Chen Xiu · Michael Gerisch · Christiane Ilg
Klaus Henle · Zhiyun Ouyang

Effects of hydrologic modifications to riparian plant communities in a large river system in northern China

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Abstract Hydrologic modifications to rivers caused by anthropogenic activity have major impacts on riparian ecosystems. Alterations to the hydrologic regime and their interactions with natural environmental parameters exert selective pressures on riparian vegetation, resulting in adaptations to specific flow attributes. However, few studies have attempted to detect these effects under multiple hydrologic conditions, especially for rivers in semi-dry and semi-humid regions. Using the “space-for-time substitution” method, we investigated the effects of hydrologic modifications to the riparian plant community along the Yongding River of northern China, by comparing community structure metrics (diversity, plant moisture affinity group, and lifespan) and a function metric (biomass) under three streamflows (perennial, seasonal and dried-up). Among these streamflows, seasonal flow reaches had the greatest plant diversity. Responses of plant moisture group and lifespan were inconsistent in different hydrologic stages, although they varied significantly ($P < 0.01$). Annuals and biennials greatly increased from perennial to seasonal

streamflow ($\sim 59\%$), while perennials decreased ($\sim 41\%$). However, from seasonal to dried-up flow, the percentage of mesics and xerics increased by 12.8 and 11.8 %, respectively, while hydrics decreased dramatically (by 24.6 %). Perennial flow had significantly greater aboveground biomass ($P < 0.05$) than the other two flows. Hydrologic conditions and their related soil nutrients were the main driving factors of community structure and function, which explained 21.0 and 18.0 % of variation, respectively. These findings reveal the response process of the riparian plant community during hydrologic modification from perennial to dried-up streamflow.

Keywords Riparian vegetation · Flow disconnection · Floodplains · Haihe River basin · Grassland

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C. Xiu · Z. Ouyang (✉)
State Key Laboratory of Urban and Regional Ecology,
Research Center for Eco-Environmental Sciences,
Chinese Academy of Sciences, 100085 Beijing, China
E-mail: zyouyang@rcees.ac.cn
Tel.: +86 10 62849191
Fax: +86 10 62849816

M. Gerisch
Aquatic Ecology and Centre for Water and Environmental
Research, University of Duisburg-Essen, Universitätsstr. 5,
45141 Essen, Germany

C. Xiu · M. Gerisch · K. Henle
Department of Conservation Biology, UFZ-Helmholtz Centre for
Environmental Research, Permoserstr.15, 04318 Leipzig, Germany

C. Ilg
Hepia-University of Applied Science Western Switzerland, Route
de Presinge 150, 1254 Jussy, Switzerland

Introduction

Hydrologic modifications to river systems caused by anthropogenic activity have major impacts on riparian ecosystems, leading to severe ecological and environmental consequences (Poff et al. 1997; Nilsson and Svedmark 2002; Stromberg et al. 2005; Steward et al. 2012). This is true in northern China, especially for rivers in semi-dry and semi-humid regions, where the flow regimes of many rivers have been modified by anthropogenic activities such as stream diversions, dams, and groundwater pumping for agricultural irrigation (Changming et al. 2001; Ren et al. 2002; Zhang and Döll 2008). For example, whole stretches of the Yongding River in Beijing have been hydrologically disconnected for several kilometers, owing to the combined effect of dams upstream and groundwater pumping in the plain area (Wang et al. 2010; Yu et al. 2011). Some stretches have been dry for more than 30 years, which may have caused extensive change to habitat and plant communities (Fig. 1) (Feld and Hering 2007). However, such changes and their relationships with environmental conditions have not been quantified.

Water flow is a major structural factor in ecological communities and is an important driving force of com-

Fig. 1 Photographs of (a) perennial streamflow (35 km from the headwaters), (b) seasonal streamflow (68 km from the headwaters), and (c) dried-up streamflow (145 km from the headwaters) along the Yongding River

munity composition in riparian habitats, because of the temporal and spatial variability of flood and drought (Walker et al. 1995; Hughes 1997; Poff et al. 1997; Richter et al. 1997; Ward 1998; Nilsson and Svedmark 2002). A number of eco-hydrological studies have identified relationships between riparian vegetation and hydrologic parameters, including frequency, timing, duration, rate of change, and magnitude of base flows (Nilsson and Svedmark 2002; Elmore et al. 2003). Vegetation can be characterized in many ways, and studies have examined effects of surface water flow regimes on plant species diversity (Katz et al. 2009; Stromberg et al. 2009a; Katz et al. 2012), species composition (Shafroth and Stromberg 2002), plant moisture group (Stromberg et al. 2005; Katz et al. 2009), and plant growth (Stromberg and Patten 1990). Flow regime adaptations of riparian and aquatic plant communities are dictated by the pattern of temporal river flow variation, which involves plant life histories and morphologies (Lytle and Poff 2004) and compositional differences between streamflow types (Stromberg et al. 2005; Leigh et al. 2010). Relationships between species diversity and hydrologic streamflow regime change have been described for a few semiarid rivers (Stromberg et al. 2009a; Katz et al. 2012), but relationships of riparian plant community metrics to those regimes have garnered less research attention.

Despite the increasing frequency of streamflow disconnection in northern China, there is still only limited information available on riparian plant community responses to hydrologic modifications. This study explores

the ecological consequences of permanent stream disconnection on riparian plant communities. Using the “space-for-time substitution” method, we investigate the effects of hydrologic modifications on the riparian plant community along the Yongding River of northern China. This is done by comparing community structure metrics (diversity, plant moisture affinity groups, and lifespans) and a function metric (aboveground plant biomass or AG-biomass) under three hydrologic gradients (perennial, seasonal and dried-up) along river reaches. To achieve these goals, we must answer two main research questions under the circumstances of permanent flow cutoff: (1) Are there differences in community metrics of riparian grassland (diversity, plant moisture affinity group, lifespan and biomass) among three streamflow types? (2) Are hydrologic factors responsible for the differences?

Methods

Study area

The study was conducted along the Yongding River, which drains a catchment area $\sim 3,600 \text{ km}^2$ over length 248 km in northern China (Fig. 2). This river is part of the Haihe River basin and is the largest river flowing through Beijing (Wang et al. 2010) (Fig. 2). The river is characterized by considerable permanent flow disconnection, which means that some reaches have been

Fig. 2 Locations of the study area, vegetation transects, and three streamflow types of the Yongding River

disconnected longitudinally for several years because of upstream water abstraction. Streambed altitudes are 10–300 m.a.s.l. The study area has a semi-dry and semi-humid continental climate within a warm temperate zone (Tian et al. 2008), and has an average temperature of 12–13 °C. Long-term mean annual precipitation is 400–600 mm and is dominated by the Asian summer monsoon during July–September, which accounts for about 70 % of annual precipitation (Zhang et al. 2000).

Vegetation and environmental variable sampling

The Yongding is an interrupted river that is influenced by hydrologic modifications along part of its length. River stretches have been categorized into three hydrologic streamflow types based on the streamflow regime in the stretch, i.e., perennial, seasonal, and dried-up (Fig. 2; Table 3). Perennial streamflow refers to stretches with continual water flow, seasonal to flow only during the wet season, and dried-up to no water flow.

A field study was conducted in August–September 2009, which focused on the riparian grassland community. We conducted an investigation before determining the study sites, and the main community types of riparian grassland were identified for each hydrologic flow type. According to each representative plant community type, an individual study site was chosen to represent the flow reaches that had a similar plant community composition. At the site for each hydrologic flow type, a vegetation transect perpendicular to the river was established. Along each transect, four 1 × 1 m plots were randomly selected within the riparian zone (0–100 m), which is a typical sample size for grassland in northern China (Wang et al. 2011). In total, 12 study sites and 36 plots were established within the riparian zone along the river. These were distributed among the three stream types, i.e., 12 plots for perennial, 16 for seasonal, and eight for dried-up.

In each plot, vascular plant taxa and numbers of individuals were recorded for each herbaceous species.

The number of individuals of each species was counted by hand. For tufted herbs, the number of stems was regarded as the number of individuals. In plots where species individuals were too abundant and were distributed evenly, individuals were counted in a smaller subplot (0.1 × 0.1 m), from which the total number of individuals in the entire plot was calculated. AG-biomass was sampled in each plot, and all litter and herb vegetation rooted in the plots was clipped to the ground surface. AG-biomass samples were air-dried, then oven-dried for 72 h at 65 °C and weighed. All samples were ashed at 550 °C for 12 h, and all AG-biomass values are reported on an ash-free dry mass basis (g/m²).

Hydrologic data were collected from monitoring data of official hydrologic gauges (at hydrologic stations of Beijing) along the Yongding River. The term “surface flow permanence” (FP) was used to represent the percentage of time that surface water was present in the river channel, which reflects the general hydrologic type of streamflows (Stromberg et al. 2005). Half-monthly surface flow presence/absence data were collected at the various streamflow plots during 2008 and 2009, and then FP was calculated based on the percentage of that presence in the streamflow plots over those years. Flow was considered present even if there was only ponding or frozen ice in the channel, without actual flow.

Several other environmental variables (Table 3) were measured. The altitude (in m.a.s.l.) of each study site was derived from GPS data. Soil samples were collected from all sample plots at depths 0–10 cm from the topsoil, using a soil sampler. The soil samples were placed in plastic-lined soil bags and transported to the laboratory. Then, 100-g sub-samples were taken from each soil sample and oven-dried at 105 °C for soil moisture analysis by gravimetric water content (Klute 1986). Bulk soil samples were air-dried, crushed and sieved with a 2-mm sieve to separate fine and coarse soil fractions. TP, pH and SOM (see Table 3 for abbreviations) were measured using standard analytical methods. TC, TN and CN were determined using a Vario ELIII Elemental Analyzer, and soil particle size (ratio of clay, silt and sand) was measured using a Mastersizer2000.

Data analysis

Alpha and beta diversity were measured to compare biodiversity within and between different stream types. Species richness was the total number of vascular plant species in each plot. The Shannon diversity index was also used as an indicator to quantify and compare species diversity. To determine floristic similarity between stream types, their degree of compositional similarity was calculated using Chao’s estimator (corrected for unseen species) for Chao’s Jaccard Abundance-based similarity index (Chao et al. 2005).

Plant species were separated into three moisture affinity groups (hydric, mesic and xeric), based on species characteristics in Flora of China (Wu et al. 1994) and the

Warming (1909) and Schimper (1898) classifications. These groups were used as an indicator to characterize plant response to water resource availability over the long term and reflect the water condition of the wetland habitats (An et al. 2003; Stromberg et al. 2005; Minggagud and Yang 2013). Similarly, the plant species were classified into three categories according to lifespan, namely, annuals, biennials and perennials. The plant moisture group and lifespan of each species were both determined by reference to the Flora of China and Beijing Flora (He et al. 1993). For species with more than one lifespan, the most commonly observed lifespan for the species within the Beijing region was identified. Nomenclature followed Flora of China and each variety and subspecies was treated as a full species. Analysis of variance (ANOVA) and the Chi squared test were performed on the community structure metrics (diversity, plant moisture affinity group, and lifespan) to test for differences among streamflow types.

Detrended correspondence analysis (DCA) was used to choose between linear- or unimodal-based methods in further numerical analyses, by estimating lengths of compositional gradients (DCA axes 1). DCA in the dataset showed gradient lengths 0.4 for axis 1, which is relatively short (< 3), and redundancy analysis (RDA) was selected for further analyses. RDA was performed to clarify relationships between community metrics, biomass, and environmental variables (Legendre and Gallagher 2001). The percentage in each plot was used to represent the value of each community metric variable, e.g., hydric referred to the percentage of hydric species in each plot. The forward-selection option was used to determine the minimum set of environmental variables that could explain the greatest variation in the species composition data. At each step, statistical significance of the environmental variable added during the forward-selection was tested by a Monte Carlo permutation test. Variables that were statistically significant ($P < 0.05$) were selected in the final model. Community metric data were log-transformed, and short lengths of community metric variables were removed because of low relevance. AG-biomass, Shannon, hydric, mesic, xeric and perennials were used as community metric variables. For statistical analysis, we used EstimateS program version 8.20 for the similarity index (Colwell 2013) and GPL software R for ANOVA, the Chi squared test, DCA, RDA, and biplot (R Development Core Team 2013).

Results

Community structure and function metrics under multiple hydrologic conditions

A total of 56 herbaceous species, belonging to 43 genera and 17 families, were recorded. The largest family was Compositae with 19 species, followed by Gramineae with 13. The remaining 15 families were represented by

Table 1 Jaccard similarity index (based on species abundance) for plant communities at the three streamflow sites (sampling dates August–September 2009)

Type of streamflow site	Seasonal	Dried-up
Perennial		
Total species	0.159	0.320
Hydric species	0.277	0
Mesic species	0.057	0.629
Xeric species	–	0
Seasonal		
Total species		0.194
Hydric species		0.015
Mesic species		0.402
Xeric species		0

Values in the table refer to Chao's estimator (corrected for unseen species) for Chao's Jaccard Abundance-based similarity index

no more than five species. The most abundant species was *Setaria viridis*, which accounted for 31.9 % of the total number of individuals, followed by *Phragmites australis* with 18.1 %. There were 32 plant species found for the perennial flow type, 22 for seasonal, and 17 for dried-up. The stream section with seasonal flow had the highest plant alpha diversity (richness and Shannon index), although it was not significantly different than the other two streamflows ($F = 2.354$, $P = 0.111$; $F = 1.932$, $P = 0.161$) (Table 2).

Floristic similarity (beta diversity), as measured by the Jaccard (J) similarity index (based on species abundance), showed different results for plant moisture affinity groups (Table 1). Hydric species had larger J values between perennial and seasonal flow sites (0.277), compared to between seasonal and dried-up flow sites (0.015); the value was zero between perennial and dried-up flow sites. In contrast, mesic species showed a different similarity composition—the largest J values were between perennial and dried-up flow sites (0.629), compared to between seasonal and dried-up flow sites (0.402). There was a smaller J value between perennial and seasonal flow sites (0.057).

Two hydric species, *Phragmites australis* and *Polygonum lapathifolium*, were present in both the perennial and seasonal flow plots, whereas only *Polygonum aviculare* was present in both seasonal and dried-up flow plots. A total of 11 hydric species (including *Arthraxon hispidus*, *Equisetum arvense* and *Roegneria kamoji*) were unique to perennial flow plots. Five hydric species (including *Echinochloa crus-galli*, *Leersia japonica* and *Eclipta prostrata*) were restricted to seasonal flow plots, and only one hydric species (*Kummerowia striata*) was unique to dried-up flow plots. Three mesic species (*Setaria viridis*, *Artemisia argyi* and *Xanthium sibiricum*) occurred in all three flow plots. Two xeric species (*Artemisia sacrorum* and *Hemarthria altissima*) were found only in the dried-up flow plots (see Electronic Supplementary Material: Table S1).

Along the hydrologic gradients, responses of plant moisture group and lifespan were inconsistent within various hydrologic stages, although they changed sig-

Table 2 Plant community structure and function metrics (diversity, plant moisture affinity group, lifespan, and aboveground biomass) for three streamflows in the Yongding River in northern China (sampling dates August–September 2009)

Community metrics	Type of streamflow site		
	Perennial	Seasonal	Dried-up
Plant moisture group (%)			
Hydric	40.6	36.4	11.8
Mesic	59.4	63.6	76.4
Xeric	0.0	0.0	11.8
Life span (%)			
Annuals	34.4	59.1	52.9
Biennials	9.4	0.0	5.9
Perennials	56.3	40.9	41.2
Diversity			
Richness	5.00 (± 0.64)	5.38 (± 0.86)	3.75 (± 0.36)
Shannon diversity index	1.41 (± 0.15)	1.43 (± 0.19)	1.11 (± 0.10)
Aboveground biomass (kg m^{-2})	1.10 (± 0.59)	0.23 (± 0.05)	0.26 (± 0.06)

Fig. 3 Biplot of the first and second RDA axes for riparian plant community metrics and biomass of the Yongding River

nificantly (Chi squared = 40.59, $df = 4$, $P = 0.001$; Chi squared = 18.69, $df = 4$, $P = 0.001$ respectively) (Table 2). From perennial to seasonal streamflow, annuals and biennials greatly increased (by $\sim 59\%$), whereas perennials decreased by $\sim 41\%$. The plant moisture group changed only slightly (Table 2). However, from seasonal to dried-up flow, the percentage of mesics and xerics increased by 12.8 and 11.8 %, respectively, whereas hydrics decreased dramatically, by 24.6 % (Table 2). Lifespan remained nearly constant as the drought deepened (Table 2). Differences in community metrics were reflected by biomass distribution; perennial flow sites had significantly higher AG-biomass ($P < 0.05$) than the other two hydrologic conditions (Table 2).

Relationships between plant community structure, function (biomass) and hydrologically related variables

RDA was performed on plant community structure metrics (diversity, plant moisture affinity group, and

lifespan), AG-biomass and environmental variables, in order to estimate the effects of hydrologically related environmental variables on riparian plant community structure and function along river reaches. Shannon refers to the Shannon diversity index. Xeric, Mesic and Hydric refer to percentage abundance of the three plant moisture affinity groups, and Perennials to the percentage abundance of perennial plants in the lifespan groups (Fig. 3). TC and TN refer to total carbon and nitrogen contents, and FP and Moist to streamflow permanence and soil moisture, respectively (Table 3). FP of perennial streamflow was calculated as 100 %, since there was surface flow throughout the year (12 months). Seasonal streamflow was 33.3 %, because surface water only flowed for four months of the year and dried-up streamflow areas had a value of zero (Table 3).

The full RDA model using all 11 environmental variables (Table 3) explained 58 % of the total variance of plant community structure and function (Table 4). Forward variable selection ($P < 0.05$, Monte Carlo permutation test) of environmental variables further reduced the environmental dataset to four variables in the final model, which explained 39.0 % of the total variance (Table 4; Fig. 3). However, the four environmental variables that significantly explained variance in community metrics were FP ($F = 4.87$, $P = 0.012$, variance explained = 13 %), Moist ($F = 3.41$, $P = 0.024$, var. exp. = 8 %), TC ($F = 4.99$, $P = 0.008$, var. exp. = 11 %), and TN ($F = 3.86$, $P = 0.032$, var. exp. = 7 %). This revealed that hydrologic variables and their related soil nutrient variables had a strong influence on plant community structure (metrics) and function (biomass). However, RDA results showed varying correlations between each metric variable and the four environmental variables. Hydric, Perennials and Shannon had strong positive correlations with Moist and FP, whereas Mesic and Xeric had negative correlations. Perennials, Shannon and Hydric had strong positive correlations with TN and TC. Shannon, Perennials and Hydric were correlated with both hydrologic variables (FP and Moist) and

Table 3 Environmental variables measured in RDA analysis. Data refer to mean values ($\pm$ SE) from three streamflow types based on hydrologic flow regimes in the Yongding River in northern China (sampling dates August–September 2009)

Variable	Unit/scale	Perennial streamflow	Seasonal streamflow	Dried-up streamflow
SWL*	m	0.55–0.80	0.20–0.35	0.00
FR*	m ³ s ⁻¹	2.95–3.07	0.96–1.71	0.00
FP	%	100.00	33.33	0.00
Alt	hm	2.55 ($\pm$ 0.10)	0.49 ($\pm$ 0.15)	1.01 ($\pm$ 0.12)
Dist	m	7.76 ($\pm$ 1.88)	14.13 ($\pm$ 4.90)	0.00 ($\pm$ 0.00)
TN	%	0.29 ($\pm$ 0.03)	0.16 ($\pm$ 0.03)	0.14 ($\pm$ 0.03)
TC	%	5.44 ($\pm$ 0.67)	3.66 ($\pm$ 0.45)	4.46 ($\pm$ 0.84)
CN		18.36 ($\pm$ 0.90)	25.05 ($\pm$ 2.34)	42.82 ($\pm$ 5.81)
Moist		0.37 ($\pm$ 0.07)	0.38 ($\pm$ 0.06)	0.11 ($\pm$ 0.02)
pH		8.08 ($\pm$ 0.05)	8.20 ($\pm$ 0.06)	8.47 ($\pm$ 0.08)
SOM	g kg ⁻¹	48.65 ($\pm$ 6.82)	34.63 ($\pm$ 7.05)	30.92 ($\pm$ 6.34)
TP	g kg ⁻¹	0.79 ($\pm$ 0.17)	0.76 ($\pm$ 0.07)	0.85 ($\pm$ 0.08)
Sand	%	0.63 ($\pm$ 0.03)	0.55 ($\pm$ 0.07)	0.68 ($\pm$ 0.04)

SWL surface water level, FR flow rate, FP surface flow permanence, Alt streambed altitude, Dist distance from river to plot, TN total nitrogen content, TC total carbon content, CN carbon-to-nitrogen ratio, Moist soil moisture, pH pH value of soil sample, SOM soil organic matter, TP total phosphorus content, Sand amount of sand in soil

*SWL and FR were not measured in RDA analysis but used to categorize streamflow type

Table 4 Summary statistics for first four axes of redundancy analysis (RDA) with the community metrics and environmental variables for the riparian grassland along the Yongding River in northern China (sampling dates August–September 2009)

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.215	0.151	0.022	0.002	
Species-environment correlations	0.663	0.76	0.392	0.142	
CV of metrics data (%)	21.5	36.4	38.8	39.0	
CV of metrics-environment relationship (%)	55.2	93.8	99.5	100.0	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues (full model)					0.580
Sum of all canonical eigenvalues (final model)					0.390

CV cumulative variance

soil nutrients (TC and TN). However, AG-biomass had stronger positive correlations with FP and Moist than with TN, but negative ones with TC (Fig. 3).

Discussion

Responses of community structure metrics

Along hydrologic gradients, the community metrics (-diversity, lifespan, plant moisture affinity group, and biomass) showed divergent responses to hydrologic regime changes. Among the three hydrologic conditions, the stream section with seasonal flow had the greatest plant diversity. This result is consistent with several studies (Stromberg et al. 2009a; Katz et al. 2012), suggesting that intermittent flow sites support higher mean richness than perennial and dried-up flow sites. This indicates that the “disturbance” of periodic drought at the intermittent (seasonal) flow sites may increase plant diversity (Tabacchi et al. 1996; Stromberg et al. 2005). This result may be related to the “Goldilocks effect” (Berlow et al. 2008), which could explain the mechanism

by which high diversity occurred at the seasonal flow sites. Compared to dried-up sites, seasonal flow sites experience more frequent surface flow events, which facilitate spatially heterogeneous moisture conditions in the riparian zone. Compared to perennial sites, seasonal flow sites experience greater “disturbance,” i.e., greater variability of surface flow (Katz et al. 2012). Overall, environmental variability at intermittent sites, combined with the immigration of species by flood flows, generates high species diversity.

Plant moisture group and lifespan changed significantly but had divergent responses between hydrologic stages. A striking change in perennial and annual herbs with hydrologic stage shift indicated that lifespan responded sensitively to the loss of water in the environment. This result can be interpreted as small changes in the physical environment producing abrupt biological responses (With and Crist 1995). Lifespan (life history) is one of the most useful characteristics for characterizing community response to disturbance (McIntyre et al. 1995), and can be used in riparian areas (Pettit et al. 2001). Perennial plants are intolerant of fluctuating flow and are favored in more stable hydrologic envi-

ronments, which provide consistently saturated soils (Lite et al. 2005; Katz et al. 2012). In contrast, in strongly disturbed environments, annual species are favored because of their fast growth rates and early and prolific seed set (Grime 1979).

In the present study, annuals had the highest percentage at seasonal flow sites, resulting from the unique hydrological “disturbance” along seasonal reaches and annuals’ response strategy. Riparian annuals like *Chenopodium glaucum* and *Digitaria sanguinalis* are fast-growing, widespread summer-annual weeds that show high phenotypic plasticity to changes in environmental conditions (Wulff et al. 1999; Huang et al. 2000; Rajcan et al. 2002; Causin and Wulff 2003). Both have intermediate strategies between R and C-R (C, S and R are short for competitive, stress-tolerant and ruderal respectively) in the established phase, according to Grime’s C–S–R model (Grime et al. 1988; Zelnik and Čarni 2008). Most annuals (both hydric and mesic species) complete their life cycle during late summer rain at seasonal flow sites, which feature inflowing groundwater or surface flow that moisten disturbed fluvial surfaces in riparian zones (Stromberg et al. 2005). The “disturbance” of periodic drought in seasonal flow reaches may provide increased opportunities for establishment of annuals (Lake 2003; Stromberg et al. 2005). Researchers of other semi-dry and semi-humid regions have also observed that annual grass species dominate riparian zones influenced by the hydrologic disturbance of flow regime (Capon 2003; Salinas and Casas 2007), suggesting that intermittent flows favor annual riparian plants (Stromberg et al. 2005).

The slight change in hydric distribution from perennial to seasonal flow sites suggests that the influence of seasonal flow cutoff on the plant moisture group was relatively weak. Researchers have found that in-channel flow or floods produced by summer rainfall contribute to homogenizing species pools by dispersing seeds within river corridors (Jansson et al. 2005; Stromberg et al. 2008). In the present study, the hydrics had greater compositional similarity between perennial and seasonal flow sites, indicating that the hydric herbs may be a nested subset of those at upstream perennial sites (Stromberg et al. 2009b). This may explain why plant composition could somehow maintain its structure after the seasonal flow cut-off. However, when there was a complete environmental change from seasonal to dried-up flow, the distribution of the plant moisture affinity group changed substantially. Respective percentages of mesics and xerics increased, while hydrics decreased dramatically. Replacement of hydric species by more mesic species has been recorded in studies of floodplains subjected to flow regulation (Bren 1992; Kingsford and Thomas 1995). Two divergent responses to flow regime change in two stages of hydrologic modification indicates that the structure of the plant moisture group had a certain tolerance to water availability loss. However, as water stress increased to a permanent level, plants suffered

restricted growth and adaptation, even threatening their survival (Porporato et al. 2001).

Response of community function metric (biomass)

The sharp decline from perennial reaches to those influenced by flow cutoff revealed that biomass of riparian grassland was associated with the gradient of hydrologic regime in the stream. The strong relationship between AG-biomass and hydrologic variables (FP and Moist) (Fig. 3) further indicates that the hydrologic regime change strongly influenced biomass, consistent with other studies (Wang et al. 2007; Debinski et al. 2010). The plant biomass distribution in the riparian plant community affects ecological functions at the stream-riparian interface by trapping sediment, stabilizing banks and reducing pollutants within the stream (Naiman 1997; Dwire et al. 2004). The sharp decline of riparian grassland AG-biomass may reduce the ecosystem function of the riparian plant community.

Environmental gradients and their relationship with community metrics

The main gradients of the riparian plant community metrics for the Yongding River were significantly related to the hydrological and related soil variables (Fig. 3). The RDA results showed that the factor Moist was positively correlated with TN, indicating that hydrologic conditions affect soil variables (Baldwin and Mitchell 2000). Our findings suggest that a stream landscape with higher nutrient levels and moister soil produces the greatest regional herb species diversity. Many studies have also found that plant species diversity in riparian zones is positively associated with perennial streamflows and high soil moisture (Tabacchi et al. 1996; Fossati 1999; Ali 2000), as well as high soil nutrient levels (Hill 1996; Young-Mathews et al. 2010).

Our results also indicate that riparian perennial species prefer an environment with high soil nutrient levels and permanent streamflow, which are key factors for successful long-term plant growth (Lite et al. 2005; Stromberg et al. 2005). The strong correlations between plant moisture group and hydrologic parameters reveal the long-term response of plants to hydrology, whereas the positive correlations between biomass and TN and hydrologic variables suggest that riparian plant community function was strong in such a moist and nutrient-rich environment (Araya et al. 2013). However, other potentially related factors such as water pollution and human physical impacts also affect the riparian plant community in rivers near urban areas (Gasith and Resh 1999; Salinas and Casas 2007), and should be considered in further research.

Anthropogenic flow intermittence in the stream is directly caused by surface water and groundwater abstraction, and indirectly by climate change (Larned et al.

2010). Climate change is in phase with regional drying, gradually reducing stream runoff and even causing permanent cessation of flow (Rupp et al. 2008). Our findings reveal the response of the riparian plant community during the hydrologic modification from perennial to dried-up streamflow, suggesting the potential effect of global change on riparian vegetation. With warmer temperatures caused by climate change, regional drought may seriously alter riparian vegetation and degrade the riparian ecosystem function (Breshears et al. 2005).

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References

- Ali M (2000) Predictors of plant diversity in a hyperarid desert wadi ecosystem. *J Arid Env* 45:215–230. doi:10.1006/jare.2000.0631
- An S, Cheng X, Sun S, Wang Y, Li J (2003) Composition change and vegetation degradation of riparian forests in the Altai Plain, NW China. *Plant Ecol* 164:75–84. doi:10.1023/A:1021225204808
- Araya YN, Gowing DJ, Dise N (2013) Does soil nitrogen availability mediate the response of grassland composition to water regime? *J Veg Sci* 24:506–517. doi:10.1111/j.1654-1103.2012.01481.x
- Baldwin DS, Mitchell AM (2000) The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. *Regul Rivers Res Manag* 16:457–467. doi:10.1002/1099-1646(200009/10)16:5<457:AID-RRR597>3.0.CO;2-B
- Berlow EL, Brose U, Martinez ND (2008) The “Goldilocks factor” in food webs. *Proc Natl Acad Sci USA* 105:4079–4080. doi:10.1073/pnas.0800967105
- Bren LJ (1992) Tree invasion of an intermittent wetland in relation to changes in the flooding frequency of the River Murray, Australia. *Aust Ecol* 17:395–408. doi:10.1111/j.1442-9993.1992.tb00822.x
- Breshears DD, Cobb NS, Rich PM et al (2005) Regional vegetation die-off in response to global-change-type drought. *Proc Natl Acad Sci USA* 102:15144–15148. doi:10.1073/pnas.0505734102
- Capon SJ (2003) Plant community responses to wetting and drying in a large arid floodplain. *River Res Appl* 19:509–520. doi:10.1002/rra.730
- Causin HF, Wulff RD (2003) Changes in the responses to light quality during ontogeny in *Chenopodium album*. *Can J Bot* 81:152–163. doi:10.1139/b03-012
- Changming L, Jingjie Y, Kendy E (2001) Groundwater exploitation and its impact on the environment in the North China plain. *Water Int* 26:265–272. doi:10.1080/02508060108686913
- Chao A, Chazdon RL, Colwell RK, Shen TJ (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol Lett* 8:148–159. doi:10.1111/j.1461-0248.2004.00707.x
- Colwell RK (2013) EstimateS: statistical estimation of species richness and shared species from samples. Version 9. <http://purl.oclc.org/estimates>
- Debinski DM, Wickham H, Kindsher K, Caruthers JC, Germino M (2010) Montane meadow change during drought varies with background hydrologic regime and plant functional group. *Ecol* 91:1672–1681. doi:10.1890/09-0567.1
- Development Core Team R (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Dwire KA, Kauffman JB, Brookshire ENJ, Baham JE (2004) Plant biomass and species composition along an environmental gradient in montane riparian meadows. *Oecologia* 139:309–317. doi:10.1007/s00442-004-1498-2
- Elmore AJ, Mustard JF, Manning SJ (2003) Regional patterns of plant community response to changes in water: Owens Valley, California. *Ecol Appl* 13:443–460. doi:10.1890/1051-0761(2003)013[0443:RPOPCR]2.0.CO;2
- Feld CK, Hering D (2007) Community structure or function: effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshw Biol* 52:1380–1399. doi:10.1111/j.1365-2427.2007.01749.x
- Fossati J (1999) Water as resource and disturbance for wadi vegetation in a hyperarid area (Wadi Sannur, Eastern Desert, Egypt). *J Arid Env* 43:63–77. doi:10.1006/jare.1999.0526
- Gasith A, Resh VH (1999) Streams in mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annu Rev Ecol Syst* 30:51–81. doi:10.1146/annurev.ecolsys.30.1.51
- Grime JP (1979) Plant strategies and vegetation processes. Wiley, New York
- Grime JP, Hodgson JG, Hunt R (1988) Comparative plant ecology: a functional approach to common British species. Unwyn Hyman, London
- He S, Xing Q, Yin Z (1993) Beijing Flora, 3rd edn. Beijing Publishing House, Beijing (in Chinese)
- Hill AR (1996) Nitrate removal in stream riparian zones. *J Env Qual* 25:743. doi:10.2134/jeq1996.00472425002500040014x
- Huang JZ, Shrestha A, Tollenaar M, Deen W, Rahimian H, Swanton CJ (2000) Effects of photoperiod on the phenological development of redroot pigweed (*Amaranthus retroflexus* L.). *Can J Plant Sci* 80:929–938. doi:10.4141/P99-134
- Hughes FMR (1997) Floodplain biogeomorphology. *Prog Phys Geogr* 21:501–529. doi:10.1177/030913339702100402
- Jansson R, Zinko U, Merritt DM, Nilsson C (2005) Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. *J Ecol* 93:1094–1103. doi:10.1111/j.1365-2745.2005.01057.x
- Katz GL, Stromberg JC, Denslow MW (2009) Streamside herbaceous vegetation response to hydrologic restoration on the San Pedro River, Arizona. *Ecohydrology* 2:213–225. doi:10.1002/eco.62
- Katz GL, Denslow MW, Stromberg JC (2012) The Goldilocks effect: intermittent streams sustain more plant species than those with perennial or ephemeral flow. *Freshw Biol* 57:467–480. doi:10.1111/j.1365-2427.2011.02714.x
- Kingsford RT, Thomas RF (1995) The Macquarie Marshes in Arid Australia and their waterbirds: a 50-year history of decline. *Env Manag* 19:867–878. doi:10.1007/BF02471938
- Klute A (1986) Methods of soil analysis. Part 1. Physical and mineralogical methods. ASA and SSSA, Madison, WI
- Lake PS (2003) Ecological effects of perturbation by drought in flowing waters. *Freshw Biol* 48:1161–1172. doi:10.1046/j.1365-2427.2003.01086.x
- Larned ST, Detry T, Arscott DB, Tockner K (2010) Emerging concepts in temporary-river ecology. *Freshw Biol* 55:717–738. doi:10.1111/j.1365-2427.2009.02322.x
- Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280. doi:10.1007/s004420100716
- Leigh C, Sheldon F, Kingsford RT, Arthington AH (2010) Sequential floods drive “booms” and wetland persistence in dryland rivers: a synthesis. *Mar Freshw Res* 61:896. doi:10.1071/MF10106

- Lite S, Bagstad K, Stromberg J (2005) Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *J Arid Env* 63:785–813. doi:10.1016/j.jaridenv.2005.03.026
- Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. *Trends Ecol Evol* 19:94–100. doi:10.1016/j.tree.2003.10.002
- McIntyre S, Lavorel S, Tremont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J Ecol* 83:31. doi:10.2307/2261148
- Minggagud H, Yang J (2013) Wetland plant species diversity in sandy land of a semi-arid inland region of China. *Plant Biosyst* 147:25–32. doi:10.1080/11263504.2012.737865
- Naiman R (1997) The ecology of interfaces: riparian zones. *Annu Rev Ecol Syst*. pp 621–658
- Nilsson C, Svedmark M (2002) Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Env Manag* 30:468–480. doi:10.1007/s00267-002-2735-2
- Pettit NE, Froend RH, Davies PM (2001) Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting western Australian rivers. *Regul Rivers Res Manag* 17:201–215. doi:10.1002/rrr.624
- Poff NL, Allan JD, Bain MB, Karr JR, Prestegard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. *Bioscience* 47:769–784. doi:10.2307/1313099
- Porporato A, Laio F, Ridolfi L, Rodriguez-Iturbe I (2001) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress: III. Vegetation water stress. *Adv Water Resour* 24:725–744. doi:10.1016/S0309-1708(01)00006-9
- Rajcan I, AghaAlikhani M, Swanton CJ, Tollenaar M (2002) Development of redroot pigweed is influenced by light spectral quality and quantity. *Crop Sci* 42:1930. doi:10.2135/cropsci2002.1930
- Ren L, Wang M, Li C, Zhang W (2002) Impacts of human activity on river runoff in the northern area of China. *J Hydrol* 261:204–217. doi:10.1016/S0022-1694(02)00008-2
- Richter BD, Braun DP, Mendelson MA, Master LL (1997) Threats to Imperiled freshwater fauna. *Amenazas a la Fauna Dulceacuicola en Riesgo*. *Conserv Biol* 11:1081–1093. doi:10.1046/j.1523-1739.1997.96236.x
- Rupp DE, Larned ST, Arscott DB, Schmidt J (2008) Reconstruction of a daily flow record along a hydrologically complex alluvial river. *J Hydrol* 359:88–104. doi:10.1016/j.jhydrol.2008.06.019
- Salinas MJ, Casas JJ (2007) Riparian vegetation of two semi-arid mediterranean rivers: basin-scale responses of woody and herbaceous plants to environmental gradients. *Wetl* 27:831–845. doi:10.1672/0277-5212(2007)27[831:RVOTSM]2.0.CO;2
- Schimper AFW (1898) *Pflanzen-geographie auf physiologischer Grundlage*. G. Fischer, Jena
- Shafroth P, Stromberg J (2002) Riparian vegetation response to altered disturbance and stress regimes. *Ecol Appl* 12:107–123. doi:10.2307/3061140
- Steward AL, von Schiller D, Tockner K, Marshall JC, Bunn SE (2012) When the river runs dry: human and ecological values of dry riverbeds. *Front Ecol Env* 10:202–209. doi:10.1890/110136
- Stromberg JC, Patten DT (1990) Riparian vegetation instream flow requirements: a case study from a diverted stream in the Eastern Sierra Nevada, California, USA. *Environ Manag* 14:185–194. doi:10.1007/BF02394035
- Stromberg JC, Bagstad KJ, Leenhouts JM, Lite SJ, Makings E (2005) Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). *River Res Appl* 21:925–938. doi:10.1002/rra.858
- Stromberg JC, Boudell JA, Hazelton AF (2008) Differences in seed mass between hydric and xeric plants influence seed bank dynamics in a dryland riparian ecosystem. *Funct Ecol* 22:205–212. doi:10.1111/j.1365-2435.2007.01375.x
- Stromberg JC, Hazelton AF, White MS (2009a) Plant species richness in ephemeral and perennial reaches of a dryland river. *Biodivers Conserv* 18:663–677. doi:10.1007/s10531-008-9532-z
- Stromberg JC, Hazelton AF, White MS et al (2009b) Ephemeral wetlands along a spatially intermittent river: temporal patterns of vegetation development. *Wetl* 29:330–342. doi:10.1672/08-124.1
- Tabacchi E, Planty-Tabacchi A, Salinas MJ, Décamps H (1996) Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. *Regul Rivers Res Manag* 12:367–390. doi:10.1002/(SICI)1099-1646(199607)12:4/5 < 3.67::AID-RRR424 > 3.3.CO;2-O
- Tian YC, Zhou YM, Wu BF, Zhou WF (2008) Risk assessment of water soil erosion in upper basin of Miyun Reservoir, Beijing, China. *Env Geol* 57:937–942. doi:10.1007/s00254-008-1376-z
- Walker KF, Sheldon F, Puckridge JT (1995) A perspective on dryland river ecosystems. *Regul Rivers Res Manag* 11:85–104. doi:10.1002/rrr.3450110108
- Wang C, Cao G, Wang Q, Shi JJ, Du YG, You RJ (2007) Characteristics of artificial grassland plant communities with different establishment duration and their relationships with soil properties in the source region of Three Rivers in China. *Chin J Appl Ecol* 18:2426–2431
- Wang W, Tang XQ, Huang SL, Zhang SH, Lin C, Liu DW, Che HJ, Yang Q, Scholz M (2010) Ecological restoration of polluted plain rivers within the Haihe River basin in China. *Water Air Soil Pollut* 211:341–357. doi:10.1007/s11270-009-0304-5
- Wang G, Li H, An M, Ni J, Ji SJ, Wang J (2011) A regional-scale consideration of the effects of species richness on above-ground biomass in temperate natural grasslands of China. *J Veg Sci* 22:414–424. doi:10.1111/j.1654-1103.2011.01279.x
- Ward JV (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biol Conserv* 83:269–278. doi:10.1016/S0006-3207(97)00083-9
- Warming E (1909) *Saxifragaceae. I. Morphology and biology*. *Meddelelser Grøn* 36:169–236
- With KA, Crist TO (1995) Critical thresholds in species' responses to landscape structure. *Ecol* 76:2446–2459. doi:10.2307/2265819
- Wu Z, Raven PH, Hong D (1994) *Flora of China*. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, Missouri
- Wulff R, Causin HF, Benitez O, Bacalini PA (1999) Intraspecific variability and maternal effects in the response to nutrient addition in *Chenopodium album*. *Can J Bot* 77:1150–1158. doi:10.1139/b99-124
- Young-Mathews A, Culman SW, Sánchez-Moreno S, Toby O'Geen A, Ferris H, Hollander AD, LE Jackson (2010) Plant-soil biodiversity relationships and nutrient retention in agricultural riparian zones of the Sacramento Valley, California. *Agrofor Syst* 80:41–60. doi:10.1007/s10457-010-9332-9
- Yu M, Wei YS, Liu JG, Liu PB, Zhang ZM, Wei W, Wang YW, Zhong J, Yang Y, Xiao QC, Yu DW, Zheng X (2011) Impact of socioeconomic development on water resource and water environment of Yongding River in Beijing. *Acta Sci Circumstantiae* 31:1817–1825
- Zelnik I, Carni A (2008) Distribution of plant communities, ecological strategy types and diversity along a moisture gradient. *Community Ecol* 9:1–9. doi:10.1556/ComEc.9.2008.1.1
- Zhang J, Döll P (2008) Assessment of ecologically relevant hydrological change in China due to water use and reservoirs. *Adv Geosci* 18:25–30. doi:10.5194/adgeo-18-25-2008
- Zhang Z, Shen Z, Xue Y et al (2000) *Evolution of Groundwater Environment in North China Plain*, 1st edn. Geological Publishing House, Beijing