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EPHEMERAL WETLANDS ALONG A SPATIALLY INTERMITTENT RIVER: TEMPORAL PATTERNS OF VEGETATION DEVELOPMENT

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Abstract: Dryland rivers are characterized by high spatio-temporal variability in water resources, with alternating wet and dry reaches and fluctuating stream flow rates. To investigate response to this dynamic, riparian plant communities from perennial, temporally intermittent, and ephemeral-flow reaches of the Hassayampa River and an ephemeral tributary (southwestern USA) were characterized over a three year period, and soil seed banks (emergence method) were assessed. Variance through time in cover and diversity of wetland (hydric) species was lowest at perennial sites and highest at ephemeral flow sites. Wetland plants established along the active channel of the ephemeral reach following a 10-year recurrence interval flood, and compositional similarity between perennial and ephemeral sites was high during this wet year. About half of the wetland species growing at ephemeral flow sites were present in floodplain soil seed banks. Wetland species emerged from soils of the ephemeral Hassayampa River (but not of the ephemeral tributary) but their density and diversity declined with distance downstream of the perennial reach. Wetland species in the seed banks of ephemeral-flow sites were a nested subset of those at wetter sites, raising the possibility of dispersal from upstream sites. These results indicate that wetlands develop episodically on ephemeral reaches of spatially intermittent rivers of the Sonoran Desert following high winter runoff, and suggest that the wetland plants arise from local seed banks and off-site sources. The study also suggests that riverine restoration success is sensitive to location within a stream network: upon re-watering, sites closer to perennial reaches will have greater capacity to self-assemble wetland plant communities.

Key Words: dryland river, intermittent flow, riparian vegetation, seed bank, temporary stream

INTRODUCTION

The longitudinal pattern of stream flow varies among dryland rivers (Nanson et al. 2002, Bunn et al. 2006). Some have ephemeral flow over their entire length, with surface water present only following major storm events; these are classified as endogenic dryland rivers. Others, classified as allogenic, have headwaters in humid mountains and sustain perennial flow in hydrogeomorphically suitable portions of the arid basin. Such rivers often are spatially intermittent, with perennial flow occurring in areas with shallow bedrock or high hydraulic connectivity to regional aquifers and ephemeral to temporally intermittent flow occurring in areas with deeper alluvial basins or greater distance from the headwaters. Given their wetter headwaters, the allogenic dryland rivers also experience larger and more sustained flood pulses than their endogenic counterparts.

Adjacent perennial and ephemeral reaches within rivers support distinct aquatic and riparian communities owing to difference in surface water permanence and ground-water hydrology (Stromberg et al. 205, Wood et al. 2005). In many dryland regions, the floodplains of perennial dryland rivers have shallow water tables, and this permanent water source sustains tall, phreatic hydric trees (Lite and Stromberg 2005, Froend and Drake 2006). In ephemeral reaches, episodic flood run-off and precipitation are the main sources of soil water, although a temporary perched water table can develop during high-flow periods; thus, xeric plant species predominate (Bloss and Brotherson 1979, de Soyza et al. 2004, Rassam et al. 2006). In some hydrogeomorphic settings, ground-water hydrology can be fairly similar in perennial and non-perennial reaches, producing more subtle differences in riparian structure and function (Birkeland 1996, Kolb et al. 1997, Stromberg 2001).

Although perennial and ephemeral stream reaches support different biotic communities, the degree of difference varies through time. Community structure and function differ most during the dry, low-flow season (Stromberg et al. 2005, Gazal et al. 2006). During wet seasons, floods create a more uniform

hydrologic environment over the length of the river, and this can result in increased compositional similarity between perennial and non-perennial reaches (Lake 2003, Wood et al. 2005) and between habitats within a reach (Thomaz et al. 2007). For example, many riparian plant species form persistent soil seed banks, and seeds that are quiescent during long dry periods may germinate during periods of flooding (Brock and Rogers 1998, Goodson et al. 2002, Nicol et al. 2003, Capon and Brock 2006, Capon 2007), increasing compositional similarity among river sites. Further, plant seeds (and plant fragments) are broadly dispersed by flood waters (Johansson et al. 1996, Jansson et al. 2005, Merritt and Wohl 2006, Vogt et al. 2006), and this may unify plant communities during the flood recession period.

The spatial patterning of wet and dry reaches on dryland rivers changes through time in response to climatic fluctuations and to human modifications of the landscape. Extreme drought, which may become more prevalent in some regions as the global climate changes, can cause long, continuous wet reaches to fragment into short, disconnected sections (Stanley et al. 1997). Anthropogenic water extraction (streamflow diversion and ground-water pumping) also can result in expansion of dry reaches (Uys and Okeefe 1997; Webb and Leake 2006). Other types of human actions can cause wet reaches to expand. For example, perennial segments can increase in spatial extent where flow-regulating dams dampen flow extremes (McMahon and Finlayson 2003) or where dry reaches receive input from interbasin water transfers, urban run-off, or urban wastewater. These "new" water sources, such as urban effluent, sometimes are used for ecosystem restoration purposes but often are discharged without considering the hydrologic context of the landscape.

The spatio-temporal patterns of wet and dry reaches within a watershed — including the length of wet reaches, their persistence through time, and the length of intervening dry reaches — may influence riverwide patterns of biota. Some plants exist along rivers as metapopulations (Menges 1990), with flood dispersal of seeds maintaining connectivity between populations. Seed dispersal distance and seed emigration rate have an important effect on metapopulation persistence in temporally dynamic habitats (Bossuyt and Honnay 2006). Connectivity may be reduced if the dispersal distance between suitable sites is too great. Such population-level phenomena may carry through to higher levels of ecosystem organization. Metacommunity dynamics have been noted to occur laterally within a riparian corridor, wherein the spatially structured communities along the stream to upland hydrogradient are linked via dispersal processes (Boudell and Stromberg 2008). A similar dynamic may occur over the longitudinal dimension. Wetland plant communities may develop at ephemeral sites along a river, and may show high seasonal similarity to those at perennial sites, only if the former are in proximity to the latter.

As the arid southwestern United States continues to urbanize and undergo climate change, landscape-scale patterns of river hydrology will be altered, heightening the need to understand consequences to riparian and aquatic biota. This investigation contrasted riparian plant communities (inclusive of the soil seed bank) between perennial, temporally intermittent, and ephemeral stream reaches of a spatially intermittent river, through multiple years, to address the roles of landscape patterns of stream hydrology and annual flow variability on vegetation patterns. We asked: 1) Does extant plant community composition at perennial and ephemeral reaches become more similar during periods of high-flow, and if so, does this reflect contributions from the seed bank? 2) Are hydric (wetland) plants present in soil seed banks of ephemeral and perennial reaches alike? 3) Are diversity and composition of the soil seed bank influenced by the spatial patterning of wet and dry reaches and, in particular, by the proximity to a wet reach?

METHODS

Study Sites

Eight study sites were established along the Hassayampa, a free-flowing (undammed), spatially intermittent river in the Sonoran Desert of central Arizona (Figure 1). One additional site was established in an ephemeral tributary (Jackrabbit Wash). The Hassayampa drains portions of the Bradshaw, Date Creek, Weaver, and Vulture Mountains. The lower watershed is in the Basin and Range physiographic province and the upper watershed is in the Central Highlands physiographic province. Elevations in the watershed rise to over 2130 m.

Of the eight Hassayampa River study sites, two were within a seven kilometer reach with perennial to temporally intermittent flow that is managed as a preserve by The Nature Conservancy in Arizona. One of the eight was in an upstream ephemeral reach, two kilometers from the starting point of perennial stream flow. Five sites were in the downstream ephemeral reach at respective distances of two, 19, 28, 43, and 48 km from the typical downstream limit of perennial surface flow. We refer to these latter sites as ephemeral-2 km, ephemeral-

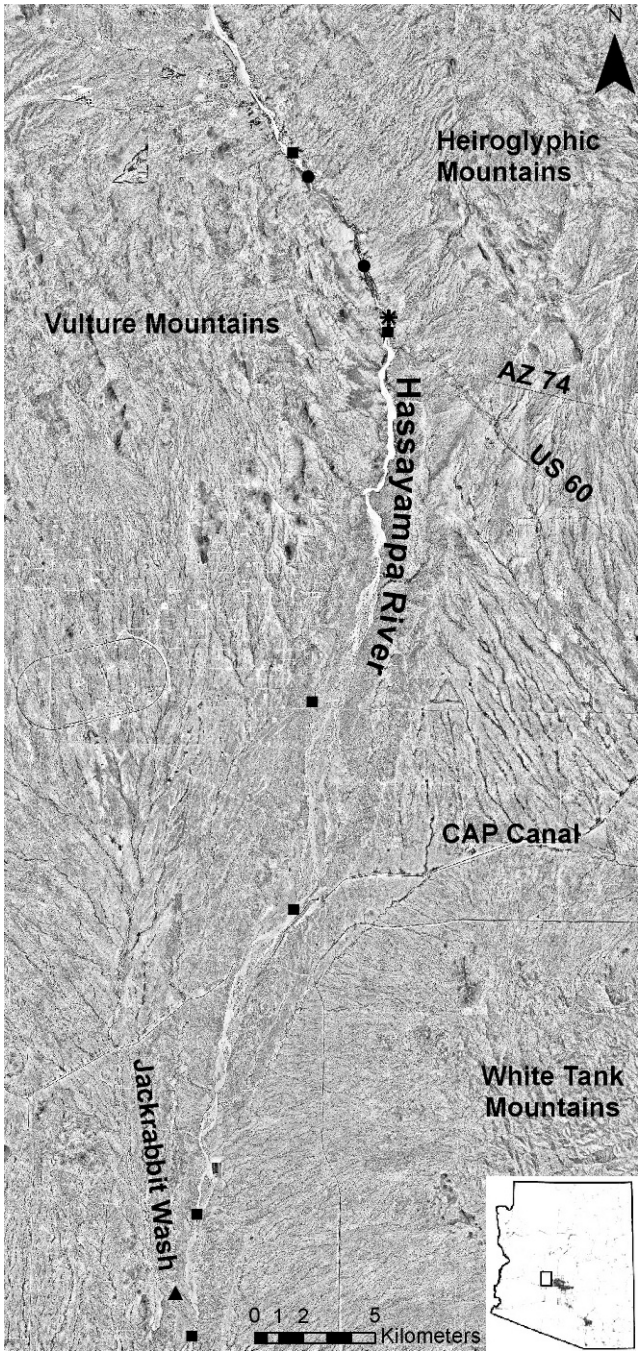

Figure 1. Location of study sites along the Hassayampa River and tributary, Arizona, USA. Site types include those with perennial or temporally intermittent surface flow (round symbols) or with ephemeral flow (square symbols). The triangle denotes the site along the ephemeral tributary. Asterisk indicates location of the Morristown stream gage (USGS #9516500).

19 km, etc. Most of the ephemeral sites were on private land; some were grazed by livestock and/or used recreationally by off-road vehicle riders. Site elevation above sea level ranged from 335 m to 603 m.

The study area is hot and arid. Mean annual temperature is 19°C and mean annual precipitation is 29°cm at the Wickenburg station (# 029287, http://www.wrcc.dri.edu). The Hassayampa River has mean annual discharge of 0.8 $m^3 s^{-1}$ at the Morristown gaging station (USGS #9516500; htp://waterdata.usgs.gov), located 0.6 km upstream of site ephemeral-2 km. The flood pattern is dominated by winter precipitation events, arising from Pacific frontal storms; floods also occur in late summer and fall following monsoonal thunderstorms and tropical storms, respectively (Sheppard et al. 2002). The coefficient of variation in annual discharge is 1.85; discharge ranges from 0.0 $m^3 s^{-1}$ in dry years to greater than 6.0 $m^3 s^{-1}$ in years with large, winter flood events.

El-Niño weather patterns occurred in 2005, and streamflow was well above average in winter/spring; the peak flow on February 12, 2005 had an approximate recurrence interval of 10 years, and flow was present at the stream gage for four months (through mid-June). Streamflow was below average in winter/spring of 2006 and 2007 (Figure 2). Based on monthly site measurements of streamflow presence/absence for an 18-month period from April 2006 through September 2007, streamflow was present 17% of the time at the upstream ephemeral site, 72% at the intermittent site, 100% at the perennial site, 22% at the nearest downstream ephemeral site (ephemeral-2 km), and 0% at all other sites. The mean streamflow rate ($m^3 s^{-1}$) at the Hassaympa-Morristown station in three-month blocks preceding each sampling period was 0.66 (June 2005), 0.06 (August 2005), 0.02 (April/May 2006), 0.00 (August 2006), and 0.00 (June 2007). Precipitation (cm) in these same blocks was 0.5 (June 2005), 2.4 (August 2005), 0.8 (April/May 2006), 2.3 (August 2006), and 0.7 (June 2007).

The floodplains of the perennial and temporally intermittent sites were vegetated mainly by *Populus fremontii -Salix gooddingii* hydric forests (moderately deep-rooted, obligate phreatophytes) and *Baccharis salicifolia* hydric shrubs. *Prosopis velutina* mesic forests (a very deep-rooted, facultative phreatophyte) and *Hymenoclea monogyra* shrublands (a xerophyte) occur at these sites on the higher floodplain surfaces where ground water is at depths of three meters or more (Stromberg et al. 1997). The downstream ephemeral sites were vegetated by xeric shrublands (*Hymenoclea*) intermixed with *Prosopis velutina*. The upstream ephemeral site supported low densities of *Populus fremontii*, suggesting the presence of a shallow water table; it thus may not qualify as ephemeral according to Meinzer's (1923) criteria which include infrequent surface flow (in response to

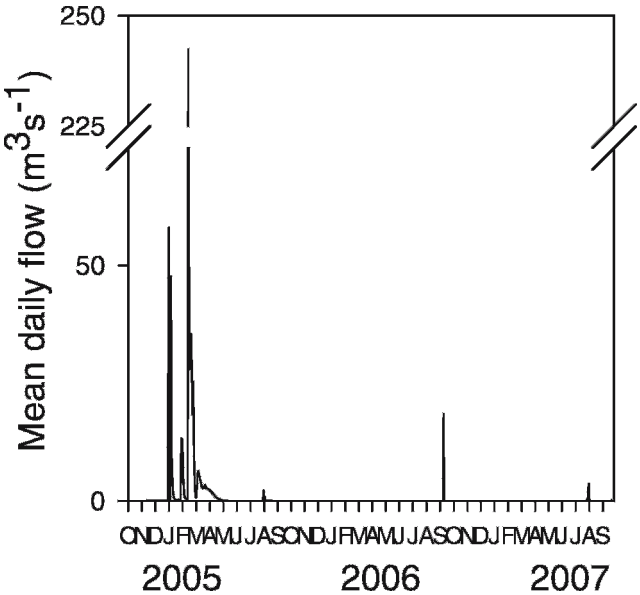

Figure 2. Streamflow rate of the Hassayampa River (Morristown gaging station) during the study period. The gage is located in an ephemeral reach, 0.6 km upstream of study site Ephemeral-2 km.

storm runoff events) and a deep water table (that consistently remains below the channel bed). However, we placed it in the ephemeral category based on our surface flow measurements.

Vegetation and Seedbank Sampling

To characterize floodplain vegetation, three, two-meter wide cross-floodplain belt transects were established per site. The transects were approximately 100 meters apart, with the location of the first being randomly selected. Each belt transect was divided into 10 equidistant segments, with the segment lengths scaled to the length of each floodplain, and species presence/absence was recorded in one, 10 m^2 plot (two $\times$ five m, long axis perpendicular to stream) per segment. To characterize vegetation along the active channel (bars and banks of the low-flow channel), cover, by species, was sampled in 18 one-m^2 plots per site (six plots within a 20-meter long segment of the active channel at each belt transect location). Data were collected in June and August 2005, May and August of 2006, and June of 2007. Not all sites were sampled at all sampling times.

The soil seed bank was assessed using the seedling emergence method (Roberts et al. 1981). Soil samples were collected in June 2005 at four of the study sites (upstream ephemeral, intermittent, perennial, and ephemeral-2 km), and again in June 2006 at eight of the sites (intermittent, perennial, ephemeral sites at 2-km, 19-km, 28-km, 43-km and 48-km, and Jackrabbit Wash). At each site, 15 soil samples were obtained (five samples from alternating segments of three transects); each sample was a composite of three sub-samples, to capture the heterogeneously distributed propagules. The sub-samples consisted of the uppermost 2.5 cm of soil (litter removed), as collected with a five-cm diameter split-core soil sampler. Species accumulation plots (not shown) indicate this sample size captures only a portion of the species present; more intensive sampling is needed to fully characterize the seed bank community (Stromberg et al. 2008).

The soil samples were spread on a sterile commercial potting soil mix and maintained for one year in a controlled environmental chamber programmed to mimic the temperature and day length of the study river. Plants were watered as needed to maintain moist soil conditions. The number and identity of all emerging plants was determined monthly. After one year, remaining unidentified samples were transferred to a greenhouse to allow for flowering and species identification. A few *Juncus* individuals remained vegetative and could not be identified beyond genus, and a few flowering individuals (e.g., *Cryptantha* sp.) could be identified only to genus. Plants were identified using Kearney and Peebles (1960) and recent treatises; nomenclature follows the USDA Plant database (http://plants.usda.gov/).

Data Analysis

Plants were classified into one of three groups (hydric, mesic, xeric) that indicate water needs and habitat affinity. Plants were placed into these categories based primarily on published wetland indicator classes (http://plants.usda.gov/), with obligate wetland and facultative wetland species classed as hydric, facultative and facultative upland as mesic, and non-wetland as xeric. For some analyses, hydric and mesic species were combined into a hydromesic group.

Sorenson's community coefficient (using presence/absence data) was calculated to assess the degree of similarity in plant community composition between perennial-flow and non-perennial sites for each sampling time (using the program EstimateS; Colwell 2005). For soil seed banks, the community coefficient was calculated using the year-round data set. To further examine patterns of floristic similarity and distinctiveness between hydrologic site types, the nestedness (i.e., the degree that species at certain sites are a nested subset of those at other sites) of hydromesic and xeric plant groups in the vegetation

and seed banks was assessed using a nestedness temperature calculator developed by Atmar and Patterson (November 1998 version of software). With this calculator, a low temperature indicates a high degree of nestedness within the flora (Atmar and Patterson 1993). This calculator can overestimate the degree of nestedness (Rodriguez-Girones and Santamaria 2006) but is useful for making relative comparisons within a study area. To determine if the seed bank plant community varied with location along the river, Pearson correlation coefficients (using SYSTAT Vers. 11) were calculated between the distance of each ephemeral-flow site from the typical downstream limit of perennial flow and the density and richness of species in the seed bank (for all species combined, and by plant moisture group). Species richness was used as our measure of diversity in this study.

RESULTS

Extant Vegetation

For the Hassayampa River active channel and floodplain vegetation, the degree of compositional similarity between perennial and ephemeral sites was highest during the period of highest stream flow (early summer of 2005) and lowest during driest periods (late summer of 2006 and early summer of 2007) (Table 1). Cover and richness remained fairly constant among sampling times at sites where flow was perennial but showed much greater variance at sites where flow was ephemeral (Table 2, Figures 3, 4).

Most of the hydric species present during the wet early summer of 2005 were recorded at perennial and ephemeral sites alike (Figure 5, upper left). Among the hydric species present along the active channel at all hydrologic site types were the annuals *Calibrachoa parviflora*, *Juncus bufonius*, *Mimetanthe pilosa*, and *Polypogon monspeliensis*, the herbaceous perennials *Polygonum punctatum*, *Typha domingensis*, and *Veronica anagallis-aquatica*, and the shrub *Baccharis salicifolia*. Xeric species also showed high overlap among hydrologic site types during early summer of 2005. Several, however, including the desert annuals *Cryptantha* sp. and *Pectocarya platycarpa*, were detected only at ephemeral sites.

During the subsequent dry sampling periods, hydric species were sparse to absent at ephemeral sites. The lone hydric species present along the active channel of an ephemeral site in June 2007 was *Polypogon monspeliensis*, with very low cover at ephemeral-2 km, and juvenile *Populus fremontii*, with very low cover at the upstream ephemeral site. Xeric species also were very sparse at ephemeral sites during the dry sampling times. Several xeric species were recorded only at perennial sites during dry time; many of these were annuals commonly associated with *Prosopis* riparian forest understory including *Bowlesia incana*, *Bromus diandrus*, *Herniaria hirsuta* ssp. *cinerea*, *Hordeum murinum* ssp. *glaucum*, and *Parietaria hespera*. During the dry sampling times, the hydromesic species and xeric species groups both showed significant nesting, with species at the ephemeral sites being a nested subset of those at wetter sites (Table 3).

Soil Seed Bank

There was a high degree of compositional similarity between the seed bank of the Hassayampa River perennial flow site and the nearby ephemeral flow sites (i.e., upstream ephemeral, ephemeral-2 km, and ephemeral-19 km; Table 1). The degree of similarity declined with increasing distance of an ephemeral site from the perennial reach (Table 1). The lowest similarity recorded (zero) was between the perennial Hassayampa site and the ephemeral tributary (Jackrabbit Wash).

Hydric species were present in soils of all Hassayampa ephemeral sites, including the most distant one (48 km) (Figure 6). However, their diversity and density declined significantly with distance downstream from the perennial reach (Table 4). Patterns for mesic species were similar to those for hydric species in that they decreased in diversity and density with distance downstream. However, in contrast to hydric species, mesic species were not present at all Hassayampa ephemeral sites, being absent from soils of the three farthest downstream sites. No hydric or mesic species emerged from seed banks of the ephemeral tributary (Jackrabbit Wash). Xeric species did not change in abundance or diversity along the distance gradient.

The hydromesic seed bank species at the dry Hassayampa River sites were a nested subset of those at the wetter sites; all but one of the hydromesic species at the ephemeral sites were also found at the perennial site, while the perennial site contained many hydromesic species not found at ephemeral sites (Table 3, Figure 5, bottom right). Among the hydric species present in soils of perennial and ephemeral sites alike were *Juncus bufonius*, *Polypogon monspeliensis*, *Typha domingensis*, and *Veronica anagallis-aquatica*; those recorded only at a perennial site included *Eleocharis parishii*, *Heliotropium currassivicum*, *Nasturtium officinale*, *Juncus torreyi*, *Polygonum lapathifolium*, and *Symphyotrichum expansum*.

Table 1. Sorenson classic similarity coefficients among riparian plant communities of hydrologic site types within the Hassayampa River drainage. Values are similarities between site pairs (i.e., perennial site vs. a non-perennial site) and are shown separately for active channel vegetation, floodplain vegetation, and soil seed banks.

Perennial site versus:	Sorenson similarity coefficient						
	Upstream Ephem.	Intermittent	Eph-2 km	Eph-19 km	Eph-28 km	Eph-43 km	Eph-trib.
Active channel vegetation							
June 2005	0.36	0.54	0.55	–	–	–	–
Aug. 2005	0.42	0.37	0.39	–	–	–	–
May 2006	0.17	0.52	0.46	0.00	0.00	0.00	0.00
Aug. 2006	0.16	0.30	0.08	0.00	0.11	0.00	0.00
June 2007	0.06	0.56	0.13	0.00	0.00	0.00	–
Floodplain vegetation							
June 2005	0.55	0.56	0.63	–	–	–	–
May 2006	0.41	–	0.46	0.10	0.00	0.04	0.04
June 2007	–	0.72	0.19	0.13	0.07	0.03	–
Soil seed bank							
2006 seed bank	–	0.52	0.43	0.40	0.21	0.13	0.11
2005 seed bank	0.39	0.32	0.60	–	–	–	–

For xeric species, the seed bank data set was not nested; many species overlapped between perennial and ephemeral sites and each site type had unique species. The majority of the xeric seed bank species were cool-season annuals: those common to soils of perennial and ephemeral sites included *Bowlesia incana*, *Bromus* sp., *Erodium cicutarium*, and *Schismus arabicus*. Ten species, all characteristic Sonoran desert annuals (e.g., *Cryptantha* sp., *Pectis papposa*, *Plantago ovata*) were detected only at ephemeral-flow sites. Two (*Herniaria hirsuta* ssp. *cinerea*, a forest understory species, and *Astragalus nuttalianus*) were detected only in soils at perennial-flow sites.

Overlap between Seed Bank and Extant Vegetation

Approximately half of the wetland species recorded in extant vegetation were detected in a site's soil seed bank. Of the 15 hydric species that grew along the low-flow channel of ephemeral-2 km during the wet early summer of 2005, seven (four annuals and three herbaceous perennials) were detected in soil seed bank samples of the site. Similarly, of the 15 hydric species growing along the low-flow channel of the perennial site at that time, six (three annuals and three herbaceous perennials) emerged from soil samples. Of the 12 hydroroparian species along the low-flow channel of the perennial site in dry 2007, six were detected in seed bank samples.

DISCUSSION

Ephemeral Wetlands and River Dynamics

Ephemeral wetlands are defined as wetlands dominated by annuals or seasonally active herbaceous perennials sustained by periodic saturation events and characterized by high year to year variability in hydrologic conditions (Deil 2005). Ephemeral wetlands develop in a variety of hydrogeomorphic settings but for the most part such plant communities have been little studied in North America. Our study documents occurrence of

Table 2. Coefficient of variation through time (five measurement periods during a three-year period) for four community traits measured on Hassayampa River active channel vegetation. Values are shown for four sites with varying surface water hydrology: perennial, temporally intermittent, and ephemeral. Sites are presented in their order along the river (far left = most upstream site).

	Coefficient of variation			
	Upper ephemeral	Intermittent	Perennial	Ephemeral-2 km
Species richness (total)	0.82	0.50	0.14	0.78
Cover (total)	0.84	0.50	0.51	1.74
Species richness (hydric subset)	0.97	0.62	0.10	1.38
Cover (hydric subset)	1.53	0.67	0.32	1.87

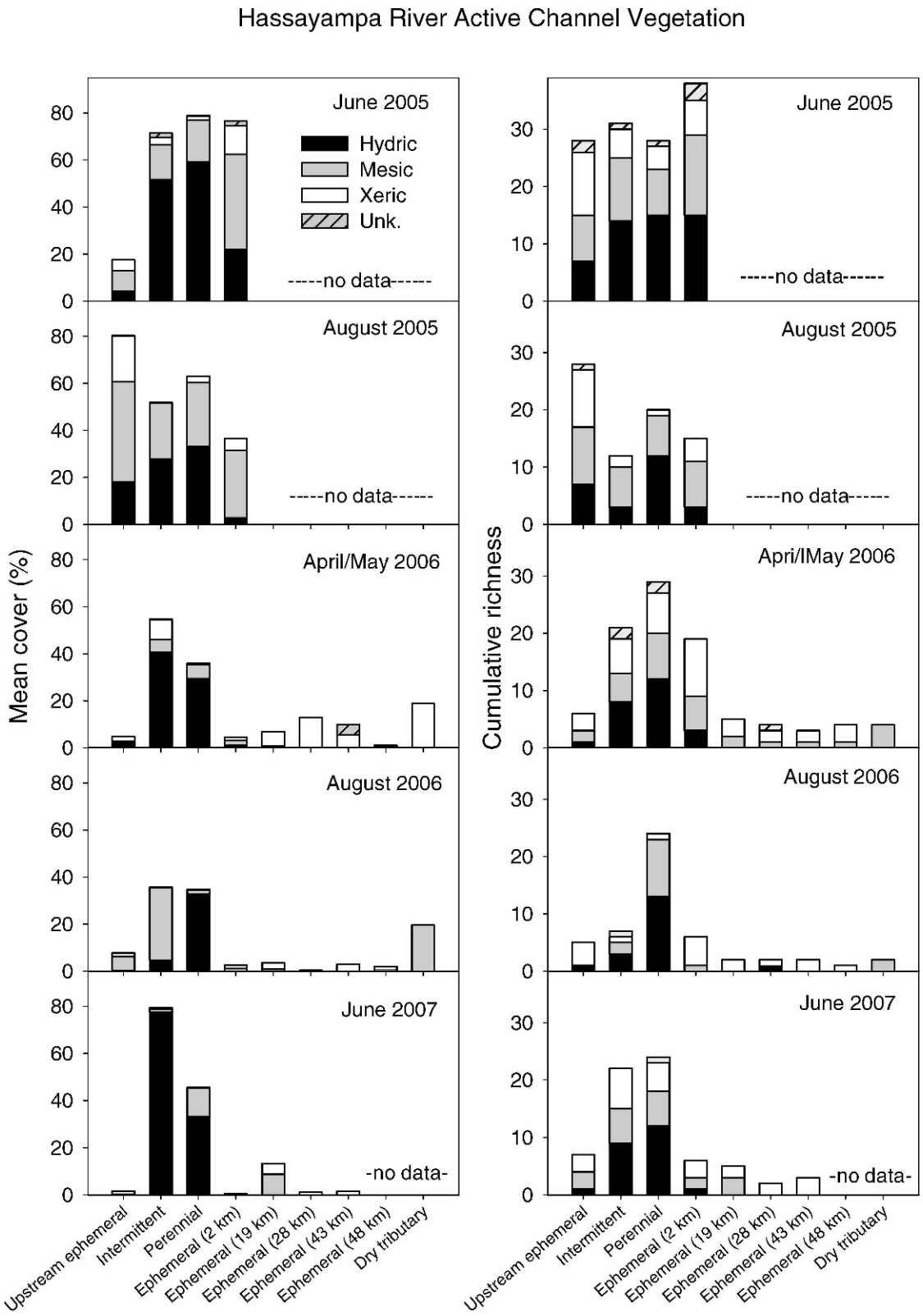

Figure 3. Cover and richness of plants growing along the active channel of the Hassayampa River during 2005, 2006, and 2007. Left panel shows mean ground cover; right panel shows cumulative species richness from 18, 1-m^2 plots. Plants are grouped by moisture affinity (hydric, mesic, xeric, unknown). Sites are presented in their order along the river (left = most upstream sites). During the study, there was a temporal shift from a wet period (uppermost panel) to a dry period (lowermost panel). Data were not collected at all study sites in all years.

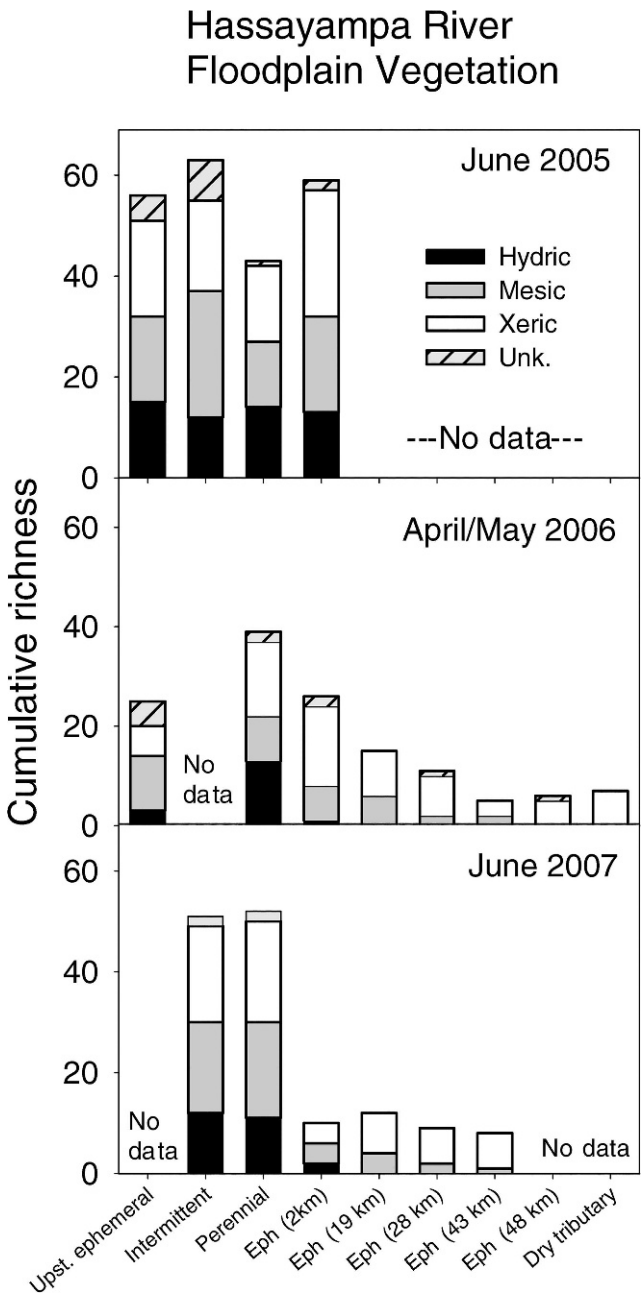

Figure 4. Richness of plant species growing in the floodplain at Hassayampa River study sites during 2005, 2006, and 2007. All panels show cumulative species richness (from 30, 10-m^2 plots per site). Plants are grouped by moisture affinity category (hydric, mesic, xeric, unknown). Data were not collected at all sites in all years.

ephemeral wetlands along an allogenic desert river with a mountainous catchment. Sampling of vegetation through a wet to dry period along the spatially intermittent Hassayampa River indicated that plant communities in ephemeral reaches had higher compositional similarity to those in perennial reaches during a period of sustained winter flood runoff. Hydric vegetation was abundant along the low-flow channel at ephemeral-flow sites during this period of above average stream flow, and was absent during the driest year.

The wetland communities in the ephemeral reaches of this spatially intermittent river are transient, fluctuating temporally with the highly variable annual stream flow pattern that characterizes arid region rivers. In some dryland regions around the world, seasonal floods occur with fairly high reliability (Gasith and Resh 1999). Rivers in the semiarid Chihuahuan Desert, for example, have reliable summer monsoonal rains and floods, and wetland vegetation establishes fairly frequently in temporally intermittent and ephemeral-flow reaches (Bagstad et al. 2005, Stromberg et al. 2005). For the Hassayampa River in the arid Sonoran Desert, the flood pattern is driven largely by winter Pacific frontal systems, which are strongly tied to the El Niño/Southern Oscillation (ENSO) global weather pattern. Floods of sufficient magnitude and duration to sustain wetland development in ephemeral reaches are more episodic and occur perhaps once or twice per decade: for the 10-year period from 1998–2007, for example, surface flows at the Hassayampa River Morristown stream gage occurred throughout the month of May during only two years (1998, 2005).

Prior studies along a perennial reach of the Hassayampa River showed that the lateral extent of marshlands (wet meadows) expands and contracts dramatically following major flooding events owing to changes in floodplain geomorphology and hydrology (Stromberg et al. 1997). This current study indicates that the longitudinal extent of the riverine wetlands along the river also can fluctuate through time (although our downstream sampling extent was limited during the flood-influenced season), as also documented for aquatic ecosystems in spatially intermittent desert rivers (Stanley et al. 1997). This pattern was evident in the extant vegetation, and also suggested by the presence of viable seeds of wetland plant species at sites many kilometers downstream in the ephemeral reach.

Mechanisms: Seed Banks and Dispersal

Many ephemeral wetlands are sustained by persistent soil seed banks. In response to periodic flooding, ephemeral plant communities develop through germination of long-lived seeds in the soil seed bank and through expansion of vegetative propagules that survive drought (Casanova and Brock 2000, Bissels et al. 2005). The similarity between the composition of the soil seed bank and

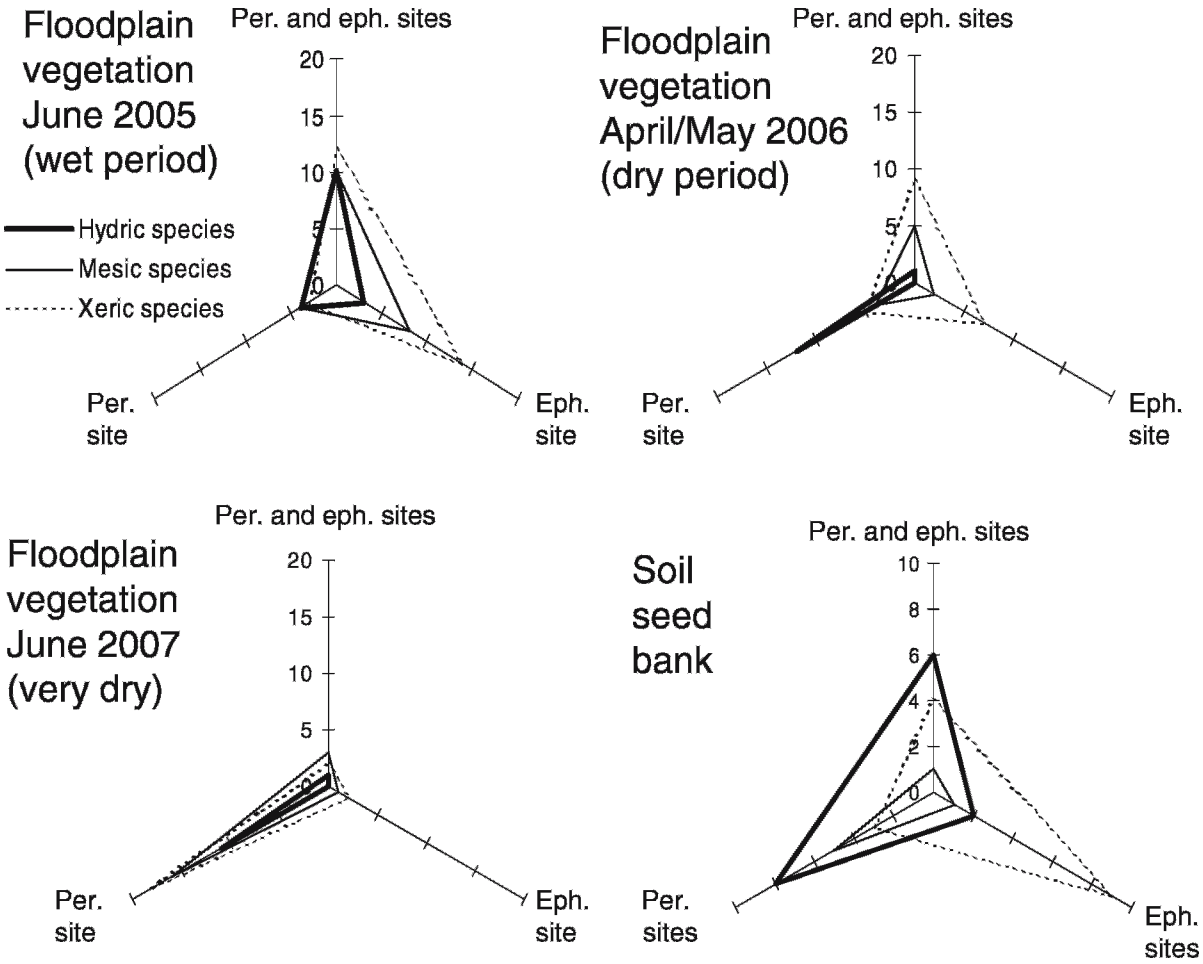

Figure 5. "Spider" charts showing the numbers of hydric, mesic, and xeric plant species occurring only at a perennial site, only at an ephemeral site, or present at both hydrologic site types. Values for floodplain vegetation are for early summer of each of three study years, and are based on data from one perennial site and one ephemeral site. Values for the soil seed bank (2006 collection) are for two wet sites (perennial and temporally intermittent) and two ephemeral sites.

Table 3. Level of nestedness in species composition, by moisture group, among sites along the spatially intermittent Hassayampa River. Low "temperature" values (close to zero) indicate a high degree of nestedness and high values (close to 100) indicate a low degree of nestedness. Values are based on data sets that include seven sites (2006 seed bank), six sites (2006 and 2007 floodplain vegetation), and four sites (2005 floodplain vegetation).

	Nestedness temperature	Probability value	Direction of nestedness
Seed Bank			
Hydromesic subset	12.0	<0.01	Dry sites nested within wet
Xeric subset	42.5	0.54	Not nested
Floodplain Vegetation			
June 2005, Hydromesic subset	44.2	0.93	Not nested
June 2005, Xeric subset	36.1	0.73	Not nested
May 2006, Hydromesic subset	7.2	<0.01	Dry sites nested within wet
May 2006, Xeric subset	31.1	0.13	Not nested
June 2007, Hydromesic subset	5.6	<0.01	Dry sites nested within wet
June 2007, Xeric subset	26.8	0.05	Dry sites nested within wet

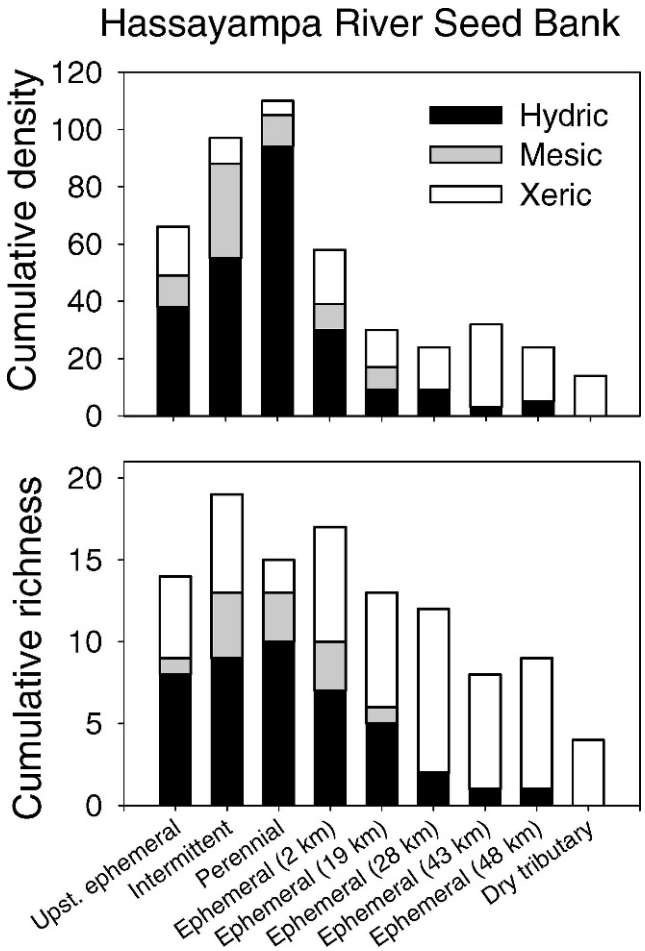

Figure 6. Density and diversity of plants emerging from soil seed banks at Hassayampa River study sites. Upper panel shows cumulative density and bottom panel shows cumulative species richness from 15, 147-cm^2 sampling areas per site. Plants are grouped by moisture affinity (hydric, mesic, xeric). Note: data for the upstream ephemeral site are from the 2005 soil collection; all others are from the 2006 soil collection.

extant vegetation can increase following flooding, in response to the establishment of the many short-lived species that often dominate soil seed banks (Capon and Brock 2006).

Soil seed banks appear to play a similar role in the ephemeral wetlands of our study system. A topic in need of further study, however, is the degree to which seed banks in ephemeral reaches develop *in situ* during major runoff events or are replenished via immigration from upstream sources. Large winter storms can produce surface runoff for several months: during a very larger winter event (1993) several years prior to our study, surface flow was present at the stream gage through August. During these major winter runoff events, soils likely are moist for a length of time sufficient to allow short-lived annual wetland plants such as *Juncus bufonius*

Table 4. Pearson correlation coefficients relating species richness and density of plants emerging from soil seed banks of ephemeral Hassayampa River floodplain soil seed banks to distance of the site from the downstream limit of perennial flow. Asterisk indicates significance at $p \leq 0.05$ ($n = 5$).

	Correlation coefficient (r)	
	Species richness	Density
Hydric subset	−0.96*	−0.89*
Mesic subset	−0.90*	−0.88*
Xeric subset	0.22	0.43
Total richness	−0.98*	−0.79

to complete their life cycle (Warwick and Brock 2003). In addition to providing a moisture source for plant establishment, the floodwaters also may transport seeds of wetland species from perennial reaches to downstream ephemeral sites; the highly fecund plant communities in the perennial reach may function as a seed source for the episodic establishment of some wetland plants in downstream dry reaches.

The density and diversity of hydric and mesic seeds in the soil of ephemeral-flow sites decreased with distance downstream of the perennial reach of the Hassayampa River. Two mechanisms — variance in *in-situ* seed bank formation and variance in seed dispersal — may contribute to this spatial pattern. Reduced seed set owing to inadequate surficial hydroperiod at the farther downstream sites is one explanation. During the period of flood recession in this allogenic desert river, the leading edge of the surface flow slowly contracts upstream; thus, the duration of surface flow will decrease with distance downstream of the perennial reach, reducing the likelihood that a germinant will complete its life cycle. Second, as seeds are entrained by floodwaters and then deposited on river margins (Goodson et al. 2003), they are longitudinally sorted with distance downstream depending on their mass, shape, and bouyancy (Johansson et al. 1996, Merritt and Wohl 2002; but see Andersson et al. 2000). This can produce a gradient in richness and density of seeds with distance from a seed-rich island. In a simulation of riverine diaspore dispersal, Andersson et al. (2000) found a leptokurtic ("super Gaussian") distribution, with peak density near the release point followed by a long tail, reminiscent of our pattern at Hassayampa. Their farthest downstream river floating dispersal distance was 152 km, well beyond our maximum downstream study site of ca. 50 km. Some riverine plants also can arise from flood-transported stem fragments, with rate of deposition

also decreasing with distance from a source population (Riis and Sand-Jensen 2006, Truscott et al. 2006). It is also possible that the seeds are being transported downstream by wind or by animals, which would also produce a sorting in terms of species composition. The few wetland species present in soils of the far-downstream Hassayampa River ephemeral sites all have small diaspores, consistent with a pattern of differential sorting along a longitudinal river gradient, but also consistent with patterns for small-seeded species to be the most common type to form persistent seed banks (Stromberg et al. 2008).

Implications for Riparian Restoration and Conservation

Many riparian restoration efforts are underway around the world, but most focus narrowly on a given piece of land, with less consideration for the landscape setting and for river-wide processes (Ward et al. 2001, Kondolf et al. 2007). Our study suggests that restoration success does depend on the landscape matrix in which a project is embedded, and on connectivity between landscape elements (Boon 1998). Specifically, our results suggest that potential for self-assembly of ephemeral wetlands varies with proximity to a perennial reach.

These results can provide guidance for riparian site selection. Assuming that our findings are representative of rivers in the region, it appears that ephemeral reaches located proximal to a perennial reach are the strongest candidate sites for flow-restoration projects; those located at greater distances are weaker candidates; and those located in completely ephemeral tributaries are least suitable. While the seeds that are present in the soil of ephemeral reaches of spatially intermittent rivers are only a subset of the riparian flora, this subset is one that is likely to be overlooked by traditional restoration seeding efforts. The composition of seeds that are present in the soil seed bank or that arrive via flood transport or other vectors from seed-rich upstream sites will vary from year to year (Andersson and Nilsson 2002, Gutierrez and Meserve 2003), contributing to temporal heterogeneity in riparian plant diversity patterns.

River-wide factors such as perennial reach length and interval length between perennial reaches are changing in some dryland rivers, and such changes will influence metapopulation and metacommunity processes. For example, changes in the degree of between-reach connectivity conferred by flood dispersal may influence the degree of genetic variability within river metapopulations (Kudoh and Whigham 2001, Carini et al. 2006). Our study raises the possibility that changes in between-reach connectivity may influence metacommunity processes. Boudell and Stromberg (2008) posited that the riparian plant communities within perennial stream reaches are linked by hydrochorous dispersal of seeds across lateral floodplain gradients, which creates a common seed bank pool in the component plant associations; this, in turn provides opportunities for establishment of hydric to xeric communities wherever flood hydrogeodynamics stochastically create suitable growing conditions. With respect to the longitudinal wet-dry river gradient, further studies are needed to determine whether hydric plants at perennial stream reaches function as a seed source for episodic development of wetlands in downstream dry reaches, and if so, how this process is affected by changes in the spatial distribution of perennial reaches within the drainage network.

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