IIa) and scour as a result of bar-scale or reach-scale topographic change (Type IIb). Type IIa uprooting has been proposed to occur because woody seedling stems can self-induce

local scour by causing flow separation in the form of a horseshoe vortex upstream of the seedling that scales with the diameter of the seedling [Schneider and Moggridge, 2009; Edmaier et al., 2011; Crouzy and Perona, 2012]. In addition, bar-scale or reach-scale scour and fill or spatially varying sediment transport may be important in decreasing  $F_R$  and driving Type IIb uprooting. Which of these scour-induced uprooting mechanisms is more likely to occur has not been evaluated to our knowledge. For both scour-related uprooting mechanisms, scour-related uprooting susceptibility likely differs between gravel-bed and sand-bed rivers, because in the latter a given scour depth may be easier to achieve [Wilcock, 1988].

Here we target persisting uncertainties in our mechanistic and quantitative understanding of the processes that influence the uprooting of pioneer woody seedlings on river bars that experience periodic flood inundation [Stella et al., 2013]. Our primary objective was to investigate the relative influence of aboveground and belowground factors controlling  $F_R$  for pioneer riparian seedlings that have recruited on bars. We expected a general relationship between plant size and  $F_R$ , with modifications to this relationship based on factors such as scour, root morphology, and species. We aimed to link  $F_R$  to root morphology, using both root morphometric variables for seedlings that were uprooted intact as well as water-table depth as a proxy for rooting depth for each seedling tested. A second objective was to evaluate the susceptibility of seedlings to uprooting during floods under alternative mechanistic frameworks, specifically from either drag forces alone acting on the aboveground portion of the plant (Type I) or these drag forces plus scour of river bed substrate (Type II).

We addressed our objectives by conducting field experiments measuring seedling resisting force ( $F_R$ ) with pull tests for seedlings ranging in species type, size, and morphology. To address how substrate scour influenced  $F_R$ , we simulated scour in our experiments. We also measured root morphology on a subset of seedlings that were excavated or uprooted intact to assess the influence of root morphology on  $F_R$ . We conducted these tests at sites that varied with respect to substrate (gravel or sand), groundwater conditions (depth to water table), and species present (*Populus* and *Tamarix*). To quantify statistically how  $F_R$  varied with the potential explanatory factors we tested, we used general linear models. We then related  $F_R$  to modeled and measured flood flows at our field sites to evaluate what flow conditions would be sufficient to uproot seedlings by Type I and Type II mechanisms. Finally, we evaluated the potential relative importance of Type IIa versus Type IIb scour-induced uprooting and compared results of our experiments to field observations of seedling uprooting. Our study, by quantifying drivers of seedling mortality by uprooting, targets a gap in understanding of the ecogeomorphic evolution of channels and provides guidance for river management.

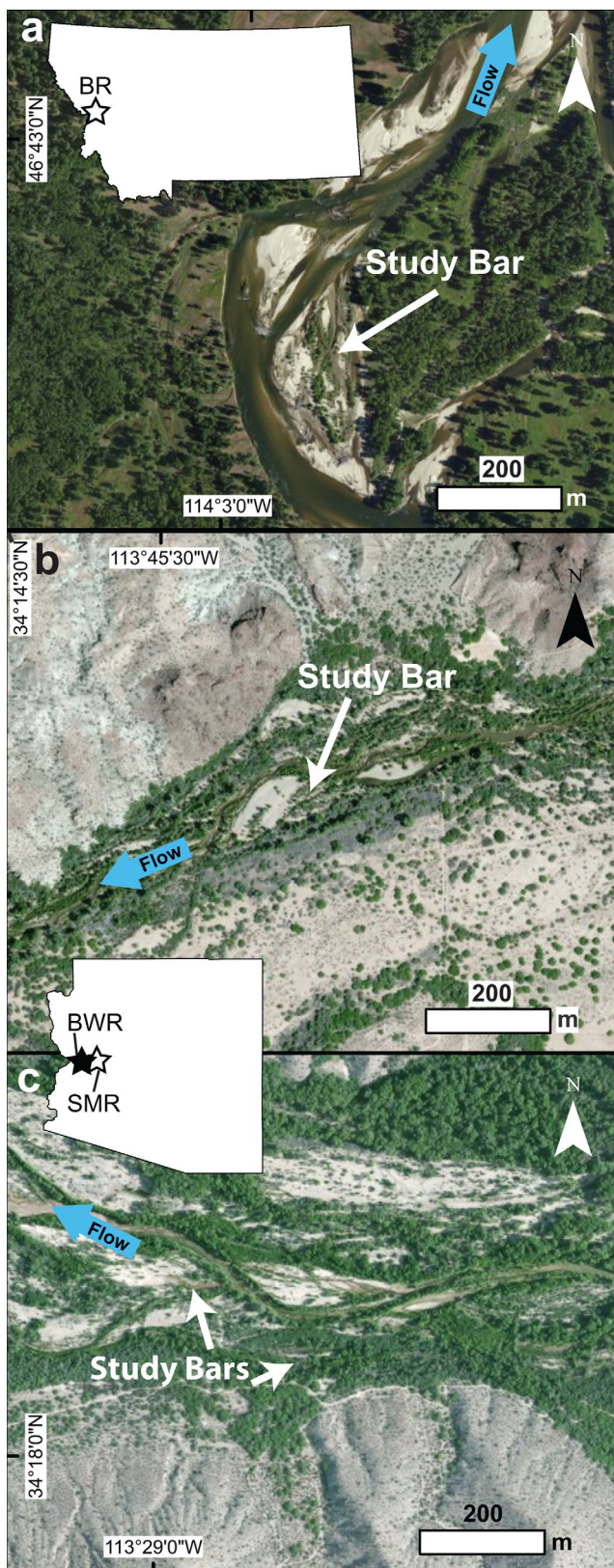
## 2. Methods

### 2.1. Site Characterization

We conducted field campaigns at three sites in order to measure uprooting susceptibility: the Bitterroot River (BR), Montana, the Bill Williams River (BWR), Arizona, and the BWR's tributary the Santa Maria River (SMR), Arizona (Figure 2 and Table 1). Using these three sites allowed us to test how  $F_R$  varied with respect to variations in groundwater conditions, species present, and grain size, which in turn allowed us to test differences in potential uprooting mechanisms (Types I, IIa, or IIb) at the sites, given the grain-size dependence of channel-bed erosion. The BR is an unregulated gravel-bed river. The BWR is a dammed sand-gravel and fine-gravel bed river where regulation has reduced flow variability and resulted in elevated, more static groundwater conditions compared to the SMR, an unregulated sand-bed river [Shafroth et al., 2000].

To characterize bed-material size, we conducted pebble counts at the BR site (supporting information Figure S1), and we used the grain size data of Dekker [2012] for the BWR and SMR sites. River water elevation and groundwater levels were measured with real-time kinematic (RTK) GPS during field campaigns representing base flow conditions (summer 2012 for BR; spring 2013 for BWR and SMR). A groundwater surface map was then derived from kriging between measurements of groundwater and river stage elevation

We chose bars at the study sites at a range of elevations above base flow stage, such that a range of water-table depths were captured. Bars contained pioneer woody seedlings (*Populus* and *Tamarix*) that were approximately 1–5 years old. Different species of *Populus* occurred at the Arizona and Montana sites (*P. fremontii* and *P. trichocarpa*, respectively). These species have different morphologies, but each represents a native foundational species within its respective ecosystem. *Tamarix* spp. were present only at the Arizona sites.



**Figure 2.** Study sites for seedling-uprooting pull tests: (a) the Bitterroot River (BR), Montana; (b) the regulated Bill Williams River (BWR), Arizona; and (c) the Santa Maria River (SMR), Arizona, which is an unregulated tributary to the BWR; Bing Imagery.

**Table 1.** Summary of Conditions at Each Field Site

Parameter	Bitterroot River (BR)	Bill Williams River (BWR)	Santa Maria River (SMR)
Hydrology	Unregulated snowmelt	Dam-regulated dryland	Unregulated dryland
Bed material	Gravel	Sand and fine gravel	Sand
Climate	Dry subhumid	Arid/subarid	Arid/subarid
Pioneer woody species	<i>Populus trichocarpa</i> , <i>Salix exigua</i>	<i>Populus fremontii</i> , <i>Salix gooddingii</i> , <i>Tamarix ramosissima</i>	<i>Populus fremontii</i> , <i>Salix gooddingii</i> , <i>Tamarix ramosissima</i>
Groundwater	Seasonally variable	Elevated/near surface	Seasonally variable
Drainage area (km <sup>2</sup> )	6,500	12,000	3,700
Median grain size (mm)	23 <sup>a</sup>	2.6	0.77

<sup>a</sup>Grain size data are presented in supporting information Figure S1.

### 2.2. Seedling Characterization

Seedlings for pull tests were selected at random and their elevations and locations were surveyed with RTK GPS. We calculated base flow depth to water table for each seedling by subtracting the water table elevation surface from the seedling's surveyed elevation. Plant height and basal area were recorded and frontal area ( $A_c$ ; equation (1)) was calculated by the method described by *Lightbody and Nepf* [2006] using a Canon Rebel XT digital camera, a blue background with a vertical and horizontal scale, and image processing in Adobe Photoshop and Matlab Image Analysis Toolbox. Difficulties in maintaining uniform photo conditions (e.g., lighting, camera angles) in the field result in error associated with this method of approximately 20% [*Lightbody and Nepf*, 2006].

To measure root frontal area, we excavated a subset of seedlings ( $n = 34$ ,  $n = 7$ ,  $n = 9$  for the BR, BWR, and SMR, respectively; Table 2) chosen at random from the same population as pull-test seedlings by carefully digging around the seedlings and extracting them. Plants were laid as they appeared in situ on a blue background, and root frontal area was extracted using the photographic method described above, using total root frontal area as a metric of biomass. In addition, we determined the depth at which the highest root density occurs by binning root frontal area in 1 cm intervals [*Pasquale et al.*, 2011] and locating the maximum, thereby allowing us to evaluate whether the depth to the greatest root density influences uprooting susceptibility, as proposed by *Pasquale et al.* [2012].

### 2.3. Lateral Pull Test Experiments

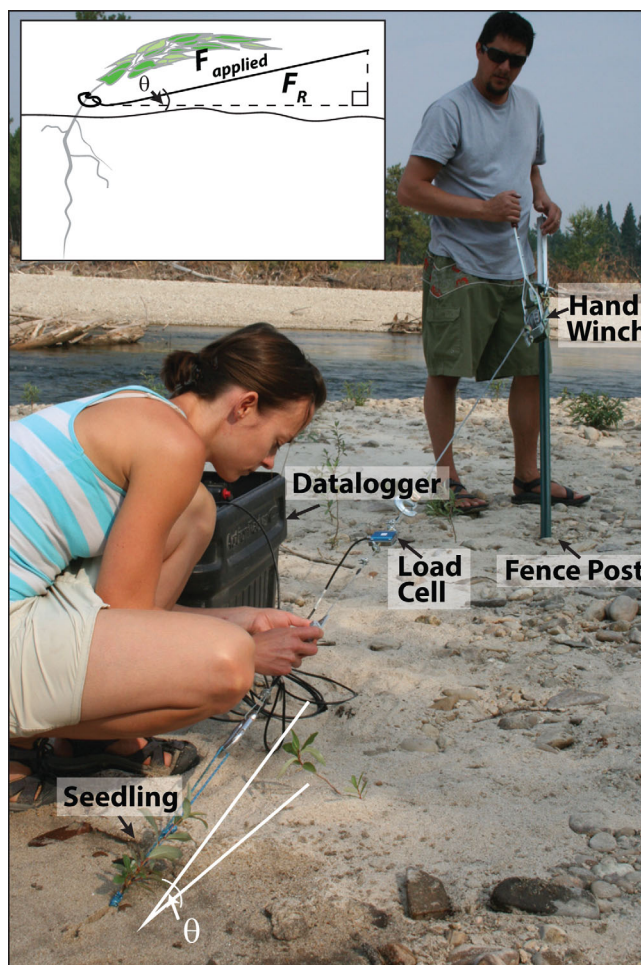
To address the challenge of measuring the forces associated with flood-induced seedling dislodgement, we used lateral pull tests [*Stone et al.*, 2013; *Peterson and Claassen*, 2013] that mimicked high-flow conditions,

while simultaneously being reproducible and mobile at the field sites, to measure the resistance of seedlings to uprooting ( $F_R$ ) by floods. To simulate the concentration of drag force below the leaves, near the base of the seedling, when riparian seedlings are submerged and bent [*Wilson*, 2007], we attached a metal cord to a rope loop placed around the seedling base and uprooted the seedling laterally in the downstream direction. We uprooted seedlings using a hand winch (assisted by a PullPal counterweight for larger seedlings) anchored to a fencepost installed 2 m downstream of the plant (Figure 3). Exerted force was continuously recorded by an Omega environmentally protected load cell (445 or 2224 N depending on plant size; manufacturer reported error = 0.25%) attached to a Campbell CR800 data logger. The sediment in a 1 m radius around the base of each seedling was wetted prior to pull tests, using 30 L of water, to simulate subaqueous moisture

**Table 2.** Sample Sizes (n) for Seedling Pull Tests and Excavations<sup>a</sup>

Experiment Type	Populus	Tamarix
BR		
Scour Depth (m)		
0	83	NA
0.1	34	NA
0.2	33	NA
0.3	34	NA
0.4	13	NA
Excavated	34	NA
BWR		
Scour Depth (m)		
0	39	34
0.2	8	8
Excavated	1	6
SMR		
Scour Depth (m)		
0	28	28
0.2	15	6
0.3	6	5
Excavated	5	4

<sup>a</sup>Pull tests were conducted for different scour depths, and a subset of seedlings were excavated (supporting information Data Set S1).



**Figure 3.** Experimental pull test setup as implemented in the field. Seedlings were pruned and  $\theta$  measured (with respect to horizontal) and uprooted using a hand winch from manually saturated sediments. The maximum pullout force,  $F_{applied}$ , was recorded using a load cell and data logger. The horizontal resisting force,  $F_R$ , was calculated as the horizontal component of the applied force (inset).

experimentation, we removed sediment in a 1 m radius around the base of each seedling until the assigned scour depth was achieved and conducted the pull tests as described previously. The 1 m radius was chosen to allow for digging down to 0.4 m depth without collapse, and for consistency among scour treatments. The 0.4 m treatment was only conducted at the BR site, and was therefore excluded from the statistical analyses. Sediment excavation completely uprooted some seedlings, resulting in zero force necessary for removal.

#### 2.4. Statistical Models

To quantify the influence of multiple factors on  $F_R$ , we developed linear mixed-effects models [Crawley, 2007], treating site as a random factor to control for environmental differences between the three river environments (e.g., with regard to grain size, climate, and discharge regime). We conducted analyses to examine (1) how  $F_R$  varied with seedling morphology, water-table depth, scour depth (Type I versus Type II conditions), and species; and (2) how root morphology influenced  $F_R$ .

Variables with nonnormal residual distributions (seedling height, seedling frontal area, seedling diameter, and seedling root length) were log-transformed to satisfy residual assumptions. The response variable,  $F_R$ , displayed increasing variance and a nonnormal residual distribution and was therefore also log transformed. For seedlings that were completely excavated with zero applied force, we assigned them a nominal force of 1 N to accommodate the log transformation. In some cases, seedlings were inundated at base flow

conditions, although full saturation may not have been achieved. We tested 83, 73, and 56 seedlings for the BR, BWR, and SMR sites, respectively (Table 2). Seedlings experienced pronation (from vertical) of  $76 \pm 9^\circ$ , consistent with flume measurements of seedling pronation during high flows [Manners et al., 2015].

We calculated the resisting force,  $F_R$ , as the horizontal component of the maximum pullout force. This entailed multiplying the maximum uprooting force, as determined using each force trace from the load-cell data, by  $\cos(\theta)$ , where  $\theta$  is the angle between the ground surface and the pruned plant, which we measured with a hand-held Kranz inclinometer (Figure 3). This approach allowed us to compare resisting force to the horizontal component of drag force.

To evaluate how scour depth influenced  $F_R$  and to measure  $F_R$  under Type I versus Type II conditions, we performed identical pull tests for seedlings chosen at random under conditions of simulated scour ( $n = 114$ ,  $n = 16$ ,  $n = 32$  for the BR, BWR, and SMR sites, respectively; Table 2). These pull tests were otherwise identical to those performed on seedlings in intact sediment. Seedlings were assigned a scour depth (0.1, 0.2, or 0.3, or 0.4 m) and prior to

**Table 3.** Pearson Correlation Coefficients Between Seedling Variables With Correlations >0.5 (Moderate Correlation) Italicized and Those >0.7 (Strong Correlation) in Bold

Parameter	Pullout Force (N)	Frontal Area (m <sup>2</sup> )	Height (m)	Basal Diameter (m)	Depth to Water Table (m)	Scour Depth (m)	Root Frontal Area <sup>a</sup> (m <sup>2</sup> )	Depth to Highest Root Density <sup>a</sup> (m)	Root Length <sup>a</sup> (m)
Pullout force (N)	1	<i>0.66</i>	<i>0.55</i>	<i>0.58</i>	0.11	0.26	<b>0.80</b>	0.41	0.38
Frontal area (m <sup>2</sup> )		1	<i>0.48</i>	<i>0.56</i>	0.02	0.04	<b>0.72</b>	0.30	0.41
Height (m)			1	<i>0.62</i>	<i>0.57</i>	0.09	<b>0.73</b>	0.33	<i>0.50</i>
Basal diameter (m)				1	0.24	0.07	<i>0.60</i>	0.31	0.49
Depth to water table (m)					1	0.27	0.24	0.03	0.25
Scour depth (m)						1	0.09	0.16	0.19
Root frontal area (m <sup>2</sup> )							1	0.36	<i>0.64</i>
Depth to highest root density (m)								1	0.22

<sup>a</sup>Root variables (root frontal area, depth to highest root density, and root length) were measured for excavated plants and for intact uprooted plants.

conditions, and therefore had a negative water-table depth. Because in the models, we considered water-table depth as a proxy for rooting depth, we assigned a value of zero for any negative values of water-table depth (i.e., inundated plants), assuming that any depth of standing water had effects on rooting depth comparable to fully saturated conditions. For all analyses, we used a likelihood-based approach to model selection, constructing alternative models from the variables of interest and comparing them via Akaike Information Criteria (AIC) and Akaike model weights [Burnham and Anderson, 2002], such that we were not choosing the best predictors. The software R (version 3.1) was used for all statistical analyses, as well as for the Monte Carlo simulations described in section 2.5 [R Development Core Team, 2014].

To develop a general relationship between how  $F_R$  varied with plant size, water-table depth, and scour depth, we conducted an all-site analysis in which those variables were continuous predictors of  $F_R$ , with site as a random factor in all candidate models. We repeated this analysis with the addition of species as a fixed factor, excluding the BR site, where the absence of *Tamarix* precluded testing of *Populus-Tamarix* differences. In specifying the candidate models, we used alternative measures of plant size (i.e., height, diameter, and frontal area), but included only one of these collinear variables in any candidate model. For model selection, we compared a full model with two-way interactions to all simpler models, and included a null model with only site as a random factor. This approach, by including multiple metrics of plant size, allowed us to determine which morphologic variable is most important in predicting  $F_R$ .

We conducted a parallel analysis for the subset of uprooted seedlings for which intact roots were salvaged. We predicted  $F_R$  by candidate models that included root frontal area or root length, because of their correlation ( $R = 0.73$ ; Table 3), depth to the greatest root density, and scour depth, with site as a random factor; the analysis was also repeated for the Arizona sites to test for *Populus-Tamarix* differences. We then included both salvaged pull test seedlings and excavated seedlings for which root morphology metrics were measured in analyses to relate the most influential root morphology metric, as determined here, to seedling size and water-table depth, with site as a random factor and, for the Arizona sites, species as a fixed factor.

### 2.5. Uprooting Velocities

As a means of evaluating seedling uprooting during floods, we calculated “uprooting velocity” ( $U_c$ ), which we define as the minimum velocity necessary to overcome the seedlings’ resisting force and cause uprooting, and then compared these values to modeled or measured flood velocities for our field sites. We calculate  $U_c$  by equating  $F_D$  (equation (1)) and  $F_R$ , then solving for  $U_c$ :

$$U_c = \sqrt{\frac{2 \cdot F_R}{\rho C_D A_c}}, \tag{2}$$

where  $F_R$  is based on measured values from pull tests,  $\rho$  is water density (1000 kg/m<sup>3</sup>),  $C_D$  is drag coefficient, and  $A_c$  is frontal area. For  $C_D$ , we use a skewed-normal distribution of possible  $C_D$  values (mean 2, standard deviation 1.3, skewness parameter 10), based on literature values for the mode [Nikora et al., 2013] and skewed range (1–10) [James et al., 2004] of  $C_D$  for seedlings and foliage. We measured  $A_c$  via photographic methods (section 2.2) and modified the resulting  $A_c$  values by a reduction coefficient to account for flow-



induced pronation [Wilson, 2007] or streamlining of leaves [Wilson et al., 2008]. We used a normal distribution of possible reduction coefficients for  $A_c$ , with a mean of 0.7 and ranging from 0.4 to 1.0 (standard deviation 0.08). These values are based on flume observations [Aberle and Järvelä, 2013; Jalonen et al., 2013; Whittaker et al., 2013; Västilä and Järvelä, 2014] indicating that seedlings are most likely to reduce their frontal area during flood events to 70% of their unpronated frontal area ( $A_c$ ), with variation around that value. We solved  $U_c$  (2) for each seedling using Monte Carlo simulations, whereby a value for the  $A_c$  reduction coefficient and value for  $C_D$  were selected randomly from the respective distributions for each seedling 1000 times. These values represent a population of seedlings that may uproot at different velocities, given a priori variability in  $F_R$  combined with variability in hydraulic properties (flexibility, streamlining,  $C_D$ ) that would be expected in a given population.

To place our  $U_c$  population in context and to assess the range of flow magnitudes under which seedlings would uproot, we compared calculated  $U_c$  values to velocities representing field conditions. To estimate high-flow velocities for our field sites, we constructed 1-D HEC-RAS 4.1.0 hydraulic models of the BR and SMR (supporting information Figure S2), and we used a calibrated HEC-RAS model (U.S. Army Corps of Engineers Hydrologic Engineering Center, 2009) for the BWR (supporting information Figure S3), for flood discharges with recurrence intervals of 2, 10, 20, and 100 years (i.e.,  $Q_2$ ,  $Q_{10}$ ,  $Q_{20}$ , and  $Q_{100}$ ). Details of methods used in the HEC-RAS modeling are provided in supporting information. The 1-D modeling used here does not resolve cross-sectional variations in velocities, which are typically lower on bars where seedlings recruit. Therefore, we consider our modeled velocities to be upper bounds on conditions experienced by seedlings. We also compared calculated values to field velocities measured within vegetation patches on the BWR during a 69 m<sup>3</sup>/s flow event in 2006 [Wilcox and Shafroth, 2013].

### 3. Results

#### 3.1. Effect of Seedling Morphology, Water-Table Depth, Scour Depth, and Species on $F_R$

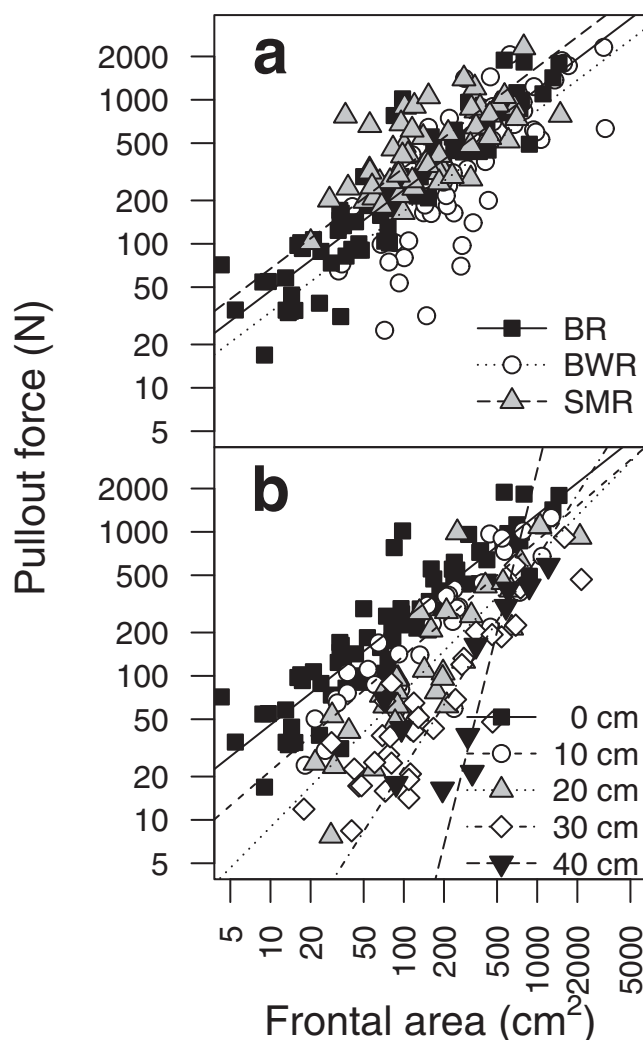
Measured pullout force ( $F_R$ ) was most strongly correlated with frontal area, height, basal diameter, and root frontal area, as indicated by Pearson correlation coefficients (Table 3). These various metrics of plant size, values for which are reported in supporting information Table S2, were also correlated with one another ( $R > 0.50$ ; Table 3).

Mixed-effects models (supporting information Tables S3 and S4) showed that frontal area was the best metric of plant size in predicting  $F_R$ . Frontal area increased pullout force ( $F_R$ ), in a power relationship (Figures 4a and 5), and had the strongest effect on  $F_R$  among variables tested. Scour depth acted to decrease  $F_R$  (Figure 4b), and water-table depth acted to increase  $F_R$  (Figure 5). Scour reduced  $F_R$  the most for small seedlings and for seedlings with greater water-table depths, as indicated by the interaction terms (Figures 6a and 6b and supporting information Table S3).

The analysis of the Arizona sites, which focused on elucidating differences in  $F_R$  between *Populus* and *Tamarix*, showed that species had an additional effect on  $F_R$ , although the effect was smaller than that of frontal area, water-table depth, and scour depth. *Populus* required less force to uproot compared to *Tamarix* for a given size. The interaction between frontal area and species shows that  $F_R$  varied more for a given size for *Populus* than for *Tamarix* (Figure 6c and supporting information Table S4).

#### 3.2. Effect of Root Morphology on $F_R$

Analyses of the effect of root morphology on pullout force, for the subset of uprooted seedlings that had intact roots, showed that  $F_R$  was most strongly correlated with root frontal area ( $R = 0.80$ ; Table 3). The best model predicting  $F_R$  by root morphology differed slightly for the all-sites versus the Arizona-only analysis, with root frontal area having the largest effect on  $F_R$  when all sites were considered (supporting information Table S5), and root length the largest effect on  $F_R$  for the Arizona analysis (supporting information Table S6). Because root frontal area and root length were strongly and positively correlated, the analyses are consistent despite these differences ( $R = 0.64$ ; Table 3 and Figure 7). The Arizona species-difference analysis indicated a species-by-root-length interaction whereby root length had a larger effect on  $F_R$  for *Populus* than for *Tamarix* (Figure 8a and supporting information Table S6). In our analysis relating the best root morphology predictor of  $F_R$  to aboveground seedling size and to water-table depth (supporting information Tables S7 and S8), interaction terms showed that for small seedlings, water-table depth had a larger effect on root morphology, with greater root frontal area and length



**Figure 4.** Pullout force ( $F_R$ ) as a function of (a) frontal area for the no-scour-treatment seedlings by site and (b) frontal area and scour depth for the BR site. Scour depth decreased  $F_R$  for a given site.

Calculated  $U_c$  values for the population of test seedlings are generally much greater than the modeled or measured velocities for our field sites, with mean  $U_c$  values of  $\sim 6$  m/s for a no-scour, shallow water-table-depth-scenario (Figure 9 and supporting information Table S9). When the maximum modeled velocities are considered ( $Q_{100}$ ), the preregulation BWR maximum modeled velocity could uproot a large proportion of seedlings under a no-scour, shallow water-table depth scenario, with fewer seedlings susceptible to uprooting with increasing water-table depths. Postregulation at the BWR and at the SMR, most seedlings would not be expected to uproot unless subjected to scour ( $\geq 0.3$  m) and/or under shallow water-table depth scenarios. For the BR, where modeled velocities are lower, seedlings would not be expected to uproot unless subjected to  $\geq 0.3$  m of scour. This analysis shows that, even given uncertainty in expected velocities and hydraulic conditions at the sites, seedlings are highly resilient to uprooting across a range of high flows and reinforces the importance of scour in uprooting.

## 4. Discussion

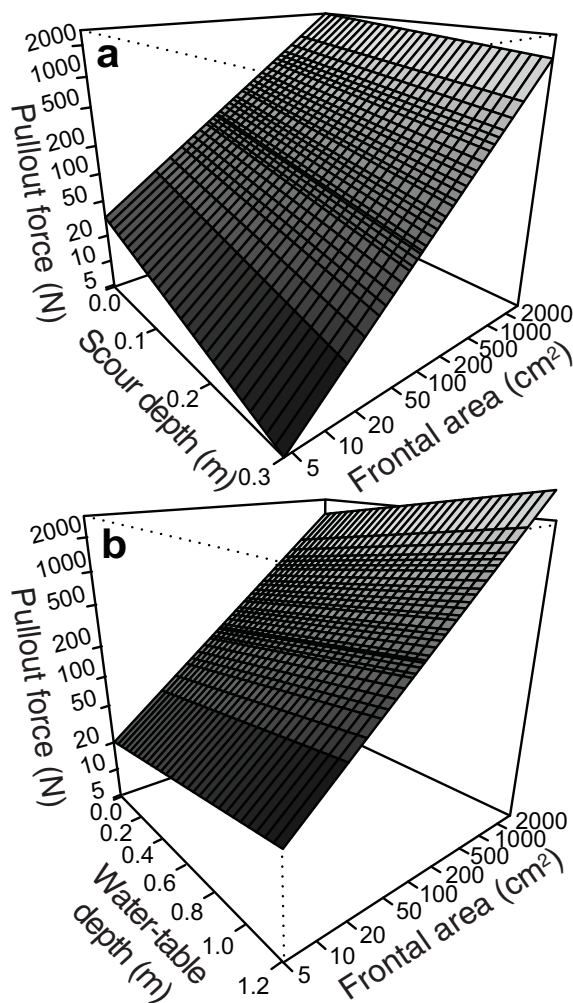
### 4.1. Controls on Seedling Uprooting Dynamics

Uprooting thresholds for pioneer woody seedlings are a function of a seedlings' resisting force ( $F_R$ ) against flood drag forces ( $F_D$ ). Our pull-test experiments quantified both aboveground and belowground aspects of

coinciding with deeper water tables. For the Arizona sites (and considering species differences), the species effect indicates root length was smaller for *Populus* compared to *Tamarix*, and the interaction between water-table depth and species indicates that the root length varied more for *Populus* with water-table depth than for *Tamarix* (Figure 8b). This is consistent with the findings (3.1) of lower  $F_R$  for *Populus* than *Tamarix* and of a larger frontal area effect for *Populus*.

### 3.3. Uprooting Susceptibility

Comparison of calculated uprooting velocities ( $U_c$ ) for our test seedlings to velocities modeled or measured at the field sites indicated that the majority of the population of seedlings would not be expected to uproot. The mean velocities modeled for flows ranging from  $Q_2$  to  $Q_{100}$  using HEC-RAS were as follows: 0.5–0.6 m/s for the BR, 0.9–1.4 m/s for the SMR, 1.6–3.3 m/s for the preregulation BWR, and 0.6–1.5 m/s for the post-regulation BWR (see supporting information Table S2 and Figures S2c and S2d for BR and SMR velocity results, Figures S3b and S3c for BWR). Measured velocities at the BWR during a flood equivalent to a post-regulation  $Q_{10}$  in which seedling uprooting was documented were up to 1.3 m/s in vegetation patches [Wilcox and Shaforth, 2013], which is consistent with the mean modeled  $Q_{10}$  velocity ( $1.2 \pm 0.2$  m/s; supporting information Table S4 and Figure S3).



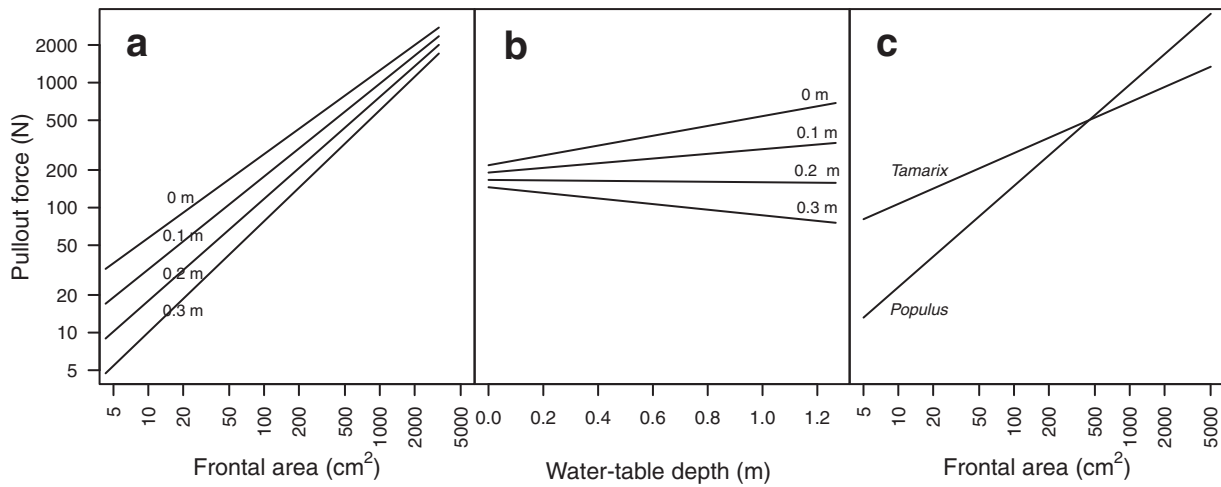
**Figure 5.** Perspective plots of factor interactions for the all-site mixed model (all species pooled, and sites as a random factor) predicting pullout force ( $F_R$ ). (a) Scour depth and frontal area, holding water-table depth constant at the midpoint of its range, and (b) water-table depth and frontal area, holding scour depth constant at the midpoint of its range. Pullout force increased with frontal area and water-table depth, but decreased with scour depth.

how and why seedlings thus become more resilient to uprooting as they grow, as well as providing insight into the role of sediment scour in predisposing seedlings to uprooting. We showed that pullout force increases in a power relationship to aboveground frontal area, a relationship that can be explained by the increase in root mass (i.e., root frontal area) and root length with increasing frontal area (Figure 7). We also illustrated that scour depth and water-table depth had additional, opposing effects on  $F_R$  (Figure 5). Scour depth was the only variable that decreased  $F_R$  and had a larger effect for small seedlings (Figure 5). Resisting forces ( $F_R$ ) increased with increasing water-table depth. Thus, seedlings are expected to be most susceptible to uprooting when they are small, experience scour, or have shallow root systems.

The positive effect of water-table depth on  $F_R$  was confirmed by our root morphometric analysis that found root frontal area and root length to be the best predictors of  $F_R$ , and the effects of each were conditional on water-table depth. Root length and root density have been proposed to influence seedlings' susceptibility to uprooting and loss [Crouzy and Perona, 2012; Pasquale et al., 2014]. We find evidence that root mass and root length are important in setting the initial  $F_R$  of a seedling in the absence of scour, which is proportional to the size of the seedling, and on water-table depths. We did not find, however, that root density influenced  $F_R$ , as has been proposed based on a field experiment using *Salix* cuttings [Pasquale et al., 2012]. This may reflect differences in root density for seedlings recruited from seeds as opposed to grown from cuttings.

Comparisons of *Populus* and *Tamarix* showed that  $F_R$  was lower and varied more with both plant size (frontal area) and root length for *Populus* than for *Tamarix* (Figure 8). As obligate phreatophytes, *Populus* rooting depths are sensitive to water table dynamics [Karrenberg et al., 2002; Stella et al., 2010], whereas *Tamarix* are considered facultative phreatophytes and likely grow deep roots independently, and less in response to environmental cues [Busch and Smith, 1995]. This difference in water table sensitivity has been postulated to explain the vulnerability of native obligate phreatophytes such as *Populus* to flow regulation, which may change water table dynamics and therefore root characteristics [Rood et al., 2010]. Our finding that root length is a primary predictor of  $F_R$  suggests that species-based differences in root length have implications for the vulnerability of *Populus* to flood flows compared to *Tamarix*. *Populus* may achieve deeper rooting depths than *Tamarix*, however, if floods recede at rates that promote *Populus* recruitment (e.g., the "recruitment box model" [Mahoney and Rood, 1998]).

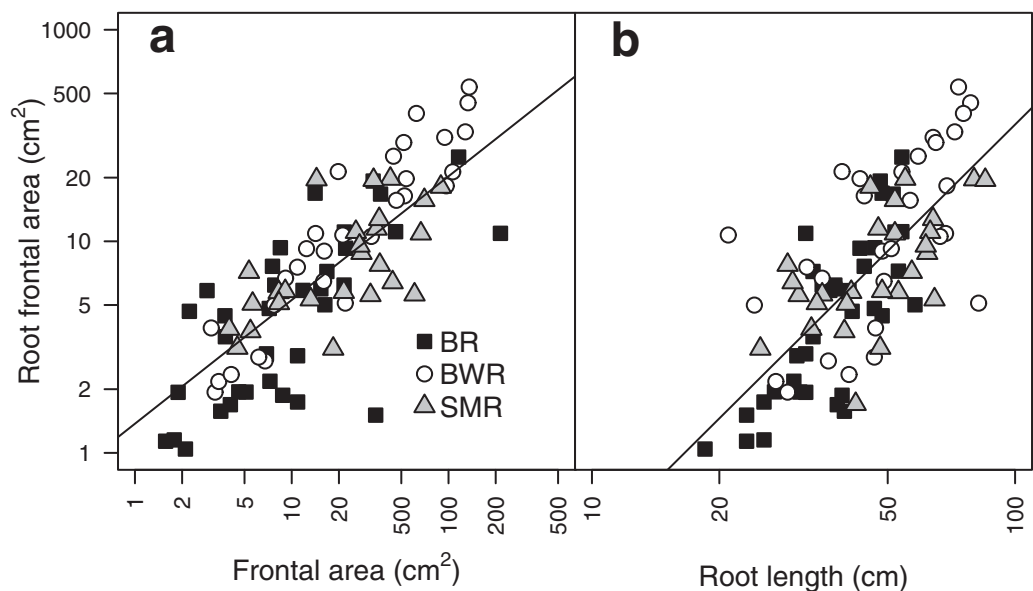
When we placed  $F_R$  in the context of uprooting susceptibility (i.e.,  $U_c$ ) for a population of seedlings with variable drag properties by setting  $F_R$  equal to drag forces, we found large values of  $U_c$  that, for the majority of the population of seedlings under conditions of no scour, are greater than modeled velocities at the sites



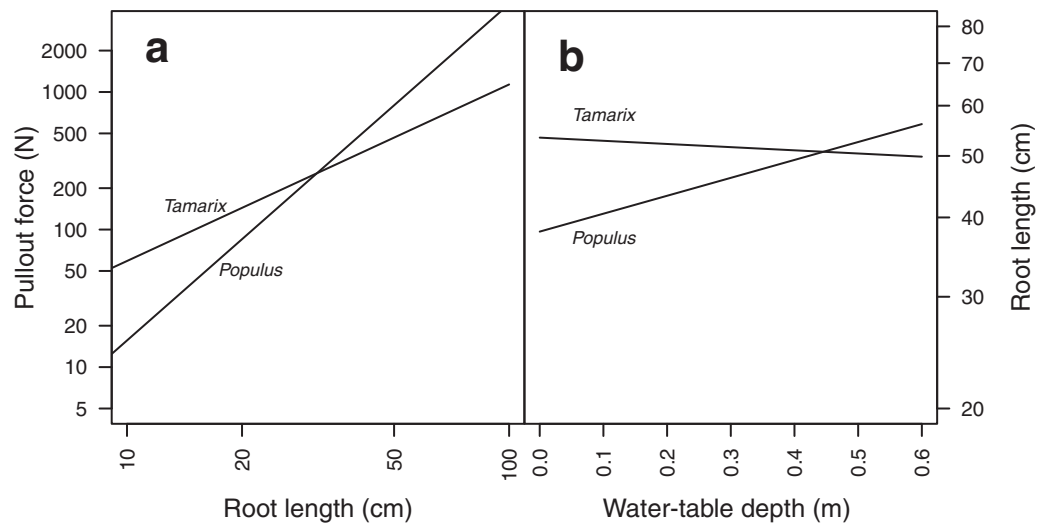
**Figure 6.** Interaction effects of (a) frontal area-scour depth and (b) water-table depth-scour depth for the all-site model. Scour reduced  $F_R$  more for seedlings with (a) small frontal areas and (b) large water-table depths. (c) The species-specific effect of frontal area on pullout force ( $F_R$ ) for the Arizona sites. Figure 6c shows pullout force varied more for *Populus* than for *Tamarix*.

across a range of flood magnitudes. This suggests that seedlings would be stable ( $U_c >$  flood velocities) under most conditions in the absence of scour and/or unless seedlings were shallowly rooted. Extreme floods (e.g.,  $Q_{100}$ ) would be expected to produce substantial bar erosion and channel reorganization sufficient to produce widespread uprooting in both sand-bed and gravel-bed systems.

Cross-section averages of velocities derived from 1-D modeling provide a simplified perspective on the velocities experienced by seedlings at the scale of individual plants or patches or plants on bars. Topographic steering and form roughness from bars, the plants themselves, instream wood, or other roughness sources [Dietrich and Smith, 1983; Lightbody and Nepf, 2006; Legleiter et al., 2011; Shields and Alonso, 2012; Brown and Pasternack, 2014; Van de Lageweg et al., 2014], as well as turbulent fluctuations around the mean velocity [Lapointe, 1992; Lawless and Robert, 2001], would cause plant-scale velocities to deviate from cross-section averages. Comparison of our modeled cross-section average velocity for the BWR with measurements within and around vegetation patches for a comparable flow in our study reach [Wilcox and Shafroth,



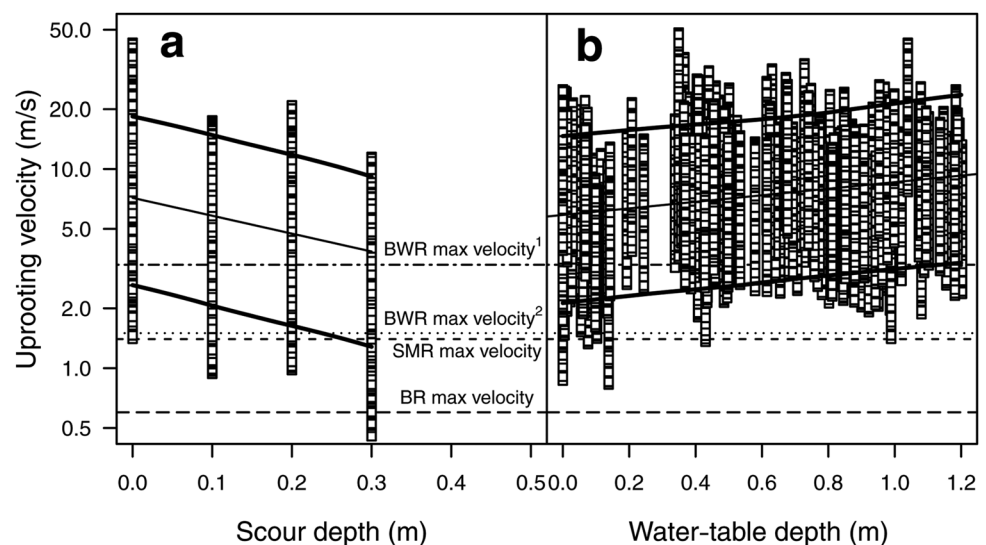
**Figure 7.** Root frontal area as a function of (a) aboveground frontal area and (b) root length. The seedlings with the largest aboveground frontal area have the largest belowground frontal area and root length.



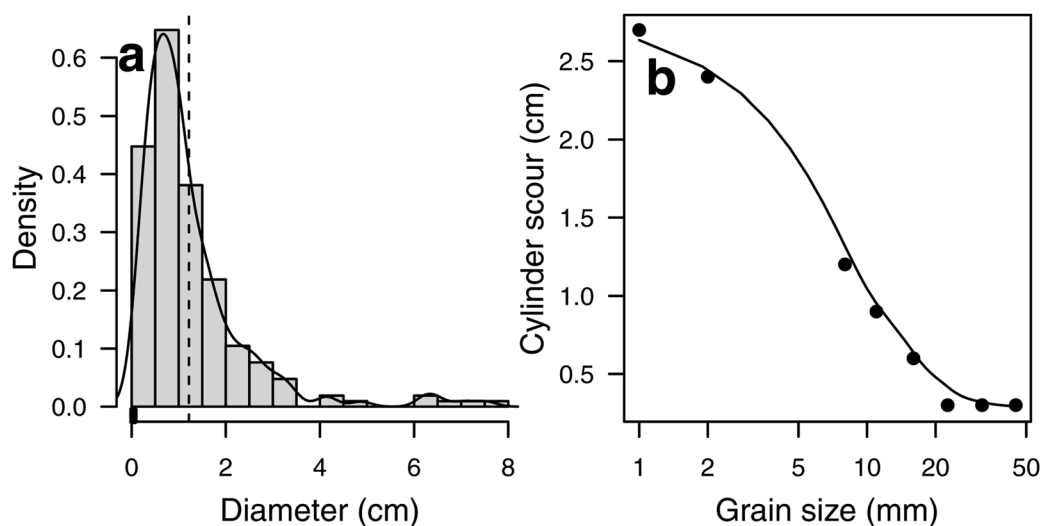
**Figure 8.** Interaction between (a) species and root length holding scour depth constant at the midpoint of its range for the model predicting pullout force ( $F_R$ ) as a function of root length for the Arizona sites indicates root length had a larger effect on  $F_R$  for *Populus* compared to *Tamarix*. The interaction between (b) species and water-table depth for the model predicting root length as a function of water-table depth indicates water-table depth had a larger effect on root length for *Populus* compared to *Tamarix*.

2013], however, shows that these modeled (cross-section average) and measured (plant-scale) velocities are similar, lending confidence in the relevance of the modeled velocities. Local-scale velocity complexities, which could be better captured using multidimensional morphodynamic modeling, are unlikely to change the overall findings here: that the majority of a population of seedlings is expected to be resilient to uprooting from drag forces alone.

Seedling size has been proposed as a determinant of whether or not scour is a prerequisite for seedling uprooting [Edmaier et al., 2011], with Type I uprooting applying to young/small vegetation and Type II to



**Figure 9.** Uprooting velocity ( $U_c$ ) as a function of (a) scour depth and (b) water-table depth with the entire Monte Carlo population (squares) and partial effect (solid line) and prediction interval (95%; bold lines) shown. An increasing proportion of the population would have  $U_c$  values less than maximum modeled values at the sites (horizontal lines) with increasing scour depth. The preregulation maximum velocity at the BWR (velocity<sup>1</sup>) would have uprooted a proportion of the population for all scour depths and water-table depths, but the reduction in flow velocities post regulation (velocity<sup>2</sup>) would allow only a small proportion of the population to uproot. With increasing scour depths, lower velocity events (e.g.,  $Q_2$ - $Q_{10}$ , velocity  $\approx 0.5$ - $1.0$  m/s) would be able to uproot an increasing proportion of the seedling population. The partial effect of water-table depth (b) remains above modeled and measured velocities for the majority of seedlings, regardless of flow, with the exception of shallowly rooted seedlings or for the preregulation BWR velocity.



**Figure 10.** Histogram of (a) seedling diameters with the mean (1.2 cm) indicated with the dashed blue line. (b) Local scour modeled by inputting the mean seedling diameter into the FDOT Scour Calculator that uses a modified *Sheppard and Miller* [2006] equation designed to calculate equilibrium bridge-pier scour for grain sizes ranging from 1 to 50 mm. The presence of the seedlings obstructing flow and inducing scour results in at most a few centimeters of scour.

older and larger plants. Our analysis, however, indicates that Type I uprooting may be exceedingly rare, even for young seedlings. We did not measure first season seedlings (<1 year), but given the recruitment strategy of *Salicaceae*, seedlings are unlikely to experience flood flows following recruitment, and survival of their first year is strongly dependent on drought conditions [Johnson, 2000].

#### 4.2. Analysis of Local Versus Reach-Scale Scour Mechanisms

Our findings regarding the fundamental importance of scour in dictating uprooting thresholds raise the question of whether local scour caused by vortices around plants (Type IIa) versus bar-scale sediment transport (Type IIb) is more likely to contribute to plant uprooting. We did not test Type IIa versus Type IIb scour mechanisms experimentally, so here we propose back-of-the-envelope calculations to evaluate their potential relative importance in seedling uprooting.

One approach to estimating the potential depth of scour associated with Type IIa scour is to apply scour algorithms developed for bridge piers [Sheppard and Miller, 2006] to seedlings. Seedlings have a more complex morphology and rigidity than cylinders [Järvelä, 2005; Wilson, 2007; Chapman et al., 2015], such that plant streamlining, pronation, and flexibility would be expected to reduce scour compared to that predicted using bridge-pier algorithms, but there is no consensus on a scour algorithm for flexible plants [Yager and Schmeckle, 2013]. We developed a back-of-the-envelope estimate of the scour magnitude that a seedling may induce through local vortices using the Florida Department of Transportation bridge-pier scour calculator. As input we varied grain size from 1 to 50 mm, used the mean seedling diameter as the obstruction diameter, and assumed a high approach velocity of 3 m/s (Figure 10). This approach suggested scour associated with stem-related vortices around seedlings (Type IIa) would occur to only very small depths ( $\leq 2.5$  cm). This magnitude of scour is far lower than our scour treatments showed is needed to increase uprooting susceptibility (at least 0.3 m) and is thus unlikely to affect uprooting, with the exception of first-season seedlings (<1 year) smaller than those tested.

The finding that Type IIa scour may be minimal suggests that instead, bar-scale and reach-scale sediment transport dynamics (Type IIb removal) may be more likely to dictate the magnitude of scour required to uproot seedlings with established root systems. Determining under which flow conditions plants and the bars on which they reside would experience erosion to scour depths of greater than 0.3 m (the amount our experiments indicated predisposes plants to uprooting) would require multidimensional morphodynamic modeling, as with treatment of local-scale velocity variations discussed above. As a simpler measure of the likelihood of bars to experience scour sufficient to facilitate seedling uprooting (Type IIb scour), we

calculated the Shields number ( $\tau^*$ ) at a dominant  $Q$  to evaluate bed mobility [Church, 2006]. The Shields number represents the capacity of a river to move its sediment at a specified discharge and is defined as:

$$\tau^* = \frac{\tau_o}{(\rho_s - \rho)Dg}, \quad (3)$$

where  $\tau_o$  is the boundary shear stress,  $\rho_s$  and  $\rho$  are the density of the sediment and water, respectively,  $D$  is the median grain size of the bed material, and  $g$  is acceleration due to gravity. We assume  $\rho_s$  of 2700 kg/m<sup>3</sup>. Values of  $\tau^*$  in excess of 0.03–0.045 tend to result in sediment mobility and transport. Church [2006] proposes that channels can be classified based on their propensity to mobilize their beds, as indicated by bankfull Shields number ( $\tau^*_{bf}$ ). Labile channels are those that can easily mobilize their beds at most flows and have  $\tau^*_{bf} > 1$ ; threshold channels, in contrast, experience flows capable of mobilizing their bed material less frequently and tend to have  $\tau^*_{bf} \leq 0.03$  [Church, 2006]. We use HEC-RAS results to determine Shields number at our field sites for two discharges that may be considered “dominant,” the  $Q_2$  and  $Q_{10}$ , recognizing the subjectivity in identifying a channel-forming discharge [Doyle *et al.*, 2005]. In many settings the  $Q_2$  may be similar to  $Q_{bf}$  [Andrews, 1980], which Church [2006] uses as the dominant discharge, whereas in dryland systems, such as the American Southwest, larger events (i.e.,  $Q_{10}$ ) may be more relevant [Tooth, 2000]. Our analysis of the bankfull Shields number shows that the SMR is labile ( $\tau^*$  at  $Q_2 = 1.4$ ,  $\tau^*$  at  $Q_{10} = 2.2$ ) and can therefore achieve scour more easily than the threshold BR ( $\tau^*$  at  $Q_2 = 0.01$ ,  $\tau^*$  at  $Q_{10} = 0.02$ ). The BWR is transitional between threshold and labile conditions at  $Q_2$  ( $\tau^* = 0.37$ ), possibly as a result of dam-induced coarsening and reduction in the  $Q_2$  discharge, but is labile at  $Q_{10}$  ( $\tau^* = 1.03$ ).

#### 4.3. Field Observations of Seedling Uprooting

Widespread seedling uprooting has been observed at one of our sites, the regulated Bill Williams River, under environmental flow releases from an upstream dam that are large within the context of regulated flow regimes ( $\sim Q_{1.5} - Q_{20}$ ) but small relative to historic floods [Wilcox and Shafroth, 2013]. Flow releases on the BWR are managed to encourage recruitment of native *Populus* and *Salix*, and baseflows are elevated compared to pre-regulation discharge levels. Proliferation of beaver in some reaches of the Bill Williams has further raised the water table [Andersen *et al.*, 2011]. These conditions may have offsetting effects on uprooting susceptibility in this system: on the one hand, elevated baseflows may increase growth rates, and therefore aboveground frontal area and  $F_R$ , but on the other hand, elevated water table levels may limit rooting depths, thus increasing uprooting susceptibility during subsequent high-flow releases. The fact that seedling uprooting occurred during modest floods can be interpreted in the context of our experiments to suggest that in the BWR case, Shields numbers during floods were high enough to cause sufficient sediment scour that seedlings were highly susceptible to uprooting, reflecting a combination of the floods’ magnitudes and the bed-material size, and that uprooting susceptibility was exacerbated by the high water table levels in the BWR.

On the Bitterroot River, in contrast, our field observations during this study indicated that seedlings were stable for a  $Q_2$  flow. Bed-material is larger and water table is lower on the BR than on the BWR, such that a  $Q_2$  would not have produced sufficient scour to promote uprooting on the BR. At our third site, the Santa Maria River, we lack the pre- and post-flood observations needed to document seedling uprooting. The labile nature of the SMR and the prevalence of unvegetated bar areas in years after which floods are known to have occurred suggest that seedling uprooting, likely in concert with bar-scale scour, is not uncommon in this system. More generally, seedling uprooting reflects the frequency of bed mobility and the depth of scour on bars achieved during floods, whereby uprooting may be more frequent in labile channels and less likely to occur within threshold channels, where only infrequent, large-magnitude floods may result in seedling uprooting.

### 5. Conclusions

Whether or not seedlings are uprooted during flood events can set the subsequent course of channel and riparian ecosystem evolution. The likelihood of seedlings growing large enough to resist flood forces, stabilize bars, and trigger other morphodynamic feedbacks depends on the relative timescale of scour-inducing floods compared to that for successful recruitment and establishment of seedlings (e.g., 2–5 years), which can occur following smaller floods [Camporeale and Ridolfi, 2010; Crouzy and Perona, 2012].

Here we found  $F_R$  to depend largely on seedling size. Water-table depth and root length covaried and increased  $F_R$ . The effect of water-table depth on root length and  $F_R$  was greater for *Populus* compared to *Tamarix*. Scour depth was found to be the only factor to shift the force balance toward the propensity for uprooting, suggesting that drag force alone is unlikely to uproot seedlings under a wide range of conditions. We conclude that *Populus* and *Tamarix* seedlings across a range of hydrogeomorphic conditions are resilient to uprooting in the absence of sediment transport that is sufficient to substantially expose roots. This magnitude of scour is more easily achieved in labile, sand-bed channels than in threshold channels, where flow events that mobilize competent bed materials are less frequent.

These findings illustrate the constraints on the scour depths and velocities required to uproot seedlings. As such they have applications for designing flow-management strategies to promote either tree establishment or, conversely, seedling scour. For example, the differing relationship we observed between water-table depth, root length, and  $F_R$  for *Populus* versus *Tamarix*, could be exploited by designing regulated flows to maximize recruitment of *Populus* by encouraging high root growth rates while maintaining the appropriate drawdown rates [Stella et al., 2010]. More generally where management seeks to increase survival and establishment of planted or naturally-recruited seedlings, measures to reduce substrate scour (e.g., location of plantings or placement of roughness objects), as well as flow releases timed and paced to promote establishment of deep roots, may increase success. Flow releases on regulated rivers aimed at uprooting nuisance vegetation (e.g., to maintain floodway clearance or promote open wildlife habitat on sandbars) must be of a magnitude and duration capable of mobilizing substrate within vegetated areas.

#### Acknowledgments

Supporting information contains seedling results (Data Set S1), mean seedling characteristics (supporting information Table S1), BR grain-size data (supporting information Figure S1), additional details on HEC-RAS modeling and results (supporting information Table S2), modeled reaches and velocities (supporting information Figures S2 and S3), and statistical analysis results (supporting information Table S3 through S8). This research was funded by the National Science Foundation (EAR 1024652 and EPS-1101342) and EPA STAR Graduate Fellowship. We thank Austin Maphis, Ben Gardner, Franklin Dekker, Abraham Schmidt, Jewel Case, Robert Livesay, Brian Reyes, and Katie Monaco for assistance in the field. We thank Paolo Perona, Nicola Pasquale, Patrick Shafroth, Rebecca Manners, Li Kui, and Krysia Skorko for insights, discussion and review of this research. We thank Mark Reiling, Philip Ramsey, and MPG Ranch for access to the BR site. We thank Missoula County and a NCALM Seed Grant for providing LiDAR, and Steve Niday for survey assistance. SMR LiDAR data acquisition and processing completed by the National Center for Airborne Laser Mapping (NCALM; <http://www.ncalm.org>). NCALM funding provided by NSF's Division of Earth Sciences, Instrumentation and Facilities Program (EAR-1043051). We also thank the Associate Editor, two anonymous reviewers, and Simon Dixon for insightful review comments.

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