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Fluvial sediment burial increases mortality of young riparian trees but induces compensatory growth response in survivors

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11   **Abstract**

12   Flooding and sediment deposition provide many benefits to riparian plants,
13 including dispersal of propagules, new seedbeds for germination, and transient pulses
14 of water and nutrients during early growth. Though many riparian species are adapted
15 to flood disturbance, sediment deposition can also be a stressor to existing plants,
16 limiting their survival and growth. Though many field studies document short-term
17 changes in plant density immediately following floods, an outstanding question remains
18 to what degree plants can survive and re-emerge following fluvial deposition events.
19 We conducted two year-long studies to quantify the response of riparian trees to
20 sediment deposition, testing a range of species, sizes and burial depths. One experiment
21 focused on long-term survival following complete burial for seedlings and saplings of
22 cottonwood (*Populus fremontii*), tamarisk (*Tamarix ramosissima*), and box elder (*Acer*
23 *negundo*). A second experiment focused on cottonwood seedling response to more
24 moderate deposition events, comparing survival and vigor (height, diameter growth,
25 and leaf production) across a range of treatments from 10–50 cm sediment depth.
26 Complete burial killed all tamarisk and cottonwood plants; however all box elder
27 survived and resprouted from the sediment surface in the following growing season. In
28 the partial burial experiment, cottonwood survival was higher in the shallower
29 deposition treatments and for larger plants across all treatments. Cottonwood seedlings
30 with exposed stem length longer than ~20 cm were highly likely to survive (> 90%),
31 whereas plant survival was severely reduced for stems with greater portions of their
32 stems buried. Seedlings that survived partial burial experienced a positive,

compensatory response in the following growing season, with height increment and canopy expansion proportional to the depth of sediment added. These results suggest that flood-borne sediment deposition events, either under natural or river management conditions, may have non-linear effects on the survival of existing riparian tree cohorts. The severity of the disturbance effects will depend on the magnitude of the event and the initial size of the plants. Together with field studies on riparian plant demography and experiments that test plants' vulnerability to flood disturbance, our study extends understanding of the drivers of plant mortality in fluvial corridors.

Key works: fluvial disturbance, sediment burial, pioneer riparian plants, plant demography, river corridor management

1. Introduction

Fluvial disturbance—the combined effects of floodwater and the sediment it carries—affects riparian plants in both beneficial and detrimental ways (Bendix and Hupp, 2000; Webb and Erskine, 2003; Polzin and Rood, 2006). Many riparian plant species have adaptations to flood regimes that allow them to mitigate damaging effects while exploiting opportunities that floods provide such as enhanced dispersal, transient resource pulses, and reduced biomass of more poorly-adapted competitors (Naiman and Decamps, 1997; Lytle and Poff, 2004; Stella *et al.*, 2006). Despite the advantageous traits that many pioneer riparian species possess, woody riparian plants often experience damage from multiple disturbance events during their lifetimes, including periods of drought and flood events that induce hydraulic scour, sediment burial, and prolonged inundation (Polzin and Rood, 2006; Stella and Battles, 2010; Bendix and Stella, 2013; Dixon *et al.*, 2015). All of these are stressors that can reduce survival, growth and ultimately the fitness of populations (Scott *et al.*, 1997; Kent *et al.*, 2001; Rodriguez-Gonzalez *et al.*, 2010). For pioneer riparian species, those that typically possess traits such as prodigious seed output, long-distance dispersal, fast growth, poor shade tolerance and short life spans, contending with abiotic stress is a necessary tradeoff when colonizing newly-disturbed environments, and ultimately allows for persistence in dynamic environments within the riparian corridor (Bornette *et al.*, 2008; Merritt *et al.*, 2010; Stella *et al.*, 2011).

Burial by sediment and uprooting by scour are two of the principal mechanisms that decrease survival of young plants during floods in addition to drought stress,

anoxia, herbivory, and wind scour (Stromberg, 1997; Cooper *et al.*, 1999; Pasquale *et al.*, 2012). For example, an experimental flood event on the Bill Williams River (AZ, USA) induced both scour and burial in different reaches and caused 86% mortality among non-native tamarisk seedlings and 36% mortality of native plants, mainly willow (Wilcox and Shafroth, 2013). Natural flood events are unpredictable, however, and quantifying the mechanisms that drive mortality in the field is challenging (Friess *et al.*, 2012). Recent experiments using live plants in flumes extend our understanding of riparian vegetation interactions with flood hydraulics and sediment, including the conditions under which plants are uprooted and/or buried, and feedbacks from the plants' own morphologies (Edmaier *et al.*, 2014; Kui *et al.*, 2014; Manners *et al.*, 2015). However, to what extent sediment burial actually kills riparian plants—and therefore influences plant demography at the population scale—is not well understood, nor are the effects of potentially mitigating factors such as plant size at the time of burial, the length of time buried, and the depth of sediment deposited (Lytle and Merritt, 2004; Harper *et al.*, 2011).

Evidence of riparian plant response to burial in field and experimental studies to data is equivocal, with survivorship largely depending on the species and the method and depth of burial (Table 1). A field study along the Elk River in the Rocky Mountains conducted by Polzin and Rood (2006) revealed that cottonwood with average of 188 cm in height could survive sediment burial that was shallower than 40 cm. Levine and Stromberg (2001) tested young (≤ 45 -day old) cottonwood, willow, and tamarisk seedlings, and found that complete burial induced 100% mortality but partial burial

96 treatments resulted >80% survivorship for cottonwood and >27% for tamarisk. Though
97 some have proposed that there may be a plant size threshold that conditions
98 survivorship (Levine and Stromberg, 2001), few studies have explicitly quantified one.
99 Burial by sediment affects both plant architecture and wood anatomy, and frequently
100 results in bent, buried trunks with multiple vertical sprouts growing upright as
101 individual trees (Everitt, 1968). Burial can increase biomass production by producing
102 more new leaves and branches (Zhang and Maun, 1992; Kent *et al.*, 2001), as well as
103 adventitious roots that sprout from the buried part of the trunk (Sigafos, 1964; Merritt,
104 2013). Burial affects wood anatomy through the creation of scar tissue, production of
105 aerenchyma, reduction in ring increment growth, and an increase in vessel cell size
106 (Sigafos, 1964; Nanson and Beach, 1977; Friedman *et al.*, 2005). In order to translate
107 the laboratory and field experiment results on plant mortality into true demographic
108 rates, and thus understand their effect on plant populations, we need to know whether
109 burial during sedimentation events kills plants outright or alternatively cause nonlethal
110 damage from which they eventually recover (Sigafos, 1964; Balke *et al.*, 2013). It
111 would be especially helpful to know this for plants older and larger than those tested to
112 date, and for burial periods that track plants across several growing seasons. In
113 addition, knowing the survival thresholds for a suite of species within the same
114 community can aid in predicting the effects of floods and flow releases for river
115 ecosystems on riparian community dynamics (Sher *et al.*, 2002; Merritt and Poff, 2010;
116 Stella *et al.*, 2013).

To better understand the vulnerability of riparian woody plants to fluvial sediment deposition, we conducted two one-year-long experiments to test the survival of tree seedlings and saplings to different levels of burial. Our studies focused on riparian species that are dominant along rivers in the southwestern U.S. One experiment tested the effect of complete burial using different sediment depths on survival of *Tamarix ramosissima* (tamarisk), *Populus fremontii* (cottonwood), and *Acer negundo* (box elder). A second experiment on cottonwood alone tested plant response to sediment addition across a range of depths, from partial to complete burial. In that study, we sought to identify a threshold of burial beyond which plants cannot recover, and to document the vigor response of surviving seedlings in the growing season following the sedimentation event.

2. Material and methods

In the two burial experiments, cottonwood, tamarisk, and/or boxelder seedlings were collected from riverine environments, transported to a protected outdoor facility and transplanted into alluvial sediments within a planting bed (Experiment 1) or experimental pots (Experiment 2) for ~3 months' recovery. Most of the transplanted plants were collected as part of two other experiments, and details of their propagation are described in Kui et al. (2014) and Manners et al. (2015). In each case, live plants were buried under a range of sediment depths at the end of a growing season and monitored for survival and emergence over the following growing season (12 months duration). At the end of the experiment, we quantified plant growth attributes of

surviving plants (height, leaf number, and basal diameter) in relation to burial depth to determine plants' response to sedimentation. Details of each experiment are explained below.

2.1 First experiment: survival response of three species to complete burial

In summer 2011, an outdoor burial experiment was set up at the San Anthony Fall Laboratory (SAFL) in a patch of alluvial sediment adjacent to the facility's Outdoor StreamLab. The planting area had no regular maintenance and the soil depth ranged from 20 cm to 50 cm. The soil was a mixture of primarily river sand, with smaller proportions of silt, clay and organic matter; the substrate was homogeneous throughout the planting area. This area was prepared prior to plant burial by clearing weeds and sparse shrubs to expose mineral substrates and eliminate biotic competition.

We tested the response of 1–3 year old seedlings to complete sediment burial for three species: cottonwood, tamarisk, and box elder. Cottonwood and tamarisk seedlings were collected from the Bill Williams River, AZ in May and shipped to SAFL by overnight mail. Most of plants were 1–2 years old with the heights ranging from 8–139 cm. The substrate of the collection location was loose sand and the excavation was carefully done; nevertheless there may have been some fine-root damage. The box elder plants native to the SAFL site were excavated and replanted for the experiment similarly to the other species. Box elder plants ($n = 9$) ranged 45–137 cm in height with an average of 96 ± 27 cm (mean $\pm$ SD). Cottonwoods ($n = 8$) ranged 11–139 cm in height with an average of 70 ± 54 cm, and tamarisk ($n = 12$) ranged 8–126 cm in height with

an average of 90 ± 44 cm. The plants were distributed by species among nine blocks, and individuals of various sizes were randomly assigned into each block and planted in the alluvial substrates. The plants were irrigated once every two weeks during a 3-month acclimation period, at the end of which (August), they were subjected to the burial treatments.

To simulate pronation that occurs during flooding, all test plants were bent over to a 30–45 degree angle using a cord connecting the mid-point of the stem to a fixed wooden stake (Figure 1A). Between nine and 12 plants from each species were randomly assigned to one of the three burial categories: (1) control, with no sediment added; (2) shallow burial, with plants completely buried under a capping layer of 1–2 cm of sediment; and (3) deep burial, with plants completely buried under a capping layer of 10 cm. For the two burial categories, a wooden box was built around the plants to hold the added sediment (Figure 1A). Sediment was carefully distributed over and around the plants until all plant parts were covered. Then, an additional 1-2 cm (for the shallow treatment) or 10 cm (for the deep treatment) was added to fulfill the treatment design. The sediment used in the burial experiment was coarse sand from a commercially-prepared mineral mixture used for the flume facility, with a median grain size of 0.5 mm ($D_{16} = 0.35$ mm, $D_{84} = 1.2$ mm) that was representative of the plants' natural setting (Wilcox and Shafroth, 2013). There was no organic matter in the sediment. It was worth noting that the burial depth became shallower over the course of the experiment due to rainfall compacting the soils; this phenomenon appeared to be

consistent across all samples. Therefore, by the end of the experiment (Aug 2012), the shallowly-buried plants had partial (1-2 cm) exposure around the stem tips.

In August of 2012, one year after the burial experiment, plants were re-surveyed to record survival. In addition, plant height was measured from the position above the soil surface and was used to compare with its pre-experimental height to evaluate the new growth of the plant.

2.2 Second experiment: cottonwood survival and growth response to partial burial.

The second experiment was conducted in summer 2013 at the Richmond Field Station (RFS) at University of California, Berkeley. Cottonwood seedlings 1–3 year old were collected from the Bill Williams River, from the same locations as the plants used in Experiment 1. Seedlings were transplanted into 19-liter experimental pots (30 cm diameter by 25 cm deep) at the RFS. Each pot contained two plants of similar height, and a total of 35 pots were placed in the full sun for a three-month recovery period (Figure 1C). The sediment in the pots was a commercially-prepared sand mixture with a median grain size (D_{50}) of 0.57 mm ($D_{16} = 0.45$ and $D_{84} = 0.75$). This size distribution was within the range of plants' natural setting (Wilcox and Shafroth, 2013), and no organic matter was added to the mineral sediment. During the acclimation period, plants were watered once a week to prevent desiccation. A total of 69 cottonwoods were used in the experiment, and their pre-burial heights ranged from 14–69 cm with an average of 44 ± 10 cm (mean $\pm$ SD). Plant diameter ranged from 2–8.8 mm with an

average of 6 ± 1 mm, and leaf number ranged from 25–189 with an average of 81 ± 34 leaves.

In August of 2013, plant attributes were recorded, including height, diameter, and number of leaves. Experimental pots were randomly assigned to one of ten burial treatments: a no-burial control (0 sediment depth) or nine burial depths from 10–50 cm at 5-cm intervals. This resulted in 2–3 pots per treatment or 4–6 plants each. Each plant remained in its natural upright position while sediment was added to meet the treatment depth. The sediment used for burial was the same as that used in the pots; no fertilizer or organic material was added. The plant pots, which had porous bottoms, were kept in an outdoor basin with a shallow water depth; the bottom 10 cm of substrate within pots was kept constantly moist. After Aug 2013, water was added into the basin three times to keep enough moisture for plants to survive. In August of 2014, one year after the burial experiment, we resurveyed and measured the heights, diameters, and leaf numbers for all the live plants (Figure 1D).

2.3 Statistical analyses

Data from the two experiments were analyzed using different methods. For the complete burial study, we compared the number of live plants remaining between the two surveys (pre-experiment and the end of the experiment), comparing the three species and three treatments. Pearson's Chi-squared test was used for determining the significance of the treatments (control, shallow burial, and deep burial) and species (box elder, cottonwood, and tamarisk) on the proportion of plant mortality.

For the partial burial study, we constructed mixed logistic models to predict the likelihood of plant mortality. Experimental pot was included as a random factor in all models to account for environmental variability that may affect survival and growth at the pot mesocosm level. The fixed predictor variables tested were antecedent plant height, burial depth, and the exposed stem length (calculated as plant height minus burial depth). We constructed alternative models among these predictor variables, with burial depth and plant height in some models (all main effects and their interaction), and other models containing exposed stem length only, as this was effectively an integrated measure of plant size and sedimentation treatment. Five candidate models were compared with different combinations of predictor variables using the second-order Akaike Information Criteria that accounts for small sample sizes (AICc). The models were ranked by their AICc values and weights, with the best models having the lowest AICc values and the highest weights (Burnham and Anderson, 2002). All models were listed and their predictors and coefficients ($\pm$ standard error) compared.

For the plants that survived the burial treatments ($n = 38$), we used linear models to quantify the effect of sediment depth on growth and canopy expansion in the subsequent growing season. We constructed three linear models, each with treatment sediment depth as the predictor, and the responses of stem height increment (final minus initial), change in leaf number, and diameter increment. Initially we considered the original stem height as a covariate in these models to account for size-dependent growth rate. However, this term was not significant in the resulting models ($p < 0.05$),

and we removed it from the final analyses. All graphs and statistical analyses were conducted in the program R (R Core Team, 2013).

3. Results

In the first experiment that compared different species' survival, no cottonwood or tamarisk plants survived complete burial, whereas box elder had 100% survival regardless of burial depth (Table 2, $p < 0.001$ in Pearson's Chi-squared test, $df = 4$, $X^2 = 173$). Survival within the cottonwood and tamarisk control groups (no added sediment) was $>65\%$ after a year, whereas both shallow and deep burial treatments caused all plants to die during that period. Although the overall sample size was limited, the strong differences between treatments indicate that cottonwood and tamarisk do not recover from complete burial. In contrast, all box elder seedlings and saplings survived all treatments, with buried plants sprouting new branches from buried portion of the main stem (Figure 1B).

In the second experiment, which tested cottonwood response to partial sedimentation, survival rates varied greatly across the gradient of burial treatments (Table 3). Importantly, plant survival was contingent on both plant height and the depth of burial (Figure 2). These two predictors and their interaction comprised the highest-ranked model predicting plant survival (Table 4; Figure 3A). In general, survival was negatively related to sedimentation depth, and for a given depth, taller plants tended to survive more than shorter plants. The relative importance of plant height increased with the severity of the treatment. For plants buried to a depth of 10 cm, the probability of survival increased by 13% for every centimeter increase in plant height,

whereas for plants buried under 30 cm of sediment, each centimeter increase in stem height conferred a 45% greater survival rate (Table 4; Figure 3A).

The second best model predicting plant survival had exposed stem length (plant height minus burial depth) as the single predictor variable (Table 4). This model predicts that plants with exposed stem lengths of 2, 12, or 22 cm would have differential survival probabilities of 10%, 50%, and 90% respectively (Figure 3B). Plants with exposed stem length longer than ~20 cm were highly likely to survive burial, whereas below that threshold, plant survival was greatly reduced until near zero at complete burial (exposed stem length = 0). Overall, there was a 23% increase in survival for each additional 1 cm of exposed stem length (Table 4). Though this model is simpler to represent than the top-ranked model as it has only one predictor, it may not be as useful under field conditions, as it does not capture the non-linear increase in survival advantage that tall plants have as sedimentation depth increases (Figure 3A).

Contrary to expectations, plants that survived the burial treatments experienced a positive growth response in the next growing season. Across all treatments, surviving plants grew 87 ± 37 cm (mean $\pm$ SD) in height following burial (Table 3). The vigor of their recovery was positively related to the depth of sediment added, as measured by change in stem height from the initial values to the end of the second growing season ($F_{1,36} = 39.53$, $p < 0.01$, Figure 4A), as well as the number of new leaves ($F_{1,36} = 5.79$, $p = 0.02$, Figure 4B). A year following the pre-treatment survey, stem diameter increased 10 ± 5 mm (mean $\pm$ SD) across all the seedlings that survived. In contrast to height and

leaf number, stem diameter was unaffected by the degree to which plants were buried ($F_{1,36} = 0.06$, $p = 0.81$; Figure 4C).

4. Discussion

These two experiments collectively tested the survival and growth responses of young riparian trees to sediment burial, both partial and complete. In response to full burial, all cottonwood and tamarisk plants died, whereas all box elder plants survived and emerged from the sediment surface and resumed growth, even when up to 10 cm of sediment had been deposited on top of the stems. The mortality rate of cottonwoods that experienced only partial burial was much lower, and plants that experienced partial burial with lengths of exposed stems 20 cm or greater largely survived. For surviving plants, partial stem burial induced height growth and canopy expansion proportional to the degree of sedimentation; this was an unexpected result. This is one of the first controlled experiments that examined a range of sediment burial depths on large seedlings and small saplings (but see Balke *et al.*, 2013; Sun *et al.*, 2014). Our results extend understanding of the drivers of plant mortality in fluvial corridors and improve the interpretation of both field studies on riparian plant demography (Wilcox and Shafroth, 2013) and lab and flume experiments that test mortality mechanisms of plant vulnerability to floods (Levine and Stromberg, 2001; Burylo *et al.*, 2012; Kui *et al.*, 2014).

309   Our finding of complete mortality for cottonwood and tamarisk subjected to full
310 burial is supported by some studies on pioneer plants, including woody riparian,
311 herbaceous and dune species (Zhang *et al.*, 2002). For example, the dune plant *Cirsium*
312 *pitcheri* was incapable of resprouting following complete burial (Maun *et al.*, 1996).
313 Possible causes of plant mortality included lack of light (i.e., a plant energy deficit)
314 and/or oxygen depletion during root respiration (Shi *et al.*, 2004). Similar phenomena
315 have been observed in field studies that tracked both sedimentation and changes in
316 plant density following floods (Cooper *et al.*, 2003; Wilcox and Shafroth, 2013). Thus,
317 extensive deposition events following floods can be expected to have a strong effect on
318 young cottonwood and tamarisk cohorts within the river corridor (Stromberg *et al.*,
319 1993; Palik *et al.*, 1998).

320   Unlike the two pioneer species, box elder in the complete burial study was highly
321 resilient, and was the only species in that experiment that resprouted new stems from
322 axillary or adventitious buds during the subsequent growing season. In contrast to
323 cottonwood and tamarisk, box elder is tolerant of shade, with a relatively slower
324 growth rate, and is considered a middle or later successional species (Johnson *et al.*,
325 1976; Saccone *et al.*, 2010). Thus it may be better adapted to types of disturbance that
326 stress plants by reducing energy acquisition (Bellingham and Sparrow, 2000), and/or
327 require them to adopt a more conservative resource allocation strategy in order to
328 survive long-term light deprivation (Harris and Davy, 1988; Brown, 1997). Other
329 studies have found that some plants have the ability to emerge from complete sediment
330 burial, including *Suaeda salsa* (Sun *et al.*, 2014), *Ulmus pumila* (Shi *et al.*, 2004), and

331 *Sarcobatus vermiculatus* (Brown, 1997). In these cases, plants survived by drawing on
332 energy stored in the buried plant tissues and relocating sufficient carbohydrates to
333 produce new stems and leaves that emerge from the sediment surface and ultimately
334 allow the plant to re-establish a positive carbon balance (Brown, 1997; Perumal and
335 Maun, 2006). In our study, box elder exhibited a stress-tolerance strategy that
336 effectively copes with the low-light environment following burial, whereas cottonwood
337 and tamarisk rely on fast growth and resprouting capacity to mitigate the long-term
338 effects of plant damage following floods, including tissue removal and root exposure
339 (Johnson, 1994; Levine and Stromberg, 2001). Though these represent different suites
340 of traits, each life history strategy can be effective for allowing persistence within
341 dynamic fluvial corridors, where gradients of both disturbance and abiotic stress are
342 steep and geographically local (Naiman *et al.*, 2005).

343   In contrast to plants that were buried completely, most young cottonwood that
344 had sizable portions of their stems exposed following sedimentation events survived.
345 These results for large seedlings and samplings are consistent with other studies in
346 which smaller plants survived moderate sediment additions (Levine and Stromberg,
347 2001; Burylo *et al.*, 2012). Larger plants and those that experienced shallower
348 sedimentation were the most likely to survive, and we found a threshold equal or
349 greater than ~20cm of exposed stem was necessary to ensure >90% survival.

350   Furthermore, we found that plants that survived partial burial showed a
351 compensatory growth response, increasing their stem extension and refoliation
352 response in proportion to the depth of sedimentation. It is possible that the increased

growth in our study was triggered as a stress response, and was achieved by spending down carbohydrate reserves. Alternatively, the excess growth may be a positive fertilization response to nutrients adsorbed to the deposited sediment; the plants' vigorous adventitious root growth within the new sediment strata may be evidence of this effect (Figure 5). Studies on sand dune plants indicate that some species respond to burial disturbance by increasing stem height and producing more new leaves; these include *Cakile edentula* (Zhang and Maun, 1992) and *Ulmus pumila* (Shi *et al.*, 2004), as well as species in the genus *Ammophilas* (Kent *et al.*, 2001). Physiological studies document a compensatory mechanism for the reduction in carbohydrate production by which some species increase growth, improve photosynthetic efficiency, and stimulate adventitious root production (Sigafos, 1964; Harrington, 1987; Shi *et al.*, 2004; Guerrero-campo *et al.*, 2006; Perumal and Maun, 2006). Another study that evaluated physiological response in riparian alders to moderate sediment deposition found a short-term drop in photosynthesis, but no long-term effect (Ewing, 1996).

Whatever the specific mechanism, it is likely that surviving cottonwood seedlings prioritized two particular growth strategies: increased height growth, which allowed the plant to emerge from the soil surface; and canopy expansion, which ensured a greater supply of photosynthate to compensate that lost in the disturbance and meet the new demand. It is notable that stem diameter increment in the following growing season did not respond proportionally to sediment depth. This is consistent with an optimal allocation strategy (Weiner, 2004), as diameter growth would be less

important than height or canopy expansion in contending with the stresses of sediment burial.

From the broader perspectives of fluvial ecosystems and river corridor management, the interaction of sediment dynamics with plant species' tolerance for burial influences the composition and dynamics of riparian communities (Stromberg *et al.*, 1993; Wilcox and Shafroth, 2013). Floods and sediment deposition are important drivers of regeneration of woody riparian communities (Mahoney and Rood, 1998), but also serve as a stressor and potential cause of mortality for existing plants (Stromberg *et al.*, 1993). On dammed rivers that trap a large proportion of the sediment supply, extensive deposition events may be less frequent and widely-distributed than historically, and burial a less important mechanism than flood scour and/or drought in controlling the distribution and density of riparian plants (Sher *et al.*, 2002; Kui *et al.*, 2014). In contrast, dam removal projects that create a *de facto* sediment addition experiment may increase the incidence and extent of both recruitment and of plant burial (Shafroth *et al.*, 2002). The few studies on riparian ecosystem response to dam removal indicate that riparian trees usually respond favorably to new sediment inputs (East *et al.*, 2015), but that the vegetation response often lags that of aquatic species and is generally on the scale of decades (Doyle *et al.*, 2005; Kim *et al.*, 2015). As plants age and grow larger, they become less vulnerable to hydrogeomorphic forces such as burial, scour, and prolonged inundation, and in turn exert feedbacks on the physical system (Corenblit *et al.*, 2007; Kui *et al.*, 2015; Manners *et al.*, 2015). Our results show that mortality rates from sediment burial are equivalent for tamarisk and cottonwood;

therefore large flow releases in sediment-rich systems may not provide a benefit to existing cohorts of native species (Sher *et al.*, 2002; Merritt and Poff, 2010). In addition, both natural floods and human flow releases could increase the areal extent and duration of plant inundation, which is another physical stressor that negatively affects growth and survival (Kozlowski, 1997; Amlin and Rood, 2001). These insights synthesized from field situations and controlled experiments such as the present study provide a greater understanding into how complex plant/geomorphic interactions in river systems change and drive the co-evolution of vegetation communities and fluvial landforms over time (Merritt, 2013).

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618 **Tables**

619 Table 1. Representative studies of seedling response to burial and other fluvial disturbances in field and experimental
620 settings.

Driver	Species and plant age/size	Location	Plant responses monitored	Key results	Reference
Field studies					
Scour and sediment burial	PRVE, TAPE, SAGO, and POFR with various sizes	Hassayampa River (AZ, USA)	Survival	~35% survival of TAPE, SAGO, and POFR on low floodplains	Stromberg et al., 1993
Sediment burial	HELA (1-2 wks old)	Field manipulation (Mu Us Sandland, China)	Plant growth traits	0–30% plants survived completed burial; partial burial had no effect on growth traits	Zhang et al. 2002
Planting technique, sedimentation, and other factors	16 different species with various sizes	Field manipulation on 5 rivers in Australia	Survival and growth	0-100% range of survival among species; 6-20 m tree height growth for EUCA	Webb and Erskine, 2003
Scour and sediment burial	POTR with various sizes	Elk River (British Columbia, Canada)	Survival	0–30% survival	Polzin and Rood, 2006
Flood disturbance	SAAL cuttings	Thur River (Switzerland)	Survival and root distribution	>90% survival	Pasquale et al., 2012
Scour and sediment burial	TARA and SAGO (1-2 yr old)	Bill Williams River (AZ, USA)	Survival and growth	14% survival for TARA; 64% for SAGO	Wilcox and Shafroth, 2013
Laboratory experiments					
Prolonged inundation and sedimentation	CARO, CAST, ALRU, FRLA	Pot mesocosms	Physiological responses	Partial burial impaired photosynthesis short term, but no long-term effect	Ewing, 1996
Burial	POFR, SAGO, TARA (<6 wks old)	Pot mesocosms	Survival	93% survival for POFR buried after two weeks; 100% survival for both POFR and TARA buried after five weeks.	Levine and Stromberg, 2001
Burial	10 sand dune species	Field, greenhouse, and growth chamber	Physiological responses	All partially buried species showed active growth and performance	Perumal and Maum, 2006

Driver	Species and plant age/size	Location	Plant responses monitored	Key results	Reference
Burial	5 woody upland species	Pot mesocosms	Survival and biomass distribution	All species survived partial burial but only ACCA seedlings emerged from complete burial	Burylo et al. 2012
Burial	SUSA (2 weeks)	Pot mesocosms	Survival, growth, and dry mass allocation	100% plants survived burial treatments; burial stimulated seedling growth	Sun et al, 2014
Scour and sediment burial	POFR and TARA	flume	Survival	99% survival under scour conditions and 86% survival for sediment burial	Kui et al., 2014
Scour and plant dislodgement	POFR and TARA	flume	Survival	32–65% survival	Manners et al, 2015

621 BASA=*Baccharis salicifolia*, PLSE=*Pluchea sericea*, POFR=*Populus fremontii*, SAEX=*Salix exigua*, SAGO=*Salix gooddingii*, TARA=*Tamarix ramosissima*.
 622 TAPE = *tamarix pentandra*, PRVE= *prosopis velutina*, POTR= *Populus trichocarpa*, CARO=*carex rostrata*, CAST=*Carex stipata*, ALRU=*Alnus rubra*,
 623 FRLA=*Fraxinus latifolia*, SAAL= *Salix alba*, ACCA=*Acer campestre*, HELA= *Hedysanum leave Maxim*, SUSA= *Suaeda salsa*, EUCA= *Eucalyptus*
 624 *camaldulensis*
 625

Table 2. Comparative survival among the three species subjected to three burial treatments (Experiment 1). Cottonwood and tamarisk had 0% survival in both of the complete burial treatments (shallow and deep), whereas all box elder plants survived across all the treatments. The Pearson's Chi-squared test on species and treatment showed $p < 0.001$.

	Box elder	Cottonwood	Tamarisk
Control	100%	67%	75%
Shallow burial	100%	0%	0%
Deep burial	100%	0%	0%

Table 3. Cottonwood seedling survival rates in Experiment 2 with ten treatments

ranging from 0–50 cm sediment addition.

Depth of sediment added (cm)	Number of plants tested	Initial plant height range (cm)	Survival rate	Percent height change (mean±SD) ¹	Percent leaf change (mean±SD) ²
Control (0 cm)	7	38–56	86%	45±38%	15±60%
10 cm	2	14–44	100%	83±15%	-2±5%
15 cm	8	39–59	100%	70±30%	-27±46%
20 cm	8	27–54	75%	87±20%	-20±50%
25 cm	8	33–69	75%	98±31%	9±36%
30 cm	8	22–61	38%	102±15%	71±16%
35 cm	4	37–54	75%	107±15%	14±42%
40 cm	8	30–60	38%	150±8%	100±21%
45 cm	8	27–47	0%	NA	NA
50 cm	8	29–66	13%	132±0%	48±0%

¹ Average percent height change (±SD) for surviving plants from the beginning to the end of the monitoring period. All plant heights were measured from the new soil surface (after sediment addition). Sample sizes for this metric include only surviving plants.

² Average percent change in the number of leaves (±SD) from the beginning to the end of the monitoring period. The initial leaf number was counted prior to burial, and the final count includes only leaves that emerged above the sediment surface. Sample sizes for this metric include only surviving plants.

644 Table 4. Model selection criteria used in ranking mixed logistic regression models with pot as a random factor predicting
 645 the probability of plant survival (N = 69 plants total). The best model (rank = 1) had the lowest AICc value and the highest
 646 Akaike weight. There were six candidate models, include a null model with intercept only (model rank = 6).

Plant survivability model rankings								Odds ratios for effects on plant survival ¹			
Rank	df	AICc	Δ AICc	Akaike weight	Cumulative weight	Log-likelihood	Deviance	Exposed stem height (cm)	Total stem height (cm)	Sediment depth (cm)	Stem height × sed depth
1	5	34.65	0	0.65	0.65	-13.01	26.02	1.23±1.05	1.00±1.12	0.48±1.34	1.01±1.01
2	3	37.12	2.47	0.19	0.85	-16.47	32.93				
3	4	37.54	2.89	0.15	1	-15.58	31.17		1.30±1.07	0.83±1.05	
4	3	68.06	33.41	<0.001	1	-22.27	44.55		2.14±1.0		
5	3	70.71	36.07	<0.001	1	-33.27	66.53			0.89±1.03	
6	2	97	62.36	<0.001	1	-46.16	92.31				

647 ¹ Values represent the odds ratio (± standard error) for each factor, which are the exponentiated coefficients from the logistic models

Figures

Figure 1. Photographs of the experimental setup for the complete burial experiment (panels A and B) and the sediment addition study (panels C and D). In the complete burial study (Experiment 1), plants were rooted in the ground, and pruned with sediment added within the plywood frames (A). Photo (B) shows box elder seedlings that emerged the following growing season. In the sediment addition study (Experiment 2), plants were initially buried within pots (C) and monitored for a full year (D).

662 Figure 2. Raw data from the sediment addition study (Experiment 2) showing the fate
 663 of all cottonwood plants tested as a function of their pre-burial stem height (vertical
 664 axis) and the depth of sediment added (horizontal axis). Symbols represent survival
 665 status following one year of burial. The solid grey line represents the threshold between
 666 full and partial burial; plants falling above the line had varying lengths of their stems
 667 exposed. All completely-buried plants died, and survival increased with greater
 668 proportions of exposed stem (i.e., moving upward on the vertical axis). The dashed line
 669 indicates a fixed increment of 20cm exposed stem length across all treatments; almost
 670 all plants above this threshold survived.

671

Figure 3. Panel A: Perspective plot of the best logistic regression model predicting survival probability in response to burial depth and plant height (Model #1, Table 4). The non-linear interaction between plant height and sediment depth indicates that as plant height increased, the lethal effects of sedimentation decreased substantially. Plants >80cm tall were able to survive stem burial up to 50 cm. Panel B: Conditional density plot of the raw data showing the probability of plant survival in response to the length of exposed stem (i.e., plant height minus sediment depth). The horizontal dashed lines indicate thresholds of 10%, 50%, and 90% survival probability; these correspond to exposed stem lengths of 2, 12 and 22 cm respectively. Completely buried plants (exposed stem length <0 cm) had little chance of survival, whereas plants with >20 cm of exposed stem length had high probability of survival (>90%).

685 Figure 4. Vigor response in surviving plants (N = 38) in the growing season following
 686 burial in terms of plant height increment (A), change in number of leaves (B), and
 687 diameter increment (C). For surviving plants, sediment addition induced a positive
 688 response in height growth and leaf flushing; stem diameter did not show a similarly
 689 positive response. Plotted trend lines indicate significant relationships ($p < 0.05$).

691 Figure 5. Adventitious root growth of cottonwood seedlings following sediment
692 addition. New roots grew from the buried segments of the stems.