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

Li Kui^{a,*}, John C. Stella^b

^a Graduate Program in Environmental Science, State University of New York College of Environmental Science and Forestry, Syracuse, NY, USA ^b Department of Forest and Natural Resources Management, State University of New York College of Environmental Science and Forestry, Syracuse, NY, USA

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ABSTRACT

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

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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,

* Corresponding author. *E-mail address:* lkui@syr.edu (L. Kui). 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 plantsand 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 treatments resulted >80% survivorship for cottonwood and >27% for tamarisk. Though some have proposed that there may be a plant size threshold that conditions survivorship (Levine and Stromberg, 2001), few studies have explicitly quantified one. Burial by sediment affects both plant architecture and wood anatomy, and frequently results in bent, buried trunks with multiple vertical sprouts growing upright as individual trees (Everitt, 1968). Burial can increase biomass production by producing more new leaves and branches (Zhang and Maun, 1992; Kent et al., 2001), as well as adventitious roots that sprout from the buried part of the trunk (Sigafoos, 1964; Merritt, 2013). Burial affects wood anatomy through the creation of scar tissue, production of aerenchyma, reduction in ring increment growth, and an increase in vessel cell size (Sigafoos, 1964; Nanson and Beach, 1977; Friedman et al., 2005). In order to translate the laboratory and field experiment results on plant mortality into true demographic rates, and thus understand their effect on plant populations, we need to know whether burial during sedimentation events kills plants outright or alternatively cause nonlethal damage from which they eventually recover (Sigafoos, 1964; Balke et al., 2013). It would be especially helpful to know this for plants older and larger than

Table 1

Representative studies of seedling response to burial and other fluvial disturbances in field and experimental 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 | ${\sim}35\%$ 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 Maun (2006) |
| 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) |

BASA = Baccharis salicifolia, PLSE = Pluchea sericea, POFR = Populus fremontii, SAEX = Salix exigua, SAGO = Salix gooddingii, TARA = Tamarix ramosissima. TAPE = Tamarix pentandra, PRVE = Prosopis velutina, POTR = Populus trichocarpa, CARO = Carex rostrata, CAST = Carex stipata, ALRU = Alnus rubra, FRLA = Fraxinus latifolia, SAAL = Salix alba, ACCA = Acer campestre, HELA = Hedysanim leave Maxim, SUSA = Suaeda salsa, EUCA = Eucalyptus camaldulensis. Download English Version:

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