

Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system

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Abstract

Intermittent streams are common worldwide, and the ability of invertebrates to recover from floods and drought is a key feature of communities from these highly disturbed ecosystems. The macroinvertebrate assemblages of Kings Creek in northeastern Kansas were sampled regularly from four intermittent and two perennial sites over 2 years (1995–1996) to investigate the response and recovery to seasonal drying and floods. A ~9 mo drying period reduced taxa richness and density to 14% and 3% of pre-drying assemblages, respectively, in 1995–1996, whereas a 2 mo drying period reduced richness by half and density to 4% of pre-drying assemblages in 1996. Floods at intermittent sites reduced densities and richness by 95% and ~50%, respectively. A > 50 y-flood reduced macroinvertebrate richness by 97% and density by >99% at a downstream perennial site. Resistance and resilience of total macroinvertebrate density was typically greater to floods than to drying, whereas resilience of taxa richness did not differ between disturbance types. The time required for recovery to pre-flood conditions (richness and density) was half as long (27 vs. 76 day) for intermittent sites compared to perennial sites. Colonization of intermittent sites was a function of distance from upstream refugia. Floods were a more important disturbance on assemblages in a downstream reach as compared to upstream reaches. In contrast, upstream reaches were more likely to dry. Recovery following flood and drought was dominated by colonization as opposed to tolerance, thus resilience is more important than resistance in regulating macroinvertebrate communities in these streams, and relative position in the landscape affects disturbance type, intensity, and ability of communities to recover from disturbance.

Introduction

Natural disturbance (or discreet events that damage abiotic properties of an environment) plays a pervasive role in structuring most ecological communities and particularly stream benthic communities (Resh et al., 1988; Lake, 2000). Ecologists have begun to isolate and quantify specific characteristics of disturbance events (Poff & Ward, 1989; Meyer & Meyer, 2000). For example, intensity, variability, return times, and predictability are characteristics of disturbance

that have been associated with shaping species traits, spatial patterns, and therefore communities. Flood and drought are the predominant abiotic agents of disturbance in intermittent streams, so these systems provide useful models for comprehensively investigating response and recovery to both of these disturbances.

Resistance is defined here as changes in a response variable caused by disturbance, whereas resilience is the rate of recovery for a variable fol-

lowing disturbance. Assemblages from frequently disturbed environments are more resilient than assemblages that experience disturbance infrequently (Reice et al., 1990; Death, 1996) because unstable environments are likely to be dominated by taxa with traits (e.g. short life cycles, dormancy) that allow them to persist in fluctuating environments (Townsend & Hildrew, 1994). If the environment is unstable, but predictable (Poff, 1992), dominant taxa are likely to possess traits that enable avoidance or reduction of stress (Slobodkin & Sanders, 1969; Southwood, 1977) or rapid colonization of newly opened space (Denslow, 1980).

Intermittent streams of the Great Plains have received less attention than perennially flowing streams of the eastern and northwestern United States (Matthews, 1988). Grasslands and wooded grasslands drain 28% of the earth's surface and contribute 27% of stream flow worldwide (Dodds, 1997). Most headwater streams draining grasslands are intermittent but little is known about the macroinvertebrate assemblages in these streams or their responses to flooding and drying. Intermittent streams of the Great Plains of North America have seasonally predictable drying associated with increased evapotranspiration and long periods with little or no rain during the summer (Jewell, 1927; Matthews, 1988; Covich et al., 1997). Prairie streams are also subjected to extreme and unpredictable floods associated with intense localized thunderstorms (Matthews, 1988; Poff & Ward, 1989). Global climate change may cause a warmer and drier habitat that impacts assemblages of small streams in the Great Plains and this potential drying is exacerbated by associated human demands on surface and groundwater resources (Matthews & Zimmerman, 1990; Covich et al., 1997). Studies that provide further understanding of how hydrologic extremes affect biota may assist in managing water resources for future sustainability and biotic integrity.

We examined the response and recovery of macroinvertebrate assemblages to hydrologic extremes (floods and/or seasonal drying) at four intermittent and two perennial sites within a prairie drainage system over a 2-year period (1995–1996). Our first objective was to determine if assemblage resistance to drying and flood varied with intensity of disturbance and position in the watershed. Our second objective

was to assess the relationships among recovery and disturbance frequency, predictability, and refugia.

Drying is generally annual, whereas bed-scouring floods occur less frequently; therefore drying is more predictable than floods in the intermittent streams studied, so we predicted that intermittent assemblages would recover faster from seasonal drying than floods. We predicted that assemblages from intermittent reaches would recover faster than assemblages from perennial reaches following flood because assemblages from the more unstable (harsh *sensu* Peckarsky, 1983) intermittent sites should contain species that are adapted to disturbance. Lastly, we predicted that in streams with nearby and/or large refugia (upstream or downstream) assemblages would recover faster from disturbance than in streams with distant and/or small refugia.

Materials and methods

Study sites

Kings Creek is located in the 3497 ha Konza Prairie Biological Station (KPBS). Six sites were sampled regularly during this study: four intermittent tributaries (N01B, N02B, N04D, and N20B) and two perennial sites (N04P and P; Fig. 1). Spring-fed reaches with surface water throughout the year were found upstream of all the intermittent sites. In most cases these reaches became isolated pools in the summer, but in a few (such as N04P), the spring outflow was sufficient to maintain continuous flow for ~100 m of stream channel. Benthic substrate at all sites consists of flat gravel- and cobble-sized particles. Benthic substrate and the hyporheic zone completely dry to bedrock for most of channel (Fig. 1) because of shallow bedrock or packed clay 10–15 cm below the surface (Gray et al., 1998). Riparian vegetation at the intermittent and perennial headwater (N04P) sites consisted mostly of tallgrass and small shrubs. In contrast, riparian vegetation at the downstream perennial site (P) was dominated by gallery forest oak species. For additional description of the Kings Creek drainage and stream communities see Gray & Dodds (1998), and Stagliano & Whiles (2000).

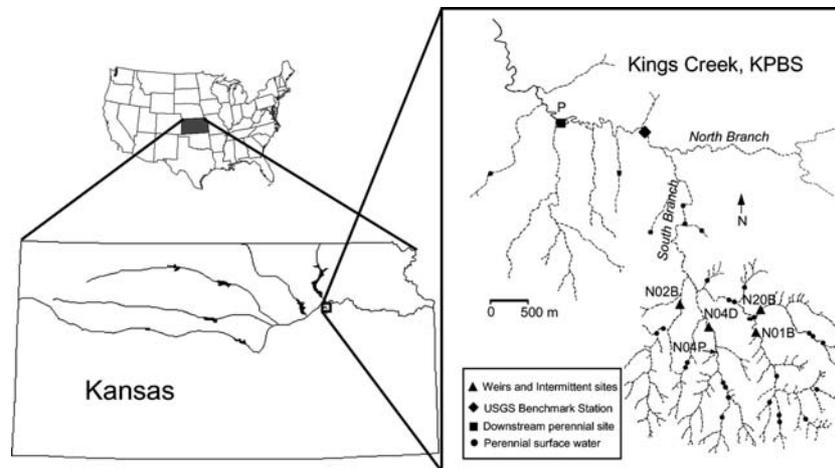


Figure 1. Locations of study sites on Kings Creek at Konza Prairie Biological Station (KPBS), Kansas, USA. Note: symbols representing perennial surface water only represent location and do not represent area of the perennial surface water.

Abiotic measurements

Discharge and water temperature were measured continuously at all intermittent study sites with trapezoidal flumes and thermocouples, respectively. Stream height during flow periods was measured manually at least weekly to maintain calibration of pressure transducers. Discharge at site P (the downstream perennial site) was estimated from United States Geological Survey (USGS) Benchmark Station (# 06879650; 39° 6' 7" N, 96° 35' 42" W) on Kings Creek (ca. 800 m upstream from P). Although discharge at the USGS gauging station is intermittent, it was used to represent relative discharge for the downstream perennial site. Because of the close proximity and the lack of major tributaries entering the channel below the gauging station, the USGS discharge values give an accurate hydrologic description for this study site.

Locations with perennial surface water were mapped (Fig. 1), and wetted surface areas were measured during fall 1995. Distances from intermittent sites and wetted area of perennial pools and springs were then used to describe colonization refugia. Unpublished data (M. Gurtz, USGS, personal communication) from the mid-1980s confirmed the stability of these refugia.

Benthic macroinvertebrate sampling

Macroinvertebrate sampling began in March 1995, within 2 days of flow resumption at the intermit-

tent sites. Samples were taken weekly from each site during the first 4 weeks of flow and biweekly thereafter, and were only sampled when surface water was present. N04P was sampled twice during 1995 (7 and 19 weeks after initiation of continuous flow at the intermittent sites) and biweekly during 1996. Samples were taken with a 20-cm-diameter stovepipe sampler (0.031 m², Merritt et al., 1996) to a depth of 10 cm into the streambed. Three samples were taken from gravel-dominated riffle habitats at each site on each date. The slope of species-area curves plateau after three samples within these streams (L. Gray; unpublished data). The mean precision (measured as D; Elliot, 1971) of total invertebrate density estimations using this sampling regime was 30%. This value is within the range (10–40%) of most benthic studies (Merritt et al., 1996). Samples were taken longitudinally upstream at 0.6-m intervals and randomly across the stream width. Samples were taken at 0.6-m intervals to minimize potentially confounding effects between sampling period and distance to upstream refugia.

Samples were sieved (250 μ m) and preserved (80% ETOH) in the field. Phloxine B dye was added to the samples, and then they were sorted under a stereoscope (12 \times). Samples were elutriated (Whitman et al., 1983) if they contained considerable amounts of mineral substrate. The gravel fraction was also sorted after elutriation in order to quantify heavier-bodied fauna (e.g., mollusks). All aquatic macroinvertebrates ≥ 1 mm (total body

length) were counted and identified to the lowest taxonomic level possible (usually species or genus). Several taxa were reared in the laboratory and adults were used to confirm identifications of immature forms. Some coleopteran larvae (i.e., Hydroporinae) were considered as separate taxa because of taxonomic uncertainty. Chironomidae were identified to subfamily after slide-mounting head capsules of representative specimens.

Data analyses

Resistance to drying and floods

Resistance was measured as the absolute value of percent change in macroinvertebrate density between consecutive samples (before and after a flood or drying event), using mean values from each date. Drying events were identified as periods when channels were completely dry for ≥ 10 day. Floods were identified as distinct (>10 day apart), rapid elevations of discharge associated with storm events. Peak discharge at intermittent sites was required to be $>0.1 \text{ m}^3 \text{ s}^{-1}$ to be considered a flood because that magnitude displaces typical streambed material at our study streams (Dodds et al., 1996). Three of the four (N01B, N02B, and N04D) intermittent sites were used as replicates in this analysis. The hydrologic regime at N20B was very episodic; therefore, separating resistance to drying and floods was not possible. Over the 2 years of study, three floods (Flood 95 I, Flood 95 II, and Flood 96) and two drying events (Dry 95–96, Dry 96) were identified that could be used for planned comparisons of percent change in density between drying and floods. Non-orthogonal planned comparisons using *t*-tests (PROC TTEST, SAS, 2001) were done to test for significant differences in density resistance. Normality was confirmed (Shapiro–Wilks test) and Satterthwaite's degrees of freedom were used when variances were unequal. Each drying event was compared to each flood, resulting in a total of six planned comparisons. To preserve an experiment-wise error rate of 0.05 for the six non-orthogonal comparisons, α was set at 0.008 (Bonferroni adjustment).

Identifying significant impact

Before comparing rates of recovery (resilience) following flood and drying, we first identified

periods when assemblage characteristics (density and richness) were significantly reduced. Significant changes in assemblage characteristics were identified using Kruskal–Wallis one-way ANOVA (PROC NPAR1, SAS, 2001). If significant differences ($\alpha = 0.05$) were detected, multiple comparison tests (Student–Newman–Keuls test) were used to determine if significant differences existed between dates immediately prior to and after floods or drying (see Boulton & Lake, 1992b).

Testing resilience predictions

Resilience was assessed by comparing recovery slopes (rate of change in assemblage characteristics over time) among: (1) disturbance type (seasonal drying vs. flood) at the intermittent sites, (2) floods at the intermittent sites vs. a downstream perennial site, and (3) separate disturbances of the same type within intermittent and perennial sites. We used the results of the Kruskal–Wallis test to identify the flood and drying events that significantly reduced macroinvertebrate density and richness. In this analysis drying is a disturbance exclusive to intermittent sites and recovery commences after rewetting. We assumed that the dry period prior to the start of the study (Dry 94–95) significantly impacted macroinvertebrate assemblages at the intermittent sites. Linear regression models were created based on days since disturbance (independent variable) and either macroinvertebrate taxa richness or density (dependent variables). Recovery slopes for intermittent streams were based on combined data from three replicate streams (N01B, N02B, and N04D). Therefore, the mean of three samples (density or richness) within each stream was treated as a replicate for a given time since a disturbance. Since only one downstream perennial site was sampled, each of the three samples within a date was treated as a replicate. Therefore, the perennial site data represents recovery over a smaller spatial scale than recovery at the intermittent streams. The duration of recovery periods used for each comparison was variable and dependent upon the onset of another disturbance (Table 1). Small sample sizes precluded comparison between disturbance types in 1996 and characterizations of recovery from the second drying event in 1996.

Table 1. Recovery comparisons and range of recovery period used for each comparison

Comparison of disturbance events	Recovery periods (d)	No. of sample periods
INT Dry 94–95 vs. Flood I 95	57–60	5–6
INT Dry 94–95 vs. Dry 95–96	20–26	3–4
INT Flood I 95 vs. Flood 96	32–35	3
P Flood I 95 vs. Flood 96	32–33	3
Flood I 95 INT vs. P	76–77	6
Flood 96 INT vs. P	32–33	3

See Methods for the procedure used to identify the recovery periods for comparisons. INT represents data from N01B, N02B, and N04D and P is the downstream perennial site.

Although the recovery periods were relatively short, they represent considerable periods of flow for these streams since water is present on average $< 90 \text{ day y}^{-1}$ at the intermittent sites (Fritz, 1997). Ideally, more than three sampling periods would be used for all recovery comparisons. However, the number of sampling periods was limited by (1) unforeseeable disturbances stopping recovery sequences, and (2) limited area of stream bottom available for sampling. The maximum number of sampling dates (or duration) in a recovery sequence was used for all comparisons, therefore for a given disturbance, the duration of a recovery sequence varied depending upon the maximum duration possible for the other disturbance in the comparison.

Data and residuals were plotted, and data were transformed ($\ln[x + 1]$) if they significantly deviated from normality (Shapiro–Wilks test). Comparisons of slopes and intercepts were made using differences in sums of squares error between reduced and combined (or full) models of the slopes tested. The difference (mean sum of squares of the differences in slope or MS_{drop} , *sensu* Ott, 1993) was then divided by the means square error of the combined model, resulting in an F statistic, and tested (PROC REG, SAS 2001) with a significance level of $\alpha = 0.05$.

Linear regression (PROC REG, SAS, 2001) was used to determine if relationships existed between upstream and downstream refugia characteristics (distance and surface area) and change in taxonomic richness and density since a disturbance event. Annual recovery from seasonal drying (Dry

94–95 and Dry 95–96) and the largest annual flood events (Flood I 95 and Flood 96) were used to test the refugia hypothesis. Significance level (α) was set at 0.05 for all analyses.

Results

Resistance to floods and drying

A larger density decline at intermittent sites was associated with the largest flood (Flood I 95; t -test, $p = 0.002$) compared to the longest drying event (Dry 95–96), but there were no differences when compared to losses associated with the shorter drying event in July 1996 ($p > 0.008$, Bonferroni adjustment). No differences in percent change of density were detected between any other flood and either drying event. However, floods with higher peak flows resulted in generally greater losses of individuals than floods with lower peak flows and in some cases density increased following low magnitude floods (Table 2). The 1996 flood was lower in magnitude than the first flood in 1995 at most sites, but percent change in densities was similar (Table 2). Likewise, response to the two drying events was similar, despite the shorter duration of the July 1996 drying event compared to Dry 95–96. Peak discharge of floods was greater at P than at the intermittent sites and was associated with greater loss of invertebrates (Table 2).

The effects of drying and flood on macroinvertebrate assemblages

Taxa richness and macroinvertebrate density varied significantly ($p < 0.05$, Kruskal–Wallis) among sampling periods for each of the sites and included significant reductions in assemblage measures between consecutive dates at all sites except N04P. Significant declines in density and richness were associated with two floods (Flood I 95 and Flood 96) and three drying events (Fig. 2 shows selected sites). Seasonal drying (Dry 95–96, > 9 mo) resulted in significant declines in both richness and density at three of the four intermittent sites (Fig. 2). Macroinvertebrate density at N20B was significantly reduced following a 17 day dry period (March 31–April 16) in 1995. Flow remained stable at the intermittent sites until June

Table 2. Resistance (as % density change across an event; negative values indicate a loss in density and positive values indicate increases), duration of drying (in days), and magnitude of floods (instantaneous peak discharge, JD = Julian date) occurring within the Kings Creek drainage, KPBS during 1995–1996

Dry 94–95		Flood I 95 JD 133		Flood II 95 JD 176		Dry 95–96		Flood 96 JD 147		Dry 96			
Site	Duration	Resistance	Q_{MAX}	Resistance	Q_{MAX}	Resistance	Duration	Resistance	Q_{MAX}	Resistance	Duration	1.67 ARI	INTDUR
N01B	108 d	-63.59	15.64 m ³ s ⁻¹	-51.92	2.84 m ³ s ⁻¹	-80.46	159 d	-80.46	15.41 m ³ s ⁻¹	-97.24	57 d	6.20 m ³ s ⁻¹	204.5 d
N02B	111 d	-75.00	5.30 m ³ s ⁻¹	+124.63	0.26 m ³ s ⁻¹	-86.00	293 d	-99.65	2.34 m ³ s ⁻¹	-	-	3.12 m ³ s ⁻¹	179.0 d
N04D	111 d	-60.36	4.49 m ³ s ⁻¹	+122.10	0.98 m ³ s ⁻¹	-71.20	280 d	-99.37	1.77 m ³ s ⁻¹	-91.75	55 d	3.61 m ³ s ⁻¹	159.7 d
N20B	300 d	+281.25 ^a	6.54 m ³ s ⁻¹	-54.10 ^a	15.85 m ³ s ⁻¹	-51.67 ^a	313 d	+215.79	83.78 m ³ s ⁻¹	-	-	6.54 m ³ s ⁻¹	348.6 d
P	-	-99.89	302.99 m ³ s ⁻¹	-77.38	21.24 m ³ s ⁻¹	-95.67	-	-	24.55 m ³ s ⁻¹	-	-	14.54 m ³ s ⁻¹	-
N04P	-	-	≤4.49 m ³ s ⁻¹	-	≤0.98 m ³ s ⁻¹	-66.79	-	-	≤1.77 m ³ s ⁻¹	-	-	≤3.61 m ³ s ⁻¹	-

Predicted magnitudes for floods with 1.67 annual return interval (ARI) and mean duration of dry periods (INTDUR) over the hydrologic records (8–17 y).

^a Channel was dry immediately prior to flood.

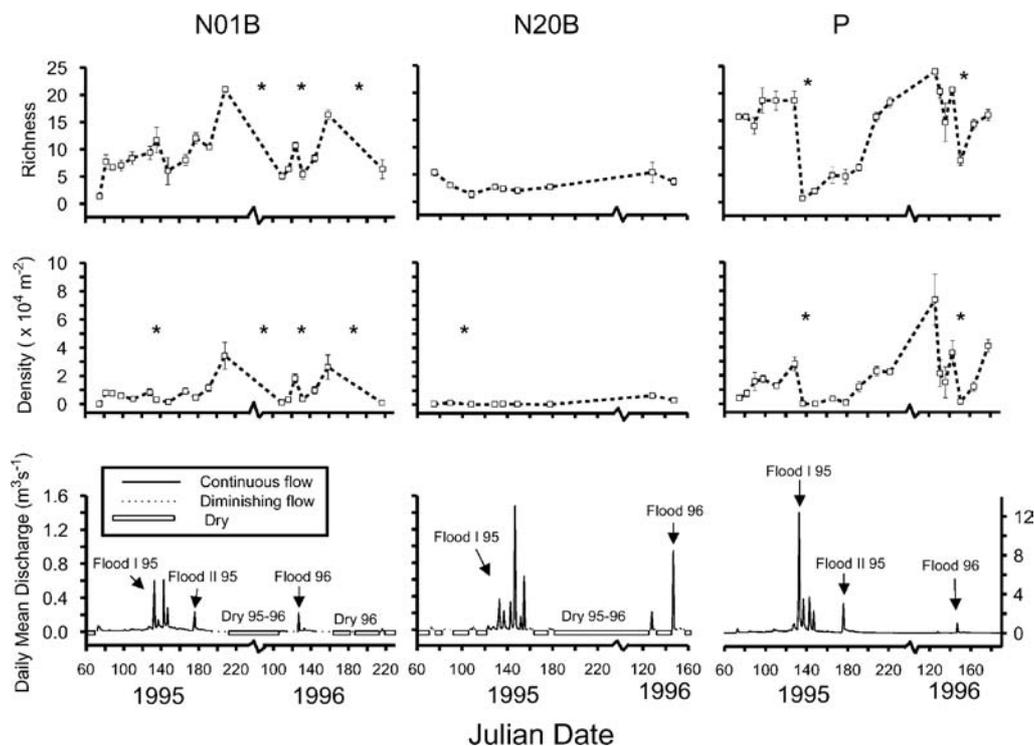


Figure 2. Taxa richness, density, and hydrologic patterns at N01B, N20B, and P. Symbols are means \pm 1 SE. Asterisk (*) indicates significant decline between consecutive samples (Student-Newman-Keuls test, $p < 0.05$). Discharge is illustrated as: open bar, completely dry; dashed line, daily mean discharge $\leq 0.005 \text{ m}^3 \text{ s}^{-1}$; solid line, daily mean discharge $> 0.005 \text{ m}^3 \text{ s}^{-1}$. Note that mean daily discharge for P is indicated on the right axis. Peak discharge of flood events and 1.67 ARI discharge for all sites are shown in Table 2.

(JD 180) and then they were dry for almost 2 months (Dry 96). Flow briefly resumed at N01B and N04D (Fig. 2). Densities and richness at these sites were significantly lower following rewetting in August when compared to pre-drying samples taken in June. In most cases, floods with peak discharge ≥ 1.67 annual return interval (ARI) were associated with significant reductions in density and richness; however, drying resulted in significant declines regardless of duration.

Resilience comparisons

Assemblages were not significantly more resilient to drying than flood in 1995 (Table 3). The recovery slopes for taxa richness did not differ significantly between drying and flood ($F_{1,29} = 0.22$, $p = 0.64$). Densities recovered faster following the 1995 flood than after rewetting ($F_{1,29} = 15.63$, $p < 0.001$). More frequently disturbed intermittent assemblages were not more

resilient to disturbance than perennial assemblages in either year (Table 3). Recovery rates for taxa richness following floods did not differ significantly between intermittent and perennial sites (1995 $F_{1,31} = 0.49$, $p = 0.35$; 1996 $F_{1,14} = 0.91$, $p = 0.36$). Macroinvertebrate density at the perennial site recovered faster following the 1996 flood than densities at intermittent sites ($F_{1,14} = 14.84$, $p = 0.002$), but there was not a difference between 1995 slopes ($F_{1,31} = 1.05$, $p = 0.31$).

The last set of comparisons was used to determine if differences in resilience were detectable between disturbances of the same type but with different timing and magnitudes. Flow resumed earlier in the year at intermittent sites in 1995 than in 1996, resulting in higher number of degree days in 1996 than in 1995 (mean at intermittent sites: 1995 = 192.11 $^{\circ}\text{C}$, 1996 = 794.10 $^{\circ}\text{C}$). Taxa richness recovered significantly faster following rewetting in 1996 than in 1995 ($F_{1,18} = 12.62$, $p = 0.002$), but recovery slopes for density did not

Table 3. Slopes of lines for the relationships between changes in macroinvertebrate richness or density and time since disturbance

Comparison	Disturbance events	Richness b (SE)	Richness r^2	Density b (SE)	Density r^2
1	INT Dry 94–95	0.10 (0.025)	0.583	46.91 (48.861)	0.079
	INT Flood I 95	0.12 (0.025)	0.552	322.56* (49.744)	0.697
2	INT Dry 94–95	0.23 (0.049)	0.690	296.55 (128.036) ^a	0.529
	INT Dry 96–96	0.55* (0.076)	0.861	1618.95 (197.489) ^a	0.909
3	INT Flood I 95	0.08 (0.070) ^a	0.175	188.07 (108.048)	0.638
	INT Flood 96	0.22 (0.080) ^a	0.454	462.33 (118.971)	0.552
4	P Flood I 95	0.15 (0.043)	0.635	128.85 (26.649)	0.770
	P Flood 96	0.31 (0.062)	0.777	1465.16* (207.702)	0.877
5	INT Flood I 95	0.14 (0.028)	0.630	372.87 (54.202)	0.773
	P Flood I 95	0.17 (0.026)	0.749	297.08 (50.409)	0.670
6	INT Flood 96	0.20 (0.075)	0.450	462.33 (182.814)	0.552
	P Flood 96	0.31 (0.075)	0.777	1465.16* (185.267)	0.877

Significantly greater slopes for each comparison are indicated by an asterisk (F -test, $p < 0.05$). Values in parentheses are standard errors.

^a Data were natural log-transformed and means given are back-transformed.

differ between years ($F_{1,18} = 3.31$, $p = 0.08$). Recovery rates following 1995 and 1996 floods at the intermittent sites did not differ for taxa richness ($F_{1,14} = 0.49$, $p = 0.50$) nor density ($F_{1,14} = 2.91$, $p = 0.11$). In contrast, macroinvertebrate density at P was more resilient to the 1996 than the 1995 flood ($F_{1,14} = 43.88$, $P < 0.001$). No differences in slope were detected for taxa richness between years at P ($F_{1,14} = 4.30$, $P = 0.06$). However, density recovered faster following the lower magnitude 1996 flood than following the larger 1995 flood. The peak discharge of the 1995 flood ($303 \text{ m}^3 \text{ s}^{-1}$, $> 50 \text{ y ARI}$) is highest on record for that station whereas the peak of the 1996 flood was only $25 \text{ m}^3 \text{ s}^{-1}$. Resilience was similar between years at the intermittent sites, where the magnitudes of the floods did not differ to the extent seen at P (Table 3).

Perennial refugia and resilience

Following rewetting (1995) and flood (1996), larger increases in taxonomic richness over time were found at intermittent sites close to upstream perennial water than at sites further from refugia, regardless of refugia wetted area (Fig. 3). Recovery from seasonal drying or flood in terms of

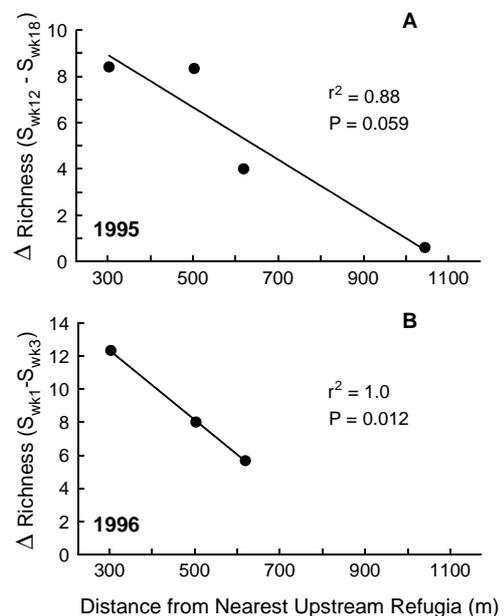


Figure 3. Relationship between change in mean richness at intermittent sites and respective distances from nearest upstream perennial water. (A) Increase in mean richness following Flood I 1995 (week 12 to week 18 since rewetting), (B) increase in mean richness following rewetting in 1996 (Dry 95–96, week 1 to week 3 since rewetting) Data from N20B was excluded from Figure 3B.

density was not significantly related with either distance from or wetted area of upstream refugia.

Discussion

Resistance to drying and flood

A flood is a 'pulse' disturbance whereas drying is a prolonged, gradual or 'ramp' disturbance (Stanley & Fisher, 1992; Lake, 2000). Because drying events are prolonged, resistance during the drying phase (resistance I, *sensu* Stanley et al., 1994) and resistance to the dry conditions (resistance II, *sensu* Stanley et al., 1994) have been considered separately. In our study, densities peaked when flow was diminishing at most of the intermittent sites. This increase in density was likely associated with a decline in area of submerged substrate (30–60 and 15–70% decreases in width and depth respectively). The site with greatest decrease in wetted width during drying was the only site where density significantly increased (N01B, JD 192–209, 1995, Fig. 2). Despite possible crowding effects associated with drying, we did not see declines in taxa richness (Fig. 2), nor were there apparent shifts in assemblage composition during the drying phase (Fritz & Dodds, 2002). The results from this and our earlier study (Fritz & Dodds, 2002) support those of other studies that have indicated macroinvertebrate assemblages in intermittent streams are resistant to the drying phase (Extence, 1981; Stanley et al., 1994; Miller & Golladay, 1996).

Aquatic macroinvertebrates in temporary habitats possess traits that enhance their resistance to water loss, such as aestivation and diapause (Imhof & Harrison, 1981; Boulton, 1989; Williams, 1998). However, macroinvertebrate resistance to seasonal drying (~9 mo) was low at our site. Resistance could be low because water is absent from our study sites for long periods of time (Table 2) relative to the physiological tolerance of most aestivating individuals (e.g., Imhof & Harrison, 1981). Also, the streambed sediments are not connected to an extensive hyporheic zone that would provide refugia. Last, our measure of resistance would not be able to detect the importance of diapausing eggs that hatched after the post-drying sample. Diapausing taxa (e.g.,

Pseudosmittia, *Perlesta placida*, *Acentrella turbida*) were present within dry sediment at our intermittent sites, but rehydration of dry sediment yielded low densities (average total density was 168 m⁻² over seven 30-day trials, Fritz, 1997).

Resistance during the drying phase will be important for the persistence of assemblages in streams with nearby perennial surface or subsurface refugia to which aquatic stages may migrate (Delucchi, 1989; Miller & Golladay, 1996). Drying resistance is most important for droughts that do not result in complete drying (Extence, 1981; Chessman & Robinson, 1987). However, in streams that: (1) completely dry and do not have nearby refugia (like those we studied), (2) have benthic organisms that do not migrate to nearby refugia during drying (Clinton et al., 1996; Rosario & Resh, 2000), or (3) have high predation pressure in nearby refugia (Boulton & Suter, 1986), resistance to drying phase will not be as critical to persistence as resistance to complete water loss or ability to recolonize from distant refugia. Streams completely shaded by a riparian canopy should have a more prolonged drying phase than streams with little or no cover (Ross, 1963; Feminella, 1996). This suggests that in forested intermittent streams, resistance to the drying phase can play a larger role in assemblage recovery and persistence than in streams with little overstory cover and high rates of watershed evapotranspiration, such as prairie streams or recently clear-cut forested streams.

Two of three floods during this study caused significant declines in assemblage density or richness among several of the study sites with the largest floods and greatest impacts occurring on macroinvertebrates downstream. In general, response to floods in the present study fall within in the range of density reductions (70–99%) observed following floods in perennial streams from other regions of the United States (e.g., Grimm & Fisher, 1989; Smock et al., 1994; Angradi, 1997). In addition to magnitude (peak discharge), timing was an important factor that governed the response to floods. For instance, drying was so severe at N20B, diversity and density often increased following floods. Floods connected distant upstream perennial water to the downstream intermittent sites, providing an avenue for rapid colonization. These low magnitude floods or 'freshets' can increase the

numbers of drifting invertebrates (Borchardt, 1993) and disperse young individuals (e.g., Anderson & Lehmkuhl, 1968).

Resistance to the drying phase and the complete loss of water will likely differ among taxa (Townsend & Hildrew, 1994). Therefore, the timing of drying will be important relative to the taxa present and vulnerability of particular life stages. Incorporating characteristics of drying events, such as timing, spatial extent, and duration, within a historical context will provide a means to better interpret biotic response and recovery across multiple environments. For instance, disturbance events can be placed in a historical context using a relative measure of magnitude (Poff & Ward, 1989). Relative measures allow comparison across different streams, and provide a way to test hypotheses regarding the role of refugia (pools or hyporheic zone) or surrounding vegetation. Predicted response curves then can be constructed for different types of intermittent stream across a range of relative magnitudes of disturbance (Fig. 4). There is a need for long-term studies to more evenly examine the effects of disturbance properties on assemblages from streams of varying size, land use, and of different climates.

Resilience to drying and flood

Macroinvertebrate assemblages recovered rapidly following seasonal drying and flood. Densities and

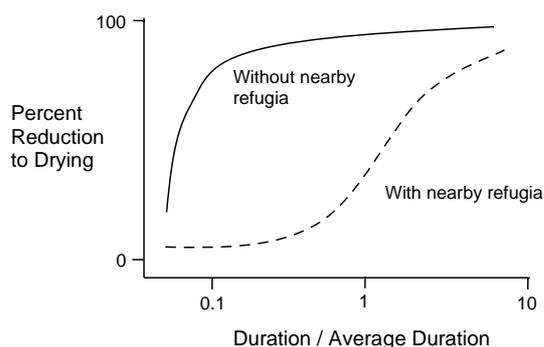


Figure 4. Hypothetical assemblage response curves by two different intermittent stream types to drying across a disturbance gradient that incorporates a historic context. Response in this example is measured as percent reduction to drying and the disturbance gradient is the ratio of the duration of a drying event to the average duration of drying events over a period of record.

taxa richness stabilized after 2–4 weeks of flow in 1995 at the intermittent sites (Fig. 2). Recovery following flood and drying in our intermittent streams was as rapid as many small scale disturbance studies at perennial streams (Lake et al., 1989; Johnson & Vaughn, 1995). The recovery slopes of macroinvertebrate density from our study were also comparable to those from a Sonoran Desert stream (Stanley et al., 1994), where density recovered in ~ 30 day. However, the duration of the annual drying events we studied lasted more than four-fold longer than those in the Sonoran Desert.

In contrast to our initial prediction, macroinvertebrates assemblages were not more resilient following seasonal drying compared to less predictable floods. In fact, densities recovered faster following the 1995 flood than following drying. Short, asynchronous life cycles and high dispersal abilities are traits that favor high resiliency following either flooding or drying (Robinson et al., 1993; Dieterich & Anderson, 1995) and this was probably important in Kings Creek. Many Chironomidae, Simuliidae and Ceratopogonidae have these traits (Williams, 1996; Langton & Casas, 1999) and were the dominant taxa at the intermittent sites (Fritz & Dodds, 2002). Life cycles as short as 18 day for the dominant mayfly (*Fallceon quilleri*) and 6 day for one of the dominant midges (*Cricotopus*) have been documented from our study sites, and were comparable to developmental times for these taxa in a Sonoran Desert stream (Gray, 1989).

Faster recovery of densities following flood compared to drying was probably related to differences in the size of area disturbed by the events. The size of the colonist pool was probably much lower following drying than flood, because most (83–98%) of the channel lengths were not occupied by active individuals. In contrast, there were greater numbers of active individuals within the channels prior to the 1995 flood, therefore the colonization distance from refugia was likely much less than after rewetting. High discharge would allow organisms to rapidly colonize intermittent sites through drift. In a Sonoran Desert stream resilience of macroinvertebrate densities following rewetting at two intermittent reaches were typically slower than following floods at a downstream perennial reach (Grimm & Fisher, 1989; Stanley

et al., 1994). The size, distance from, and longitudinal position of refugia relative to a disturbed reach are directly correlated with rate of recovery.

Despite experiencing hydrologic disturbance annually, density and richness of assemblages from intermittent sites were not more resilient to floods when compared to the assemblage from the downstream perennial site. However, because richness and densities were reduced to a greater degree at P, recovery to pre-flood conditions took twice as long compared to recovery at the intermittent sites (ca. 27 vs. 76 day, Fig. 2). There was substantial taxonomic overlap between intermittent and downstream perennial sites (41% of the total number of taxa collected were found at P and the intermittent sites). There were very few taxa that were exclusive to intermittent sites (17% of the total number of taxa collected that were not collected at P or N04P) and these contributed <1% to total densities (see Fritz & Dodds, 2002 for complete taxa list). With the exception of the most ephemeral flowing site (N20B), faunal composition at intermittent sites became more similar to that of perennial sites over time during both years (Fritz & Dodds, 2002). Because the intermittent assemblages were subsets of the dominant taxa present at the downstream perennial site, it is reasonable that resilience was not greater at intermittent sites. Several comparisons of intermittent and perennial streams have found overlap of taxa and very few that are exclusive to intermittent sites (Delucchi, 1988; Boulton & Lake, 1992a; Feminella, 1996; Miller & Golladay, 1996).

Recovery was faster following the 1996 flood at P compared to intermittent sites and the 1995 flood at P. Since this flood had a much lower magnitude than the 1995 flood, we suggest that the faster recovery at P in 1996 was associated with a larger pool of nearby colonists compared to the 1995 flood. Although we were unable to compare recovery rates following drying and flood in 1996 at the intermittent sites, we were able to compare recovery following rewetting between years. Taxonomic richness recovered significantly faster in 1996 compared to 1995. Since flow resumed later in 1996 (May), air and water temperatures were higher than in 1995 (March). Colonization rate has been shown to increase as a function of ambient temperature and invertebrate activity levels in other studies (Mackay, 1992; Robinson et al.,

1993). Additionally, it is likely that there were more taxa present as ovipositing adults in May than in March and this contributed to faster recovery in 1996.

Role of refugia

Paltridge et al. (1997) concluded that the relative importance of a colonization mechanism (pathway) in intermittent streams was dependent upon the harshness (duration) of the dry season, type of substratum, and distance from refugia. Aerial colonization or drift from upstream perennial refugia was the dominant colonization mechanism in streams with severe harshness. The assemblages of intermittent sites in the present study were determined primarily by taxa colonizing from upstream refugia. In most years, distance and short periods of flow limit upstream migration from downstream perennial water to intermittent sites.

The rate of colonization in ephemeral habitats likely is related to distance from refugia and the size of the refugia (MacArthur & Wilson, 1967). Island biogeography theory has been applied successfully to temporary ponds (e.g., Ward & Blaustein, 1994), however some investigators disagree with this application because presumed carrying capacity is never reached (Wiggins et al., 1980). Even so, it has been hypothesized that distance and area effects of refugia are crucial in recovery from disturbance in intermittent streams (Delucchi, 1988; Stanley et al., 1994), although few watershed-level tests of this model exist (see Paltridge et al., 1997).

Conclusion

The interactions seen among drying, flood, and longitudinal position along Kings Creek resulted in four distinct successional patterns of the macroinvertebrate assemblage. These patterns were apparent over both years of this study. Macroinvertebrate assemblages had unique responses to disturbance events at two sites for very different reasons. The headwater site (N4P) did not dry and was not affected by floods since runoff was likely moderate near the top of the watershed. At the other extreme, N20B usually did not differ in assemblage parameters between sampling periods; this is because N20B is always in an initial state of

recovery from either drying or flood. The longer flow duration at the other three intermittent sites allowed for development of more stable assemblages, and these intermittent sites were less impacted by flood than the downstream perennial site.

The impacts of drying and flood were detectable at most intermittent study sites. Among the stresses associated with varied hydrologic regimes of these sites, resistance was greatest to diminishing flow, followed by floods, and was lowest to complete loss of water. This pattern of resistance was determined by the availability of refugia and the physiological tolerance of the taxa to these stresses. Predictability of disturbance type or frequency of disturbance between perennial and intermittent sites did not determine assemblage resiliency.

The predominant life history strategy of having short, asynchronous life cycles provides equally rapid recovery from drying and flood, regardless of stream permanence. Upstream perennial refugia determined the diversity and resiliency of assemblages at intermittent sites downstream. The function of perennial surface waters as refugia has important implications for maintenance of longitudinal stream connections, even the brief ones found in these streams. It is likely that many intermittent streams of the Great Plains do not have nearby refugia, and therefore persistence of many taxa depends upon very localized reaches or spring seeps with perennial surface water. Impoundment of or diversion of water from spring-fed reaches may eliminate vital refugia necessary for persistence of lotic taxa without stages resistant to drying within these low order streams.

Although there were declines in assemblage parameters associated with loss of water, these events do not meet the definition of disturbance proposed by Resh et al. (1988) because seasonal drying witnessed in this study was not outside a predictable range in time and intensity for these streams, organisms are expected to be 'adapted' to the recurring loss of water. In a sense this may be true because most taxa occurring in Kings Creek utilize an opportunist life history strategy (i.e., short, asynchronous life cycles), however the intensity of drying is so great, that individuals that have not already emigrated prior to complete

water loss are exposed to desiccation. Complete drying in these streams may not be outside the predictable range of intensity, but these harsh conditions are outside the range of adaptation by the majority of macroinvertebrates colonizing these streams. The contingent flow regime however, does produce a predictable succession of taxa that are able to colonize following resumption of flow. Our results indicate that resiliency (colonizing ability) and not resistance (tolerance to water loss) is responsible for the stability of assemblages, and that position in landscape can determine both disturbance intensity (i.e., bigger floods downstream, longer droughts upstream) and recovery (i.e., closer upstream refugia encourage rapid colonization). Further work will need to be done to determine if these patterns hold for other biotic components (e.g., meiofauna, chironomids identified to species, algae) of tallgrass prairie streams.

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