



Floods, drought, and seed mass of riparian plant species



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ARTICLE INFO

Article history:

Received 23 August 2012

Received in revised form

13 March 2013

Accepted 27 May 2013

Available online 25 June 2013

Keywords:

Arid

Disturbance

Ephemeral stream

Floodplain

Plant community

Water

Wetland

ABSTRACT

Plant communities in dryland riparian ecosystems are influenced by flood disturbance and water availability. As global climate change alters stream flow regimes, there is increasing need to understand which traits allow plant species to persist under increased stress and disturbance. Small seed mass is part of a strategy that adapts for disturbance, but the role of seed mass as an adaptation for drought is less well documented. For dryland riparian plant communities, we asked, does seed mass vary with water availability and flood frequency? We compared community seed mass between sites that vary in flow permanence (longitudinal water gradient) and between hydrogeomorphic surfaces within sites (lateral gradients of moisture and disturbance). Using data from four rivers in Arizona, we contrasted seed mass between plant groups. We found community seed mass to be greater at sites with ephemeral than perennial flow, and to increase laterally from wet, frequently-flooded channel edges to dry, less disturbed terraces. Seed mass varied by moisture group (smallest for hydriplant species) and by disturbance group (smallest for disturbance species), and showed a trend for being greater in introduced species. We conclude that small seed mass is independently associated with wet and disturbed conditions in dryland riparian ecosystems.

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1. Introduction

Many regions of the world, including southwestern United States, are becoming drier and experiencing more intense storms (Seager et al., 2007). As climate changes globally, scientists are increasingly called upon to explain how fundamental changes in resources and in disturbance regimes will influence biotic communities. Increasingly, such questions are being addressed by focusing on plant traits (Kyle and Leishman, 2009a). Although a suite of traits collectively influence a plant's ability to establish and persist under a given set of conditions, it is also true that a single trait can influence a plant's response to myriad environmental factors, necessitating studies that range from reductionist to holistic.

Seed mass exerts strong influence on plant distribution, and is commonly used as a disturbance indicator in ecological classification schemes (Westoby, 1998). It is well established that small seed size is a component of a ruderal strategy in which short-lived plants produce many propagules, each with small maternal investment of resources (Grime, 1974). Seedlings that arise from small seeds

typically require bare moist soil in light gaps to produce sufficient photosynthate. Conversely, high seed mass is a component of a competitive strategy, and allows seedlings to establish in the presence of neighbors (Gross, 1984; Jensen and Gutekunst, 2003; Salisbury, 1974; Shipley et al., 1989).

In addition to influencing colonizing vs. competitive ability (Turnbull et al., 2004), seed mass influences a seedling's ability to tolerate various environmental stresses. For example, high maternal investment in seeds provides an advantage for seedlings growing in areas with low nutrients, low soil moisture, low light high, or high risk of seed burial by sediment (Hewitt, 1998; Hodkinson et al., 1998; Moles and Westoby, 2004; Parolin, 2000; Stromberg et al., 2011). Large seed mass also, however, increases risk of being eaten by granivores.

In riparian ecosystems of arid regions, plants are strongly influenced by flood disturbance and water stress. Although there is some evidence that large seed size is adaptive in dry habitats, patterns are not strong or universal. Baker (1972) observed higher seed mass for species in California habitats characterized by high risk of drought, with the difference most pronounced between wetland and dryland habitats. In a region with a humid continental climate, however, water availability explained only a small fraction of the variance in regional seed weight (Mazer, 1989). In semiarid Australia, Leishman and Westoby (1994) found large-seeded

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species to have survivorship advantage over small-seeded species under dry conditions in a glasshouse, although these results were not borne out in the field. Theoretically, large seeds would be advantageous in dryland riparian zones by allowing seedlings to grow roots to deep and/or rapidly declining water tables, and to increase the size of their 'foraging' area for soil water. As a trade-off, however, such plants would have reduced ability to produce large numbers of seeds, thereby reducing their effectiveness as colonizers of disturbed sites.

In this study, we focused on seed mass in arid region riparian zones and asked whether community seed mass varies along both a resource/stress gradient and a competition/colonization gradient. Specifically, we expected 1) wetland species to have smaller seeds than those of dryland species, 2) species adapted to disturbance to have smaller seeds than those associated with more stable environments, and 3) sites with the combination of perennially wet soils and frequent flooding to have the smallest seeds overall. Finally, given the high number of introduced species in dryland riparian zones, we asked whether seed mass differs from that of the local (native) species.

2. Methods

We used two approaches. First, we analyzed field data to determine whether community-level seed mass varied along environmental gradients of water availability and disturbance frequency. Second, we classified riparian plants a priori by moisture class and by disturbance adaptation, and then compared seed mass among moisture and disturbance groups. Given the recognized influence of plant growth form on seed mass (Moles et al., 2007; Westoby et al., 1996), we included growth form as part of our analyses. Differences between native and introduced species were assessed using a priori classification of plants collected from regional rivers.

2.1. Field studies

We examined community-level seed mass along 1) longitudinal gradients of surface flow permanence and 2) lateral gradients encompassing linked changes in moisture availability and disturbance frequency. The longitudinal studies were conducted at two interrupted perennial rivers, each of which has areas with ephemeral, intermittent, and perennial flow (Stromberg et al., 2009a, 2009b) (Fig. S1). Near Wickenburg, Arizona, the Nature Conservancy's Hassayampa River Preserve encompasses a 5 km stretch of perennial to intermittent flow within an otherwise ephemeral portion of the river. At the Hassayampa River we sampled 11 study sites, all within the Nature Conservancy Preserve or in the downstream ephemeral reach (335 m–600 m elevation). Pima County's Cienega Creek Natural Preserve, east of Tucson, Arizona, has short stretches of perennial to intermittent flow separated by longer reaches with ephemeral flow and deep water tables. We sampled eight sites within the Preserve (965 m–1090 m elevation). We sampled over a 3-year period at the Hassayampa and a 2-year period at Cienega Creek, during which time we assessed presence of stream surface water monthly at each study site. We used flow presence/absence data for each 12-month period prior to vegetation sampling as an index of annual flow permanence. At each site, we recorded plant cover by species in 18, 1-m² plots distributed along the edge of the low-flow channel. The sampling zone consisted of a 2 m wide strip bordering the low-flow channel, inclusive of banks and bars, and extending for 20 m. We sampled vegetation during the summer dry season (May) to avoid the confounding effects of late summer floods. We calculated median seed mass per site using plant presence data (values were not

weighted by a plant's abundance in the community) and then used Pearson correlation analysis to test for relationships, within years, between flow permanence and median seed mass of the plant community.

We examined lateral seed mass patterns at three rivers (Hassayampa, San Pedro, Verde). Data for the Hassayampa River were collected at intermittent and perennial sites within the preserve. Data for the San Pedro River were collected at 18 intermittent to perennial sites (600 m–1285 m elevation) (Lite et al., 2005). At the Verde River, three sites were sampled within perennial sections of the river, all on preserves (965 m–1285 m elevation). At all three rivers, vegetation plots (100-m² for woody plants and 1-m² plots for herbaceous) were distributed from the low-flow channel edge to river floodplains and terraces. Vegetation was sampled in early and late summer to capture seasonal diversity, and, except at the Verde (1-year), was sampled in multiple years. Species presence was then compiled by hydrogeomorphic zone. Zones were low-flow channel edges, low floodplains, high floodplains, and river terraces. At the Hassayampa River, these latter three zones were respectively <2 m, 2–3 m, and >3 m above the channel bed; at the San Pedro River they were <2.5 m, 2.5–5.0 m, and >5 m above the channel bed (based on cross-sectional topographic surveys). At the Verde River they were <2.5 m, 2.5–4.5 m, and >4.5 m above the water table. We tested for differences in median seed mass between zones within rivers using general linear models (GLMs) and Tukey's tests. Seed mass was not weighted by plant abundance.

2.2. Plant classification and seed mass

We derived a list of 431 riparian plants based on vegetation sampling at four rivers in arid to semi-arid Arizona (Fig. S1). Long-term mean annual temperatures in the study areas are 20 °C (Cienega Creek), 19 °C (Hassayampa River), 17 °C (San Pedro River), and 16.5 °C (Verde River). Long-term mean annual precipitation is 29 cm (Cienega Creek), 29 cm (Hassayampa River), 35 cm (San Pedro River), and 30 cm (Verde River).

Plants were identified to species using Kearney and Peebles (1960) and recent taxonomic treatments (<http://nhc.asu.edu/vpaperbarium/vpap.html>). Seed mass for most species was obtained by collecting lots of 5–100 seeds from three herbarium plant samples (Arizona State University herbarium) or from at least three individuals in the field (the minimum recommended sample size; Cornelissen et al., 2003) and then weighing them to a precision of 0.01 mg (0.001 mg for the smallest-seeded species). For one third of the species, seed mass data was obtained by accessing the Kew Royal Botanical Gardens Seed Information Database Version 7.1 (<http://data.kew.org/sid/>).

All plant species were placed into one of three moisture groups: hydroriparian, mesoriparian, and xeroriparian. Plants were considered to be hydroriparian if their Wetland Indicator Status (obtained from <http://plants.usda.gov>) was obligate wetland or facultative wetland; as mesoriparian if they were facultative or facultative upland; and as xeroriparian if they typically grow as upland species at low elevations in the region.

For disturbance classification, we used multiple approaches. For woody plants, we distinguished floodplain pioneers (i.e., shade-intolerant plants that characteristically establish on flood-scoured sites) from non-pioneers based on habitat preferences. This latter group included riparian species associated with high floodplains and terraces as well as Sonoran Desert upland species for which traditional successional models do not apply. Given that dispersal mechanism is linked with successional status (Drezner et al., 2001) we also classified species into one of three primary dispersal categories – anemochores (those with pappus, plumes or dust-like seed), zoochores (diaspores with barbs, hooks or spines, fleshy

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