

# Differences in seed mass between hydric and xeric plants influence seed bank dynamics in a dryland riparian ecosystem

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## Summary

**1.** Dryland riparian zones have steep spatial gradients of soil moisture and flood disturbance, and the component hydrogeomorphic surfaces support hydric to xeric plant species. These systems undergo extremes of flood and drought, a dynamic that may select for persistent soil seed banks. We asked if reliance on this strategy differed among plants in three moisture groups (hydric, mesic and xeric), and if patterns were related to diaspore traits.

**2.** We assessed the composition of soil and litter seed banks (emergence method) and extant vegetation along a riparian hydrogradient, and measured seed persistence (using an indirect method) and diaspore mass and shape variance of the component species.

**3.** Hydroriparian species had smaller diaspores than xeroriparian species, corresponding to differences in selective pressures on seedlings in their respective habitats, but the two groups formed persistent seed banks at approximately equal percentages. Persistent seeds were smaller than transient seeds, but within the persistent seed group there was separation between the smaller-diaspored hydrophytes and larger-diaspored xerophytes.

**4.** Distribution patterns of extant vegetation, in concert with diaspore trait differences among moisture-affinity groups, gave rise to divergent spatial patterns of diaspores within the soil: hydroriparian diaspores were abundant not only along wet channel bars but also in deep soils under floodplain forests and shrublands, presumably owing to dispersal by flood waters. Xeroriparian diaspores were largely restricted to the litter and upper soil layers of their drier, higher, floodplain habitats. With increasing depth in the soil of floodplain forests and shrublands, viable diaspores became smaller and rounder, and plant composition shifted from xeroriparian to hydroriparian species.

**5.** The wide distribution of hydroriparian diaspores in floodplain soils influences disturbance dynamics, increasing the probability that ephemeral wetland communities will develop wherever suitable conditions are stochastically created by floods. Persistent seed banks also allow many xeric annuals to be maintained in dryland riparian zones throughout extended drought, similar to processes that occur in desert uplands.

**Key-words:** diaspore, dryland, floodplain, river, vegetation

## Introduction

Riparian zones of dryland rivers are spatially structured systems that are characterized by steep gradients of water availability and flood disturbance (Hupp & Osterkamp 1996;

Stromberg, Tiller & Richter 1996; van Collier, Rogers & Heritage 2000). Stream bars and banks in perennial-flow reaches have moist to saturated surface soils, are frequently disturbed by floods, and are vegetated by emergent aquatics and other hydrophytes (Stromberg *et al.* 2005). Many older river floodplains and terraces are elevated several meters above the water table and have dry surface soils except following rare floods or rains; they are vegetated by hydromesic phreatophytes and by

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shallow-rooted xerophytes sustained by episodic moisture pulses (Scott *et al.* 2003).

Riparian ecosystems of dryland regions are exceptionally dynamic (Tooth & Nanson 2000; Capon 2003). Spatial patterns can shift rapidly through time, as pulses of flood water and sediment disrupt existing communities and alter local site potential (Hauer & Lorang 2004; Parsons *et al.* 2006). Patches supporting hydric plant communities can be replaced by those supporting more xeric communities, and vice versa (Stromberg, Fry & Patten 1997). Typical forest successional dynamics also occur; in arid and semi-arid Southwestern United States, for example, pioneer tree species such as *Populus* and *Salix* cede to successional species such as *Prosopis* as the floodplain surfaces aggrade through time during small, depositional flood events.

One mechanism that allows plant species to persist in highly stochastic environments is formation of persistent soil seed banks. Persistent seed banks are common in areas that are frequently disturbed, such as stream edges (Abernethy & Willby 1999; Goodson *et al.* 2001; Holzel & Otte 2004). They also occur in some dryland areas that have highly episodic resource pulses, such as desert scrublands (Guo, Rundel & Goodall 1999). Many species in dryland riparian zones do form seed banks (Capon & Brock 2006; Pettit & Naiman 2006; James *et al.* 2007; Porter, Kingsford & Brock 2007), but the relative importance of this strategy for the various types of plants that populate different hydrogeomorphic surfaces and successional stages is not well understood.

Differences in selective pressures between habitats of hydriparian and xeriparian plants may give rise to differences in seed traits that influence the probability of seed persistence in soil. Seed mass and shape are key factors that influence whether a species forms persistent seed banks, with smaller and more regularly shaped seeds more likely to be buried in sediment and larger seeds more likely to be consumed by herbivores (Thompson, Band & Hodgson 1993; Thompson *et al.* 1998). Seed traits are subject to many evolutionary pressures, and may, like other life-history traits, vary along riparian hydrogradients (Lamb & Mallik 2003). Seed mass, for example, can be greater in drier habitats (Baker 1972), and morphological adaptations for zoochory can prevail in later, drier seres (Drezner, Fall & Stromberg 2001); thus, there may be linked patterns of seed morphology and seed bank usage along riparian hydrogradients.

If seed traits do differ between hydrophytes and xerophytes, this may give rise to differences in spatial distributions of seeds in dryland riparian soils, thereby influencing plant community dynamics and response to ecosystem disturbance. Water flows in freshwater ecosystems can homogenize riparian seed pools to a certain degree, creating a common seed bank that underlies the various plant communities (Welling, Pederson & van der Valk 1988; Brock & Rogers 1998; Robertson & James 2007; Boudell & Stromberg in press). However, hydrochory also can produce spatial patterning of seeds at the landscape scale because of inter-species differences in traits such as seed floating ability (Nilsson *et al.* 2002). In between episodic flood dispersal events, the local vegetation makes

ongoing contributions to the soil and litter seed pool, further shaping the landscape scale spatial patterns.

Studies that link population-level traits (e.g. seed traits) with community-level traits (e.g. abundance of plant types) and landscape patterns (e.g. zonation within a riparian corridor) are important in furthering our understanding of ecosystem dynamics. This study, conducted along a perennially flowing reach of a dryland river, asked if plants affiliated with different habitat types show differences in seed traits, and if these differences shape the spatial patterns of seed banks at landscape scales that influence vegetation response to ecosystem disturbance. Our objectives were to determine: (i) whether diaspore mass and shape vary among plant species classified as hydrophytes, mesophytes and xerophytes, and with vertical and lateral position in riparian soils; and (ii) whether these moisture-affinity groups differ in seed banking strategies (i.e. prevalence of formation of persistent vs. transient seed banks) and in spatial zonation of diaspores within the soil profile and along the lateral hydrogradient. An additional objective was to speculate as to how these differences might influence plant community response to floods and drought.

## Methods

The study was conducted along a perennial reach of the Hassayampa River, in the Sonoran Desert of Arizona, USA (33°93'20" N; 112°69'60" W). Mean annual temperature is 19 °C and mean annual precipitation is 29 cm (Wickenburg station no. 029287; <<http://www.wrcc.dri.edu>>). The Hassayampa River has mean annual discharge of 0.8 m<sup>3</sup> s<sup>-1</sup> (Morristown gauge, USGS no. 9516500; <<http://waterdata.usgs.gov>>); stream flow has high variance, with a coefficient of variation in annual discharge of 1.85.

Study sites were established in four zones that spanned the range of hydrogeomorphic surfaces present: (i) channel bars, (ii) *Populus-Salix* forests on low floodplains adjacent to the channel, (iii) *Hymenoclea* shrublands on floodplains of intermediate elevation, and (iv) *Prosopis* forests at the floodplain perimeter on the highest surfaces with the deepest water tables (Boudell & Stromberg in press). *Populus* and *Salix* establish after floods on moist substrates, and cede to *Prosopis* during forest succession; *Hymenoclea*, a xeriparian pioneer, establishes after floods on drier substrates (Stromberg *et al.* 1997).

To assess extant plant communities, foliar canopy cover and ground cover, by species, was inventoried in 15, 1-m<sup>2</sup> study plots in each of the four zones. This plot size captures the few woody overstorey species as well as a portion of the herbaceous plants that comprise the majority of the flora. Data were collected during two time periods (May–June and September–October of 1998), to capture seasonal turnover. The May–June survey sampled cool season species that persisted late in the year due to a prolonged winter/spring rainy season. The September–October survey sampled warm season species, including those that established during the monsoonal thunderstorm season. Cover data are presented for the year as a whole, using the maximum value recorded by each species in any season; richness data are presented as cumulative species recorded across sampling times.

The soil seed bank was assessed using the seedling emergence method (Thompson, Bakker & Bekker 1997). Litter and soil samples were collected during October–November 1998, from the same 60 study plots sampled for extant vegetation, with three subsamples pooled per plot. Soil was collected from three depths (0–2, 2–5 and 5–8 cm) using a 5-cm diameter split-core soil sampler. The litter and

soil samples were placed in a controlled environmental chamber, with each sample spread to a depth of 3-cm on commercial pasteurized soil substrate. Day length and temperature in the chamber were programmed to mimic local conditions. Temperature ranges were based on average monthly maxima and minima for the Wickenburg, Arizona Global Historical Climate Network Station No. 42572278009 <<http://data.giss.nasa.gov/>>; temperature settings were changed c. 10 times a day to mimic gradual diurnal temperature fluctuations. Average day length data for 33°58' N, 112°44' W was used to program the growth chamber light timers. Plants were bottom watered and top sprayed with distilled water to maintain moist soil conditions. Twice a year, with each seasonal change in the growth chamber, the sample soil was gently stirred to bring any seeds at the bottom of the sample close to the surface to increase the likelihood of germination. To minimize competition, plants were counted and removed from trays when they could be identified. At the end of 2 years, mature plants that had not flowered were transferred to a greenhouse for identification to species. Voucher specimens were deposited in the Arizona State University herbarium.

The 101 plant species that were recorded in either the seed bank or extant vegetation were placed into one of three categories (hydroriparian, mesoriparian and xeroriparian) that differ in water needs and habitat affinity: hydric plants are associated with wetland conditions and permanent water sources, mesic species require supplemental water beyond that supplied by local precipitation, and xeric species can survive on local precipitation alone (see Supplementary Appendix S1). The classification was based on published regional values for Wetland Indicator classes <<http://plants.usda.gov/>> in conjunction with field observations, as follows: obligate wetland and facultative wetland species were classified as hydroriparian, facultative and facultative upland species as mesoriparian, and upland species as xeroriparian. In a prior paper on metacommunity dynamics, plants were classified into two categories, upland and wetland (Boudell & Stromberg in press); here we subdivide the wetland group into hydroriparian and mesoriparian. Plants also were classified by life span and growth form.

In the absence of direct data on seed longevity and persistence, we placed species into seed bank categories (persistent and transient) using an indirect approach of relying on cues from spatial distribution patterns (Thompson *et al.* 1997; Holzel & Otte 2004; Yu *et al.* 2007). Persistent seeds (= emergent seedlings) were (i) abundant in the soil, (ii) present in deep soil depths, and (iii) present at sites not vegetated by the species. Transient seeds were either (i) rare or absent in the soil, or (ii) restricted to the litter or shallow soil layer of sites vegetated by the species. This approach overestimates transient species, because all species that are rare in the community will be classified as transient.

For 72 of the 101 species, diaspore mass data was obtained from published sources (e.g. <<http://www.kew.org/data/sid/Kew/>>). (Diaspores are disseminated propagules, and can be the seed or the fruit depending on species; in this study, 55% of the diaspores were fruits including achenes, caryopses and nutlets). For the remaining species ( $n = 29$ ), lots of from 5 to 100 diaspores were collected from three plant samples (from Arizona State University or Desert Botanical Garden herbaria) and weighed to the nearest 0.1 mg. For all species, diaspore shape (three dimensions) was measured for six seeds per species, using samples from herbarium specimens. An index of diaspore shape variance (Thompson *et al.* 1993) was calculated by first transforming the length, width and depth measurements so that length is unity and then calculating the variance of the three values. The shape variance value ranges from 0 for spherical diaspores to about 0.3 for those that are needle shaped.

Analysis of variance, followed by means separation (Tukey), tested for differences in diaspore mass (natural log-transformed) and shape variance between moisture-affinity groups and between seed-banking groups. ANOVA (plus Tukey) also tested for differences in mean diaspore mass and shape, by soil depth, among vegetation zones. Here, mean diaspore traits were calculated as a weighted average by multiplying each species' diaspore density (per soil layer) by its diaspore trait values. Significance level was set at  $\alpha = 0.05$ . Analyses were conducted with MINITAB version 15.

## Results

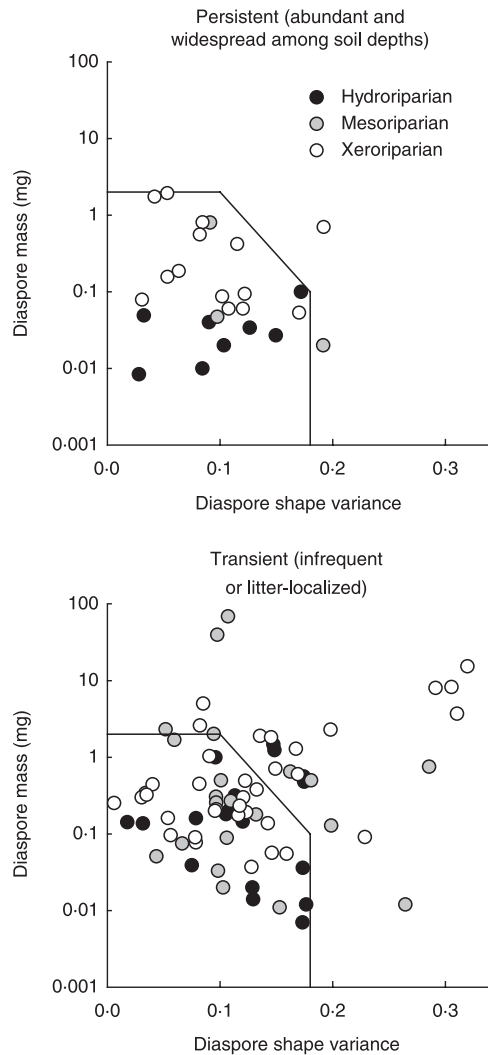
### PATTERNS BY PLANT MOISTURE GROUP

Hydroriparian species had significantly smaller diaspores than mesoriparian and xeroriparian species (Table 1, Fig. 1). Half (50%) of the hydroriparian species produced diaspores lighter than 0.1 mg, while only 27% of the xeroriparian group were in this weight category. Persistent-seed species had significantly smaller diaspores than transient-seed species, and within the persistent seed group, there was separation between the smaller-seeded hydrophytes and larger-seeded meso/xerophytes. Diaspore shape variance did not differ between moisture affinity groups, but diaspores of persistent-seed species were somewhat ( $P = 0.08$ ) rounder than those of transient-seed species.

Hydroriparian and xeroriparian plants formed persistent seed banks at approximately equal rates (31% and 29%, respectively), with the percentage lower for mesoriparian species (12%). Most (75%) of the hydrophytes and all (100%)

**Table 1.** Diaspore mass and shape variance, by moisture-affinity group (top rows) and by seed-banking category (bottom rows) for Hassayampa River riparian plant species. Values are means ( $\pm 1$  SD) followed by median. Different superscript letters within a row indicate significant difference at  $P < 0.05$

	Hydroriparian ( $n = 26$ )	Mesoriparian ( $n = 26$ )	Xeroriparian ( $n = 49$ )	<i>F</i> -ratio
Diaspore mass (mg)	0.25 $\pm$ 0.40 (0.08) <sup>a</sup>	4.6 $\pm$ 15.2 (0.26) <sup>b</sup>	1.3 $\pm$ 2.7 (0.30) <sup>b</sup>	7.23
Diaspore shape variance	0.11 $\pm$ 0.05 (0.12)	0.12 $\pm$ 0.08 (0.12)	0.12 $\pm$ 0.07 (0.12)	0.11
	Persistent (abundant and widely distributed) diaspores ( $n = 25$ )	Transient (infrequent or litter-localized) diaspores ( $n = 76$ )		<i>F</i> -ratio
Diaspore mass (mg)	0.32 $\pm$ 0.52 (0.08) <sup>a</sup>	2.40 $\pm$ 9.20 (0.26) <sup>b</sup>		6.71
Diaspore shape variance	0.10 $\pm$ 0.05 (0.10)	0.13 $\pm$ 0.07 (0.12)		3.07

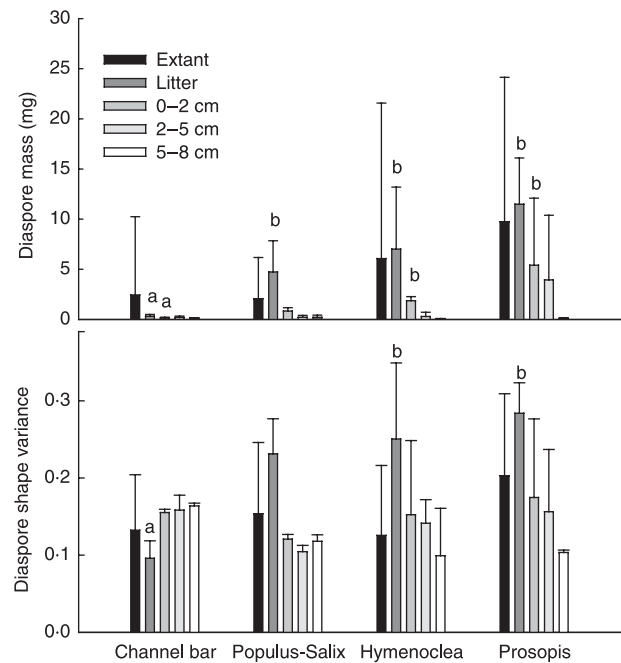


**Fig. 1.** Distribution of Hassayampa River riparian plant species along gradients of diaspore mass and shape variance. Plants are classified according to moisture affinity (hydic, mesic and xeric) and according to seed bank categories (persistent vs. transient). Also shown as inset lines are approximate boundaries (from Thompson *et al.* 1993 and Funes *et al.* 1999) that delineate diaspores with long-term (*c.* 5-year) soil persistence for a variety of ecosystems.

of the xerophytes in the persistent seed bank were annuals or biennials (vs. perennials); respective percentages within the extant vegetation were 36% (hydrophytes) and 85% (xerophytes). Overall, the majority (88%) of all persistent-seed species were annuals or biennials (vs. perennials), as were most (71%) species in extant vegetation. By life-form, 88% of persistent-seed species were forbs and 12% were graminoids, compared to 57% (forb), 31% (graminoid), and 12% (woody) for extant vegetation.

#### SPATIAL PATTERNS WITHIN THE RIPARIAN ZONE

Mean diaspore mass of extant vegetation increased along the lateral hydrogradient, with values low for channel bars and



**Fig. 2.** Diaspore mass and shape variance for riparian vegetation in each of four zones along the Hassayampa River. The zones span a hydrogradient from low, wet surfaces (channel bar) to high, dry surfaces (*Prosopis* forests). Values are shown for extant vegetation and for plants that emerged from the soil litter layer and three soil depths. Values are means  $\pm$  1 SD. Different letters indicate significant difference between zones, within soil strata, for seed bank comparisons.

*Populus-Salix* forests and high in *Prosopis* forests (Fig. 2). Diaspore mass within the litter and shallow soil layer also increased along the hydrogradient, while values within the deeper soil layers remained invariant. For the litter and the shallowest soil layer, there were significant differences in diaspore mass between channel bar and floodplain plant communities. Diaspore shape within the extant vegetation and litter layer became more variable from low to high surfaces, with significant differences evident for the latter.

For channel bars, diaspores within all soil layers had low mass (Fig. 2). In contrast, diaspore mass declined with soil depth for the floodplain plant associations. In *Prosopis* forests, for example, diaspores in litter averaged 11.5 mg while those in deepest soil (5–8 cm) had values (0.10 mg) equivalent to those in channel bar soils. Diaspores became rounder with depth in the soil for floodplain associations, but showed the opposite pattern within channel bar soils.

Most plants emerging from litter and soil samples of channel bars were hydroriparian (Fig. 3). Hydroriparian species also dominated channel bars with respect to extant plant cover, although plants from all moisture groups occurred in this zone (Fig. 4). For the floodplain associations, xeroriparian species dominated the seed banks of the litter and 0–2 cm soil depth (mirroring patterns in extant vegetation of the ground layer), while hydroriparian species were abundant in the 2–5 and 5–8 cm depths.

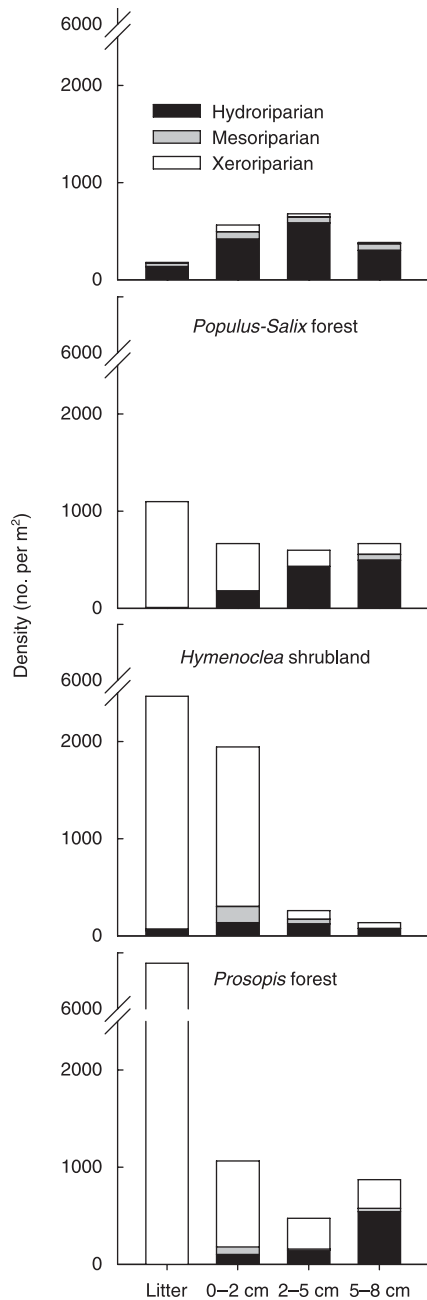


Fig. 3. Density of plants emerging from four zones in the Hassayampa River riparian corridor, by depth in the soil and by plant moisture group.

## Discussion

### DIASPORE TRAIT DIFFERENCES AMONG PLANT TYPES AND PLANT COMMUNITIES

Within the riparian zone of a dryland river, we found differences in diaspore mass between plant moisture groups and plant communities. Hydrophytes produced significantly smaller diaspores than meso/xerophytes, and diaspore size within the extant plant community and associated litter and shallow soil increased along a hydrogradient from channel bar to high floodplain communities. These patterns are consistent with regional

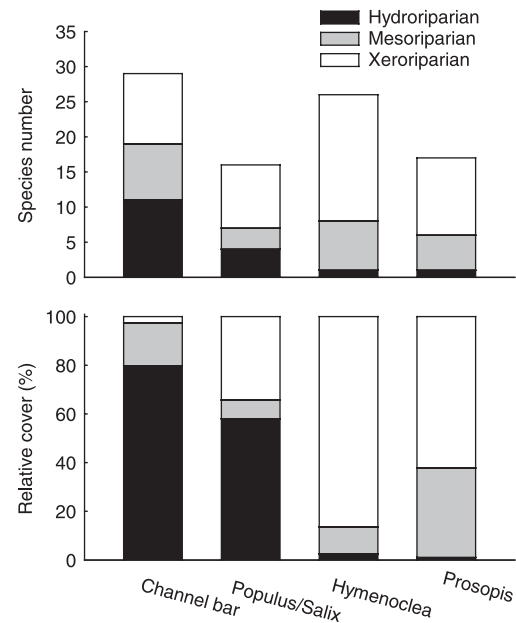


Fig. 4. Cumulative numbers of species recorded over two seasons (top panel), and their relative cover (bottom panel), by moisture group, for extant vegetation within four zones of the Hassayampa River riparian corridor.

trends (Baker 1972) for large-seeded species to prevail in drier habitats, but run counter to positive (Moles *et al.* 2005) associations between seed mass and precipitation at global scales.

The diaspore mass differences between the moisture-affinity groups conform to environmental pressures on seedlings in their respective habitats, although selection at the seedling stage is, but, one of many influences on seed mass (Leishman, Westoby & Jurado 1995; Guo *et al.* 2000). The channel bar habitats of the hydrophytes have abundant soil moisture, space and light, and are frequently disturbed by floods. Theory predicts that small-seeded species should be favoured under high disturbance although empirical studies show mixed support (Grime 1979; Kleyer 1999; Schippers *et al.* 2001). Xerophytes, in contrast, are common in the dense shade and deep litter of mature floodplain forests, or in the dry, open soils of the sparse *Hymenoclea* shrublands, both underlain by deep water tables. This finding is consistent with theoretical predictions and with empirical data showing that large seed size confers seedling survivorship advantage under conditions of drought, deep water tables, deep litter and dense shade (Salisbury 1974; Hodgkinson *et al.* 1998; Moles & Westoby 2004).

Persistent seeds often differ from transient seeds in having smaller seed mass and/or more rounded shape (Thompson *et al.* 1993, 2001; Funes *et al.* 1999; Cerabolini *et al.* 2003; but see Leishman & Westoby 1998; Moles, Hodson & Webb 2000; Holmes & Newton 2004; Yu *et al.* 2007), and this pattern held for the Hassayampa riparian flora. However, despite differences in seed mass, the hydric and xeric types had approximately similar percentages of persistent-seeded species in the seed bank (with mesic species having lower percentages). Globally, there appears to be a pattern for persistent seed banks in humid regions to be populated by small and com-

pact seeds and for those in arid regions to be populated by larger seeds (Gutierrez & Meserve 2003; Yu *et al.* 2007): our results along the Hassayampa moisture gradients mirror this large-scale climatic pattern, with the persistent seeds of xerophytes being larger, on average, than the persistent seeds of hydrophytes.

In contrast to diaspore mass, diaspore shape did not vary between moisture-affinity groups. Diaspore shape is linked to dispersal adaptations, and although plants in different moisture groups at the Hassayampa River differ in dispersal syndromes, they have approximately equal percentages of variably-shaped seeds: many hydriparian species have diaspore structures adapted for anemochory, and many mesoriparian and xeroriparian species are adapted for ecto-zoochory (Drezner *et al.* 2001). Diaspore shape did, however, become more variable across the hydrogradient within extant vegetation and seed bank communities of the litter and shallow soil. Community-level patterns at the Hassayampa show that richness of anemochorous species remains constant with distance from the river while richness of zoochorous species increases sharply (Drezner *et al.* 2001).

#### SPATIAL PATTERNS

The moisture-affinity group and the diaspore traits of the litter and shallow-soil seed banks generally mirrored that of extant plant cover across the lateral riparian hydrogradient, but this linkage between seed banks and vegetation was decoupled for the deeper soil layers. Hydriparian species prevailed along the wet, stream channel and produced small diaspores that were abundant not only in channel bar litter and soils but also in deep soil layers of the floodplain forests and shrublands. Xeroriparian species prevailed in the higher, drier and less disturbed areas, and produced larger seeds that were most abundant in the litter and shallow soil layer of the floodplain.

Many studies in freshwater ecosystems report lateral zonation in composition of extant vegetation and seed banks along gradients of soil moisture, water depth or hydroperiod (Abernethy & Willby 1999; Capon & Brock 2006; Yuan *et al.* 2007). Seed traits of extant vegetation also vary along such gradients (Parolin 2000; Lamb & Mallik 2003). Variation of seed bank seed traits along such gradients, however, has received less attention; its occurrence in this dryland riparian ecotone appears to be a product of sharply divergent physical environments that select for different life-history traits.

Along with lateral zonation, vertical zonation was apparent as well, with moisture affinity group and diaspore morphology both changing with depth in the soil profile of floodplains. The observed shift towards wetland plant species with depth in soil has been reported in other riparian areas (Richter & Stromberg 2005; also reported in Boudell & Stromberg *in press*), and the shifts toward smaller and rounder seeds with depth are common in many ecosystems (Bekker *et al.* 1998). The pattern contrasts, however, with that observed in North American deserts, where large seeds are common in deep and shallow soils alike (Guo, Rundel & Goodall 1998).

#### PROCESSES SHAPING SEED BANK ZONATION

In this dryland riparian zone, aquatic and terrestrial processes interact to create distinct spatial patterns in seed banks of plants in different moisture-affinity classes. One key process is hydrochory, wherein large floods periodically entrain seeds during the ascending phase and then disperse them broadly across the floodplain (Merritt & Wohl 2002; Goodson *et al.* 2003; Jansson *et al.* 2005). Although flood waters transport a variety of propagule types (Vogt, Rasran & Jensen 2006) the diaspores of hydrophytes may have a higher probability of entrainment because of their small size and abundance (given trade-offs between seed size and number; Harper 1977) and their location in low portions of the riparian corridor. In between flood events, *in situ* processes dominate, and the seed banks are shaped by extant vegetation. On aggraded floodplains, there are increasing inputs from larger-seeded xerophytes into the litter, while the smaller seeds move downward in the sandy soils soil via rainfall at greater rates (Benvenuti 2007). Thus, zonation develops. We note, however, that our methodology detected only viable seeds. If larger diaspores are dispersed laterally and/or buried at equal rates as smaller ones, but lose viability more quickly, this also would contribute to horizontal and vertical zonation.

#### PLANT COMMUNITY DYNAMICS

In various freshwater ecosystems, a diverse suite of species in seed banks creates a mosaic of potential floras (Hughes & Cass 1997; Casanova & Brock 2000; Nicol, Ganf & Pelton 2003). For dryland rivers with intense floods, such as the Hassayampa, the presence of hydrophyte seeds throughout the floodplain soils is a key factor influencing disturbance dynamics (Capon & Brock 2006). The wide vertical and lateral distribution of diaspores of annual (e.g. *Calibrachoa parviflora*, *Juncus bufonius* and *Mimetanthe pilosa*) and perennial (e.g. *Veronica anagallis-aquatica*) hydrophytes in the riparian soils increases the probability that ephemeral wetland plant communities will develop wherever floods stochastically create suitable hydrogeomorphic conditions (Boudell & Stromberg *in press*). Deeply buried seeds do not contribute to future plant communities in terrestrial ecosystems (Traba, Azcarate & Peco 2004), but they likely do for dryland sandbed rivers with highly mobile sediments. Transient-seeded hydrophytes utilize other means to populate moist, flood-scoured sites: the dominant trees and shrubs (*Baccharis salicifolia*, *Populus fremontii* and *Salix gooddingii*), for example, each year produce moderately-sized, wind-dispersed seeds.

Persistent and transient seed banks also collectively maintain the many xerophytes that occur along dryland rivers, most of which are annuals. The rain or flood pulses that stimulate the germination and seed-set of xeric annuals such as *Amsinckia intermedia* and *Bowlesia incana* do not occur every year; but persistent soil seed banks allow them to be maintained through extended drought. This strategy parallels that of the many annual species that populate desert uplands (Guo *et al.* 1999; Gutierrez & Meserve 2003). Transient-seeded xeric

annuals adapted for ecto-zoochory, such as *Bouteloua barbata* and *Bromus rubens*, also occur in floodplain forests and shrublands. Such species may be maintained during dry cycles by soil moisture provided by riparian-zone processes such as hydraulic lift (Hultine *et al.* 2004), or by source-sink dynamics; if dispersed into wet microsites by zoochory they may establish small populations whose progeny are subsequently dispersed back into the drier portions of the riparian zone.

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## Supplementary material

The following supplemental material is available for this article:

**Appendix S1.** *Functional Ecology*. Stromberg JC, JA Boudell, AF Hazelton. Differences in seed mass between hydric and xeric plants influence seed bank dynamics in a dryland riparian ecosystem.

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