Life on the Edge: The Ecology of Great Plains Prairie Streams

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Great Plains streams are highly endangered and can serve as model systems for studying disturbance ecology and related issues of resistance and resilience in temperate freshwaters. These streams exist in a precarious balance between flood and drying. In general, microbial activity recovers in days to weeks after drying or flooding, and invertebrate and fish species are quick to follow. In lower forested reaches, floods may be more intense but drying less common. Upstream reaches of prairie streams are characterized by frequent drying, little canopy cover, and limited leaf input. Life history and adaptations alter the ways in which stream organisms respond to these linear patterns. Human modification has altered these patterns, leading to large-scale loss of native grassland streams. The future for Great Plains streams is bleak, given the land-use changes and water-use patterns in the region and the large areas required to preserve intact, ecologically functional watersheds.

Keywords: disturbance, drying, flood, prairie, streams

Prairie streams and rivers historically formed a critical part of Great Plains ecosystems. However, such streams have received less attention from ecologists than streams in forested regions (Matthews 1988). Prairie streams not only are vital habitats that control downstream water quality but also can serve as model systems for studying disturbance ecology and related issues of resistance and resilience in temperate fresh waters. Biological responses to disturbance are particularly easy to document, because prairie stream organisms have exaggerated life-history characteristics that are well suited to survival in such habitats (Lytle 2002). Understanding the ecology of Great Plains streams is imperative, because they represent a component of the ever-dwindling North American supply of unpolluted surface freshwater resources and are home to a number of threatened or endangered species, including the Topeka shiner *(Notropis topeka)*, the Neosho madtom *(Noturus placidus)*, and many freshwater mussels in the United States.

North American prairie once covered 160 million hectares, but it is now one of the most endangered biomes on the continent (Samson and Knopf 1994). For instance, about 95% of the once-extensive tallgrass prairie has been lost (Samson and Knopf 1994). Streams in prairies are even more endangered, because many of the remaining fragments of prairie are not large enough to encompass a significant, functional watershed. Most areas of the Great Plains that were formerly prairie are now heavily affected by agriculture or urbanization, resulting in pollution, hydrologic disturbance, and physical modification (e.g., channelization and alteration of riparian vegetation) of streams. In addition to the aboveground insults, vast areas of the Ogallala–High Plains aquifer and other large aquifers under grasslands have been overexploited, literally sucking dry many streams of the Great Plains.

Understanding the ecosystem function of small streams in the Great Plains region is essential, because those streams represent a key interface between terrestrial habitats and downstream areas, and substantial in-stream nutrient processing may control downstream water quality (Peterson et al. 2001). Thus, physical and biological factors that influence the ecosystem function of native prairie streams, including even small headwater reaches, must be studied to help assess current water quality issues on both local and continental scales. Knowledge of community and ecosystem dynamics will help in designing such studies, and these dynamics are driven in large part by the variable hydrology that results from the climate of the Great Plains.

Hydrology is one of the most fundamental components of the physical template of all streams, and flooding and drying

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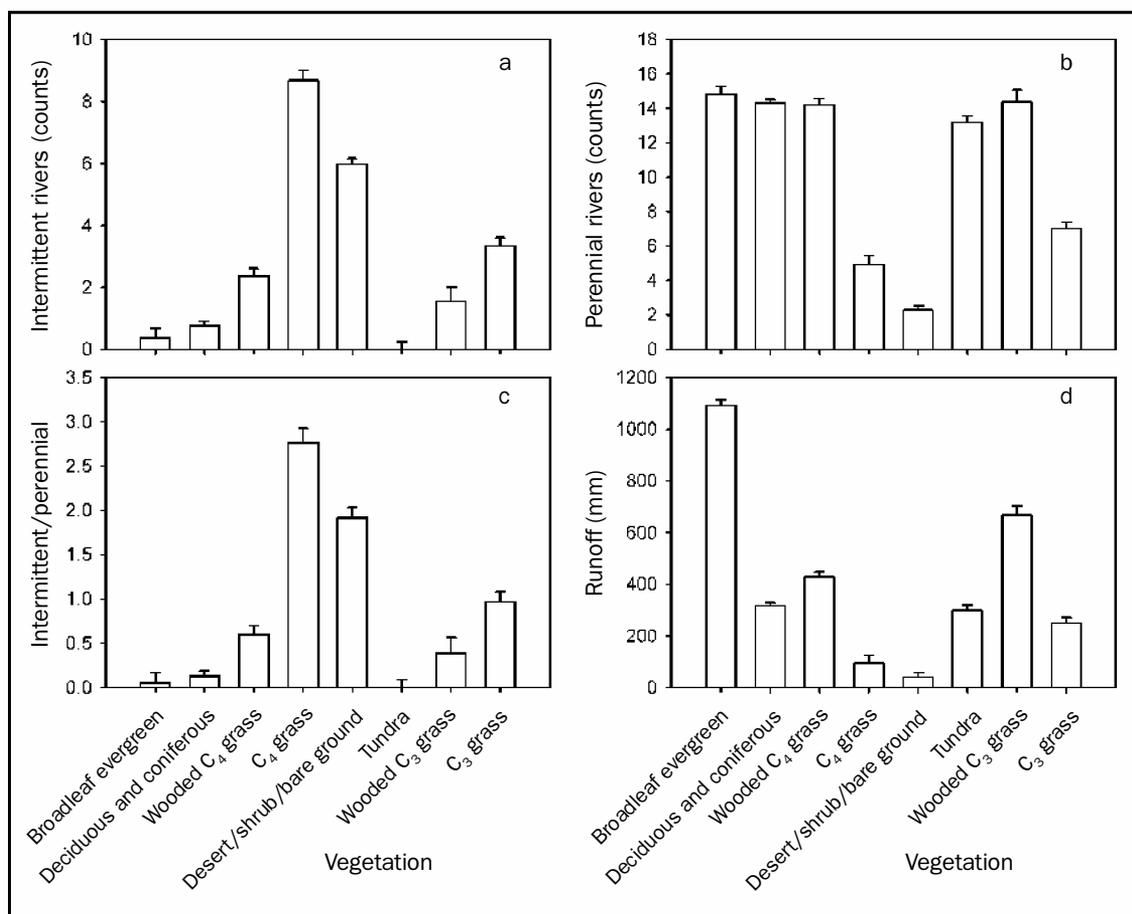
Figure 1. (a) Number of intermittent rivers, (b) number of perennial rivers, (c) ratio of intermittent to perennial rivers, and (d) runoff (in millimeters), as these measurements relate to different types of vegetation worldwide. River counts and vegetation cover are based on a 1° × 1° grid; runoff is based on a 2° × 2° grid. Error bars represent 95% significance levels; analysis of variance indicates that differences are highly significant. The number of grids for each vegetation type ranged from 454 to 4059. See Dodds (1997) for a description of the strengths and weaknesses of data sets and data sources. Vegetation classifications include broadleaf evergreen (mostly moist tropical forest); deciduous and coniferous (seasonal tropical, temperate deciduous, and high-latitude forest); wooded C_4 grassland (trees interspersed with dry grassland); C_4 grassland (dry grassland); a composite of desert, shrubland, and bare ground; tundra (high-latitude and high-altitude habitat); wooded C_3 grassland (trees interspersed with moist grassland); and C_3 grassland (moist grassland).

are particularly characteristic of Great Plains streams. From a global perspective, intermittent streamflow is a feature of most grasslands. Areas dominated by grasses that do well in hot, dry climates (C_4 grasses) have relatively low runoff, a relatively high number of intermittent streams, and a high proportion of intermittent streams relative to the number of perennial streams (figure 1). The correlation between runoff and the ratio of intermittent to perennial streams is negative and highly significant ($P < 0.01$). Cool-season (C_3) grasslands, wooded C_3 grasslands, and wooded C_4 grasslands have intermediate numbers of intermittent streams, and forested areas and tundra are characterized by more abundant perennial streams. Grasslands historically dominated the Great Plains, and, consistent with global patterns, intermittence is

common in hydrographs of Great Plains streams. In the Great Plains, mid-continental weather patterns are characterized by large convective cells (thunderstorms) that regularly lead to intense localized floods. Climatic variability and thunderstorms result in highly variable annual runoff patterns in smaller streams, where drying and floods are both common (figure 2). This pattern is widespread across the Great Plains, where most small streams are characterized as harsh, intermittent, or perennial, but with high flood frequency and low predictability (Poff and Ward 1989). How this intermittent hydrology affects community and ecosystem function is a central question in our prairie stream research.

Hydrology influences organisms that subsequently affect ecosystem function. In one study, for example, almost all the
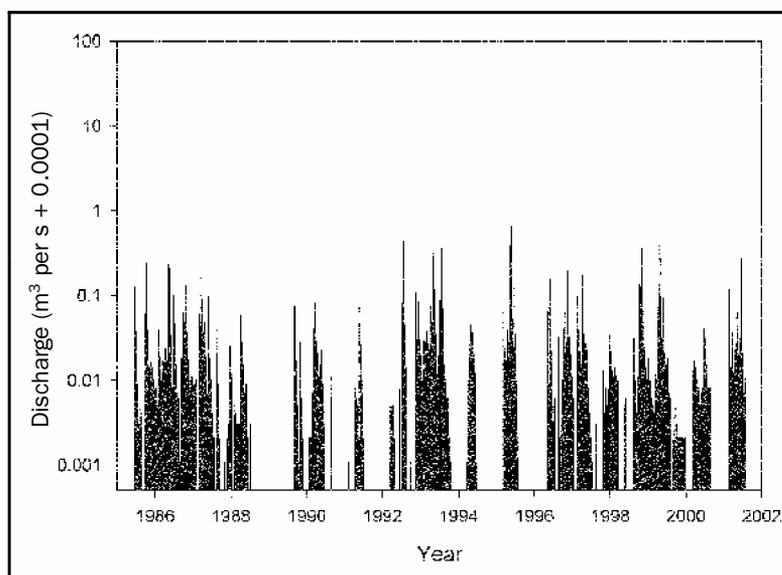
Figure 2. Hydrograph of the 134-hectare Watershed N04D of Kings Creek at Konza Prairie Biological Station. Mean daily discharge (in cubic meters per second) has had a value of 0.0001 added to each value to facilitate plotting on a log plot. Areas without dark bars are times of no flow. Note that any month can have no flow or a flood, although floods and flow are more likely in late spring or early summer. Data courtesy of the National Science Foundation's Konza Prairie Long Term Ecological Research program.

nitrogen assimilated by microbes in a prairie stream moved into the primary consumers, indicating that animals are intimately involved in nutrient cycling (Dodds et al. 2000). Primary consumers and omnivores strongly influence primary production (e.g., Evans-White et al. 2001, Gido and Matthews 2001), either by reducing algal biomass through consumption, stimulating algal growth by excreting limiting nutrients, or both. We are only beginning to document how the variable physical conditions that are typical of the harsh environment of Great Plains streams govern the effects that stream consumers and producers have on the ecosystem and how those organisms interact with each other.

The upper reaches of grassland streams often do not have a riparian canopy of trees, so stream ecosystem structure and function may differ from that in forested systems (e.g., Wiley et al. 1990). With the exception of several reviews on the conservation of prairie fishes (e.g., Cross et al. 1985, Cross and Moss 1987, Fausch and Bestgen 1997), there is only a modest amount of published research on Great Plains streams. Much of the research on invertebrate and microbial responses to flood and drying has been conducted in Kings Creek at Konza Prairie Biological Station, one of the few preserved tallgrass prairie regions large enough to have complete watersheds protected. Hence, our overview is based on available literature with an emphasis on the ecology of Great Plains streams.

Great Plains streams play a vital role in ecosystem services, support a unique and sometimes endangered biota, and

are endangered. These streams may differ from more studied streams in the vegetation of their watershed and in their variable hydrology. Thus, our picture of prairie stream ecology is painted from a nonequilibrium viewpoint; these streams exist in a precarious balance between flood and drying. And it is life on the border of the terrestrial–aquatic ecotone that is vital to determining how anthropogenic disturbances are transmitted into the aquatic realm. This "life on the edge" makes prairie streams exciting arenas for ecological research.

Hydrologic disturbance in prairie streams
While flooding and drying clearly have the potential to alter stream communities, a single definition of disturbance remains elusive. For most, but not all, aquatic organisms, drying and severe flood can remove most individuals from a stream. Intermediate-level floods (e.g., 1-year return time) or partial drying may have considerably less effect than severe events that completely rearrange cobbles and rocks on the bottom of the stream or dry the entire stream channel.

Our view of hydrologic disturbance in streams explicitly recognizes that *disturbance* is a general term encompassing the magnitude, frequency, and predictability of stream drying or flooding, and that consideration of disturbance must be placed in the context of adaptations of individual organisms (i.e., both ecological and evolutionary time scales should be considered; Poff 1992). Two types of response to disturbance are quantified: resistance, or the ability of organisms not to be affected by a particular disturbance, and resilience, or the ability of organisms to recover after disturbance.

For example, for our research in eastern Kansas, we have defined drying as complete loss of water in all but spring-fed reaches of intermittent first- to third-order stream channels. (Stream order is a method of categorizing stream size; first-order channels are the smallest, two first-order channels merge to form a second-order channel, two second-order channels form a third, and so on.) We use the term *drying* to mean loss of surface water in the stream channel and *drought* to imply an unusual dry period in any ecosystem. Because channel drying may be a typical seasonal feature in many Great Plains streams even in years with normal precipitation, the length of a dry period can also be important when defining drought conditions. Here we consider drying intensity at the watershed scale, as indicated by the number of days since the channel was contiguously flowing and the length of wetted periods between dry periods. We define *flooding* as high flows with at least a 1.67-year return interval of bankfull discharge (Poff 1996), because such disturbances move cobble in stream channels (Dodds et al. 1996).

Relatively soon after flood or drying (within days to weeks), we observe a rapid recovery of ecosystem activity and biodiversity. Thus, the resilience of prairie stream communities is

1st order intermittent small floods	Diversity following drying	Diversity following flooding	Routes of colonization	Production and respiration	Dominant riparian vegetation	Grazers and shredders
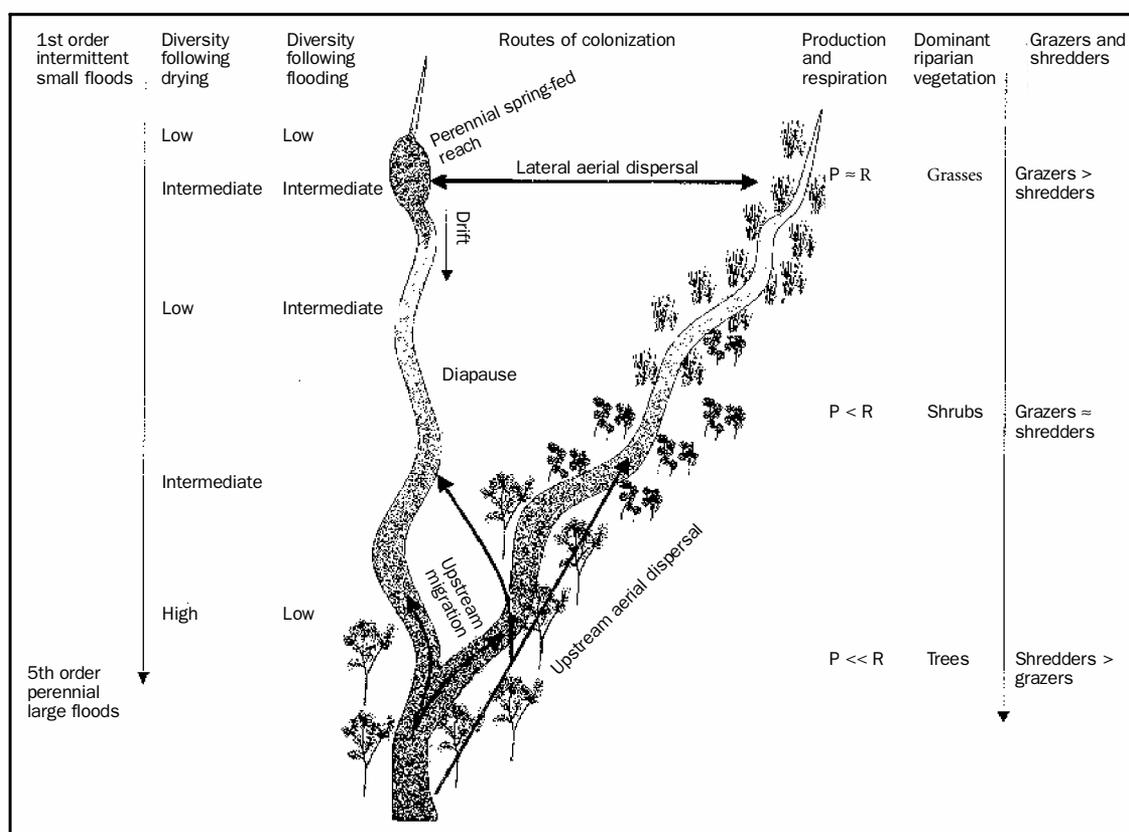
Figure 3. A conceptual diagram of community and ecosystem dynamics in intermittent prairie streams. Abbreviations: P, primary production; R, respiration.

high. This recovery is dependent on the physical characteristics of the habitat and the natural history of the organisms involved. In general, microbial activity recovers first, but invertebrate and fish species soon follow, depending on their mobility and proximity to source populations. We focus here on microbes, macroinvertebrates, and fishes. Other biotic components of prairie streams (e.g., microfauna, waterfowl, and amphibians) may be equally important, but they have not been as closely studied.

Disturbance and prairie streams as a linear landscape

In Great Plains streams, the natural hydrologic variance that occurs when water flows across the surface of the land is exaggerated. In most streams, the uppermost reaches of the watershed have intermittent flow. In continuously wet climates, the intermittent stretches may only be short rivulets that form during intense rainy periods. In contrast, streams that occur in drier regions (e.g., prairie and desert streams) have intermittent stretches that are much longer.

Watershed geometry makes it likely that floods will be more intense (greater discharge, somewhat higher velocity, much greater sediment loads) in midorder reaches than in upland reaches, as long as the cross-sectional shape of the channel is comparable and precipitation is relatively even across the watershed (Leopold 1994). Discharge increases with

watershed area, so floods may be more intense in the lower reaches. Applying discharge patterns to the ecology of stream organisms leads us to think of prairie stream habitats as linear landscapes (figure 3), in part because hydrology depends on the position of the stream reach in the watershed. Small upstream segments are more prone to drying (except for isolated pools and reaches fed by springs), and midorder downstream reaches are more prone to intense floods. The larger rivers will dilute floods, in many cases, because increases in discharge are often dissipated by lateral expansion of the river into the floodplain, and rain usually does not fall hard across the larger drainage area. The large rivers also will almost never dry. Of course, this linear model is only a generalization and will not hold for all Great Plains streams. For example, first-order streams in the Sand Hills of Nebraska can be spring fed, resulting in constant flow and extensive riparian canopy cover (DeNicola and Hoagland 1996).

A downstream change in types of vegetative cover also influences stream communities. Little canopy cover and limited leaf litter inputs characterize the upstream reaches of many unimpaired Great Plains streams, compared with forested streams (Wiley et al. 1990). In drier environments such as shortgrass prairie, minimal riparian cover was present historically, even on rivers (Cross and Moss 1987). In more mesic grassland habitats such as tallgrass prairie, a riparian tree cover develops in perennial reaches, leading to a down-

stream increase in detritivory and a decrease in grazers. Life history and feeding adaptations alter organism response to these linear patterns. Predatory invertebrates are not heavily affected, whereas shredders (animals that subsist on terrestrial leaves that enter streams) may be limited by food supply in the upper reaches of the stream. Larger animals (crayfishes and fishes) are often omnivorous and can thus cope with variable food sources across space and time; such omnivores are ubiquitous in streams of all biomes, but they do particularly well in prairie streams, where food sources can change rapidly and be spatially variable.

For organisms that are unable to swim, crawl, fly, or otherwise disperse upstream, the stream habitat landscape has a highly directional component as well as a linear constraint. Organisms may be able to move upstream or across the watershed relatively quickly if they have areal dispersal as adults or desiccation-resistant propagules that can be moved by wind. The ability to swim rapidly or hitchhike on other organisms can allow organisms to move upstream. Fishes move upstream easily but are more laterally constrained, since they are unable to move out of stream or river channels. Once an organism colonizes an area after disturbance, growth and reproduction rates dictate how quickly its abundance will increase. Most species must reproduce relatively quickly to survive in prairie streams, but some are able to reproduce more quickly than others. Thus, life-history characteristics influence how organisms will respond to disturbances.

Taxonomic groups have different adaptations to desiccation. Groundwater-fed pools or hyporheic zones (wetted habitat below the stream bed surface) may provide important refugia from dry conditions in an otherwise inhospitable stream channel. Such refugia are an important component of streams in dry climates worldwide (Lake 2003). Microbial activity resumes in less than a week; if desiccation-resistant mats (dense layers composed of algae and heterotrophs) are present, activity may resume in hours. Microbial propagules wash in quickly if they are upstream or present in hyporheic refugia, and doubling times are hours to days. A few invertebrates may be found within days after rewetting, and moderate populations can be found within a few weeks, particularly if there are upstream or hyporheic refugia. Rapidly reproducing invertebrates have doubling times in the range of days to weeks. Fishes and larger macroinvertebrates with longer life cycles take anywhere from hours to weeks to find their way into rewetted reaches, depending on their proximity to perennial waters (Larimore et al. 1959). The generation times of fishes and large invertebrates are generally long enough that a sustained wet period of weeks or months is necessary for successful reproduction in intermittent reaches; thus, refugia are particularly important for these species.

Similar adaptations offer resistance to flooding, allowing rapid colonization by microbes and slower recovery by invertebrates. Larger macroinvertebrates and fishes may have behaviors, such as the ability to move to side channels or backwaters, that allow them to find refuge from floods and thus to repopulate flooded areas more quickly than smaller invertebrates. Resistance to floods in prairie streams is generally greater than resistance to dry periods, although the magnitude of floods and the length of dry periods are important factors in an organism's overall resistance to hydrologic disturbance.

The expected sequence of colonization allows us to predict how ecosystem processes will develop after floods and rewetting. Microbial activity (e.g., photosynthesis, respiration, denitrification) will be low immediately after severe disturbance, but it should increase quickly. Metabolic rates after disturbance may actually exceed those observed following long periods of stable flow, because of increased resource availability and decreased consumption by animals such as grazing invertebrates. Early colonizing invertebrates that are primary consumers will probably find abundant resources and grow and reproduce quickly in recently disturbed habitats. Predatory invertebrates will be less productive until a substantial prey base becomes established. Once the largest invertebrates and fishes arrive (particularly the omnivorous species), complex trophic interactions will dominate, making predictions about ecosystem responses more difficult. Testing these predictions is one of the challenges facing future stream ecologists. Understanding the nonequilibrium dynamics of stream ecosystems will be central in efforts to understand and protect these unique and endangered systems. We approach these dynamics by considering the major groups of organisms in the streams—microbes, invertebrates, and fishes—in more detail.

Microbial processes and primary production

Microbes form the key component of nutrient cycling in prairie streams, as they do in all other habitats. Primary production by microalgae can be substantial in low-order prairie streams, because canopy cover is limited and clear water allows light to penetrate to the stream bottom (Hill and Gardner 1987, Stagliano and Whiles 2002). The ratio of primary production to respiration is higher in desert and grassland streams than in most other stream habitats (Mulholland et al. 2001), although community respiration rates can slightly exceed gross primary production. Thus, nutrient cycling capacity and the recovery of primary producers are linked and contribute to observed responses of prairie stream ecosystems to flood and drying.

In Kings Creek on Konza Prairie, algal biomass took less than 2 weeks to recover after normal streamflow rewetted the rocks (Dodds et al. 1996). Recovery was just as fast on bleached and scrubbed rocks (i.e., rocks with desiccation-resistant propagules removed) as on dried rocks, indicating that they were colonized primarily by upstream or airborne propagules. In contrast, a severe flood in Kings Creek (with a return time of nearly 100 years) lowered chlorophyll for 3 weeks, followed by a rapid increase to levels substantially above preflood chlorophyll biomass. Within 2 weeks after this extreme flood, primary production equaled that measured before the flood, and within 3 weeks it exceeded the production measured before the flood. In a reversal that is characteristic of the

dynamic nature of prairie streams, the studied reach was completely dry about 6 weeks after the flood. The sequence of microbial recovery after the flooding in Kings Creek is very similar to that in Sycamore Creek, a desert stream (Fisher et al. 1982).

The native prairie streams of Konza are highly nitrogen retentive, maintaining relatively low concentrations of nitrogen even in the more ephemeral streams, where microbial populations may have a limited amount of time to respond to flow (Dodds et al. 2000). Thus, fairly high nitrogen retention can be maintained at all times, which could in part be due to the rapid response to environmental conditions by the microbial assemblage. When prairie sediments were transferred from low-nitrogen streams to high-nitrogen streams containing agricultural runoff, they exhibited nitrification rates characteristic of the substantially higher values observed in agriculturally influenced waters within 6 days (Kemp and Dodds 2002).

After 5 months of continuous flow, the rates of nitrogen cycling in a tallgrass prairie stream (Dodds et al. 2000) were indistinguishable from those in streams from a wide variety of other biomes, including a tropical forest, deciduous and coniferous forests, a desert, and tundra (Peterson et al. 2001). This indicates that intermittent streams (both desert and prairie) can attain rates of ecosystem function typical of permanent streams over a period of months.

Microbial communities are also a major biological determinant of organic matter decomposition rates, another important energy and nutrient pathway in streams. Few studies have examined the consequences of variable hydrology and intermittency on decomposition in streams. In general, inputs of allochthonous organic matter into prairie streams are lower than those of forested systems, and upland prairie streams tend to retain less of this material because of frequent scouring floods and a lack of retentive structures such as large wood (Gurtz et al. 1988). Decomposition of leaf litter that enters and is retained in prairie streams is influenced by inundation patterns, with generally slower decomposition in intermittent reaches compared with perennial reaches (Hill et al. 1988). However, litter that is subjected to periodic inundation in an intermittent stream channel decomposes more rapidly than that in adjacent terrestrial habitats, because the amount of time moisture is available to decomposers is greater in the intermittent stream channels (Gurtz and Tate 1988).

Microbes inhabiting prairie streams are resilient. However, much remains to be investigated with regard to the temporal sequences of microbial recovery from flood and drying. Virtually nothing is known about microbial assemblage succession, about the detailed temporal sequences of recovery of most nutrient cycling functions, or about the routes of inoculation of microbes in stream channels. Work on Sycamore Creek, a desert stream, has documented ecosystem succession upon rewetting (see Fisher and Grimm 1991) and after a severe flood (Fisher et al. 1982). The timing and sequence of colonization was very similar in Kings Creek and Sycamore Creek, with algal assemblages reaching preflood levels within 2 weeks and with diatoms colonizing early, followed by filamentous green algae, in both streams. The results from the two intensively studied intermittent streams suggest that the ecosystem function and response to disturbance of open-canopy intermittent streams may be broadly similar across biomes. Further research on additional comparable systems is required to verify this speculation.

Macroinvertebrates

Within a week of resumed flow or after a very intense flood, macroinvertebrates reappear in prairie streams (Fritz 1997). How do these animals get there? Are they different from the inhabitants of more permanent waters? How long does it take the assemblage to completely recover from the disturbance?

The first colonists in prairie streams following dry periods are those that survived in refugia such as upstream permanent pools and subsurface water (Miller and Golladay 1996, Fritz and Dodds 2002, Boulton 2003). These survivors and initial colonists are followed by taxa that reproduce rapidly, such as chironomid midges that have very rapid life cycles (high somatic growth and reproductive rates) and aerial reproductive adults. After 1 or 2 months, larger invertebrates with slower life cycles, such as many stoneflies and caddisflies, move in. Hence, most initial colonization is by drift from upstream reaches, followed by deposition of eggs by aerial adults that colonize in a sequence reflecting the length of their life cycles. In general, most species found in the intermittent reaches also can be found in nearby downstream perennial reaches. Apparently few species experience a diapause in the dry sediments of intermittent streams and emerge upon wetting (Fritz and Dodds 2002), although some insects (e.g., stoneflies) have eggs and early instars that resist drying (Snellen and Stewart 1979), and crustaceans with desiccation-resistant stages were found to be important in a prairie stream in Alberta (Retallack and Clifford 1980). In intermittent streams in Oklahoma, permanent pools were an important source of colonists after a period of drying (Miller and Golladay 1996). Wetted refugia dominate recovery from drying in intermittent Australian and English streams (Boulton 2003), suggesting that the importance of such refugia is a general characteristic of intermittent streams regardless of biome.

A more complex story evolved when studying flood effects on Konza streams. A very large flood (50-year return time or greater) almost completely removed the macroinvertebrate assemblage of lower Kings Creek (fifth-order reaches) and somewhat decreased the density of communities in the upper reaches. Recovery in the downstream reach took several months (figure 4), a rate similar to that observed in the desert Sycamore Creek following a flood (Fisher et al. 1982). If there are permanent spring-fed pools upstream, smaller floods can actually increase diversity in intermittent reaches by transporting invertebrates from upstream. Thus, reach-level heterogeneity (proximity of localized spring-
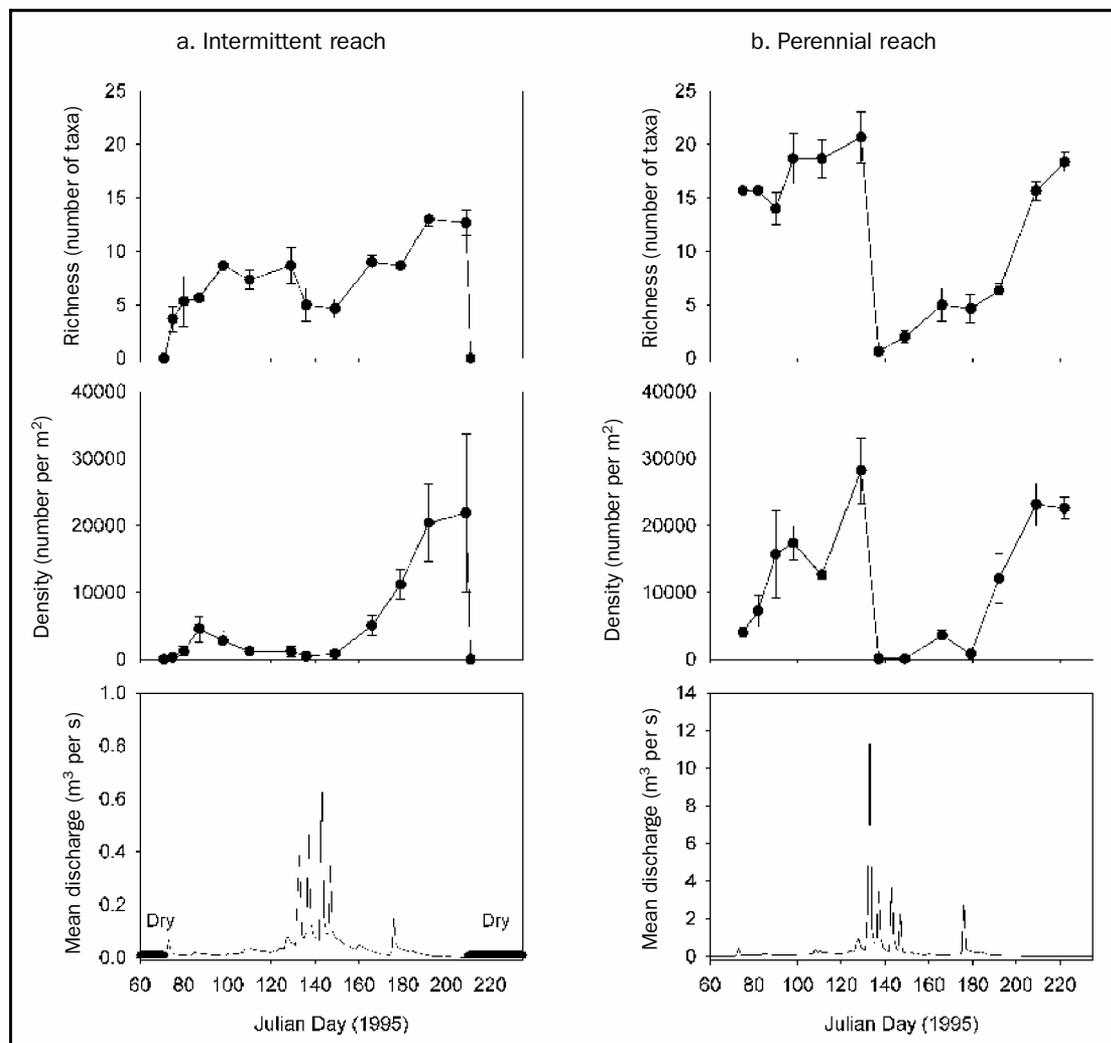
Figure 4. Response of macroinvertebrate species richness (number of taxa; top) and density (number of individuals per square meter; center) to flood and drying in (a) an intermittent reach and (b) a downstream perennial reach. Lower panels show mean daily discharge, in cubic meters per second, at the two reaches (Fritz 1997). Drying in the intermittent reach caused a drastic lowering of diversity and abundance, but recovery was fairly rapid. A large flood caused much lower species richness and density at the downstream perennial reach, whereas the same flood upstream was followed by a rapid increase in species richness and density.

fed reaches) as well as whole-watershed position can alter response to floods. Even smaller-scale heterogeneity can affect response to floods, and species associated with more stable substrata are generally more resistant to flooding. Meiofauna (invertebrates with body sizes greater than 50 micrometers but less than 1 millimeter) associated with large pieces of wood had higher resistance to flood washout than sediment-dwelling meiofauna in a North Texas prairie stream, and recovery of the sediment habitat was aided by recolonization of small invertebrates that used wood as refugia (Golladay and Hax 1995). Insects in an Oklahoma prairie stream that were associated with stable substrata (particularly the mayfly *Caenis*) were also more resistant to spates, whereas chironomid midges, which were generally associated with less

stable substrates, were highly susceptible to flooding (Miller and Golladay 1996). Although not very resistant, chironomids were very resilient because of their rapid life cycles.

Given that both flooding and drying are important disturbances that affect invertebrate communities, and that both can occur (sometimes more than once) in a single year, how do we assess their combined effects on invertebrate assemblages? Our approach was to construct an index of harshness that incorporated the frequency and intensity of a disturbance as well as its spatial characteristics. We constructed the index by adding a series of 11 scores, each on a scale from 1 (benign) to 7 (harsh). The index incorporated three annual characteristics indicative of harshness: low mean annual discharge, high number of days with no flow, and high

number of floods (events with an annual return interval greater than 1.67). In addition, four historical characteristics indicative of harshness were included: low long-term average discharge, high variance in discharge between years, high flood frequency, and low flow predictability. Finally, the index included four refugia characteristics leading to high harshness scores: greater distance to upstream permanent water, greater distance to downstream permanent water, low surface area of nearest upstream permanent habitat, and low surface area of nearest downstream permanent water. A comparison of harshness scores and of macroinvertebrate communities from streams representing a gradient of conditions on Konza revealed that both total abundance and diversity (measured as species richness) of macroinvertebrates correlated negatively with harshness scores (figure 5).

While we are beginning to understand the responses of many macroinvertebrates, including most insects, to hydrologic disturbance in prairie streams, less is known about crayfishes and many other noninsect groups. Crayfishes are a large component of the biomass and a common feature of many prairie streams, including those on Konza, and they are intimately involved in community and ecosystem processes
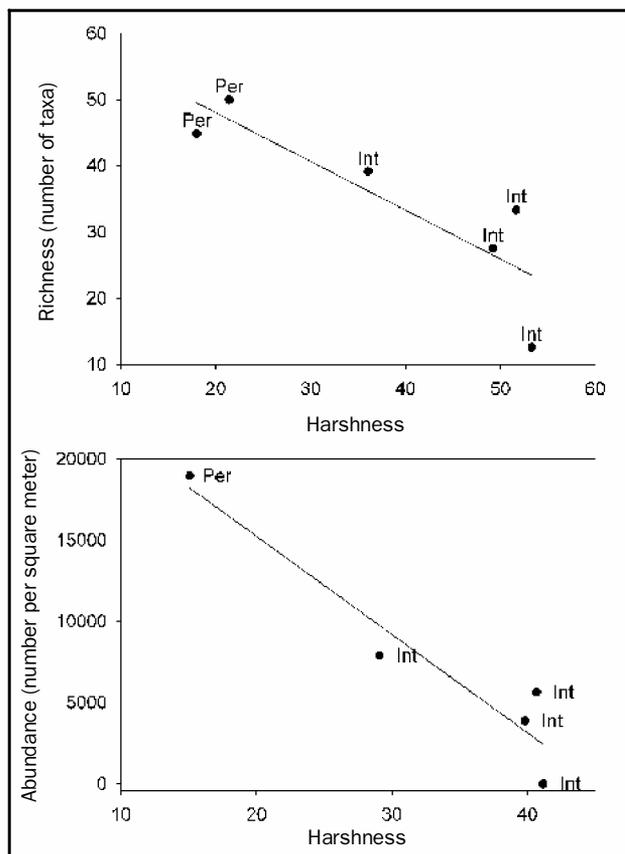
Figure 5. Total annual macroinvertebrate richness and abundance as a function of system harshness at Konza Prairie. Both relationships were significant (p < 0.05). The harshness index includes intensity of flood, drying, and distance from source of colonization (Fritz 1997). Abbreviations: Int, intermittent reaches; Per, perennial reaches.

(Evans-White et al. 2001). Their burrowing abilities could be important for avoiding hydrologic disturbances in prairie streams, but there is little quantitative information regarding crayfish resistance and resilience to flood and drying. Several Great Plains species have been found to be more abundant in intermittent reaches of streams than in nearby perennial reaches (Flinders and Magoulick 2003). Presumably, crayfishes can survive in burrows, crawl upstream, or drift downstream to colonize disturbed reaches.

Fishes

Fishes are a highly mobile component of stream ecosystems, and their abundance is regulated not only by hydrologic variability but by spatial position in the landscape (Fausch et al. 2002). Although it is hard to monitor movement patterns of prairie fishes after disturbances, most adult fishes move freely within a stream network to avoid drying pools or excessive current during flooding. These movements can range from a few meters (m) to many kilometers, depending on the location of the refuge habitat and the mobility of the fishes. For example, headwater species have been reported to move downstream during extended periods of drought (Deacon 1961, Ross et al. 1985), suggesting a retreat from harsh conditions in low-order stream reaches. Alternatively, some fishes (e.g., orangethroat darter, *Etheostoma spectabile)* have been observed along stream margins during severe flooding; from these areas, they could rapidly recolonize midchannel habitats when flows diminished. The effects of disturbances on prairie stream fish assemblages depend not only on proximity to refugia habitat (Larimore et al. 1959) but also on the fishes' ability to rapidly reproduce after the disturbance (Fausch and Bestgen 1997). Because of the high frequency of disturbances in prairie streams, fish assemblage structure is clearly linked to the spatial position and connectivity of the stream network as well as to the life history traits of each species.

Fish assemblages can be characterized by reduced abundance and dramatic changes in assemblage structure immediately after a flood (Harrell 1978). In particular, young fishes that are unable to maneuver in the increased current get washed downstream (Harvey 1987). If the stream channel is highly incised and there are few low-velocity habitats or eddies, most fishes cannot maintain themselves in the current. Because the swimming strength of a fish is proportional to its size, smaller species and juveniles may not be able to resist displacement. For example, the Topeka shiner, a federally endangered species unique to Great Plains streams, can maintain itself in current velocities of 0.3 to 0.4 m per second for over 3 hours, but it can last only up to 10 minutes in current velocities between 0.4 and 0.75 m per second (Adams et al. 2000). Thus, larger floods in less complex habitats decrease the probability that a fish will find refugia and eventually return to the stream channel as floodwaters recede.

The timing of floods can dictate the effect on fish populations (Harvey 1987). If a flood occurs early in the year,

when most fishes are spawning or have just spawned, the increased current will flush eggs and larvae from the stream. Alternatively, if a flood occurs between late summer and early spring, most fishes will have spawned, and the young will have grown to a large enough size to be efficient swimmers. Although most flooding in Great Plains streams occurs during the spring, many prairie stream fishes can rapidly colonize disturbed habitats from upstream or downstream areas and reinitiate spawning almost immediately. In Kings Creek, fish abundance was reduced after catastrophic flooding in 1995 (Fritz et al. 2002). However, these changes were undetectable by the following year (figure 6).

Flooding also can potentially increase the connectivity of stream habitats by providing fishes access to off-channel habitats that are rich in resources and by allowing movement upstream past barriers and through ephemeral reaches. For
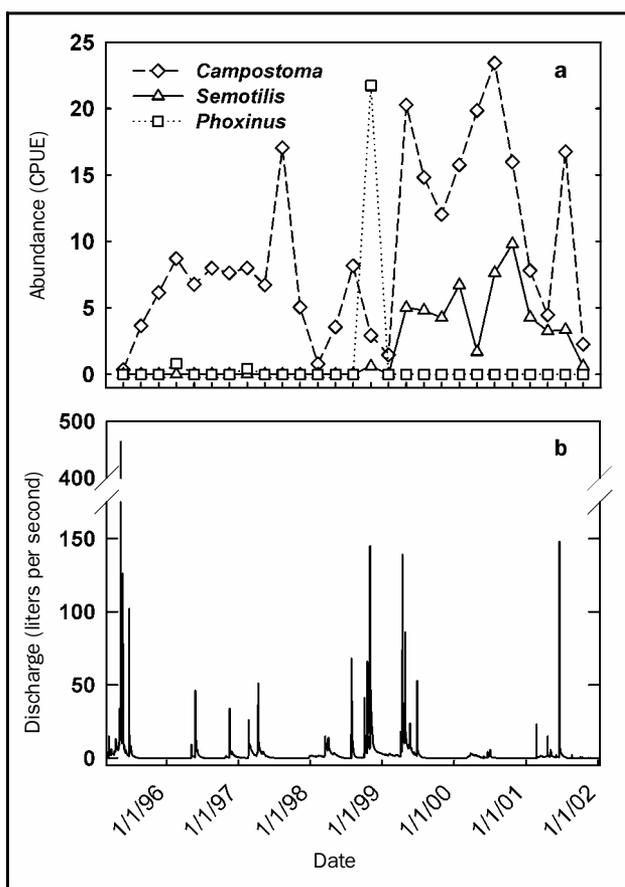
Figure 6. (a) Catch per unit effort (CPUE), or number of fish caught per minute of electrofishing, for three fish species in a permanent headwater prairie stream pool located at Konza Prairie Biological Station and (b) discharge (liters per second) in an intermittent reach immediately below the pool. This pool is isolated from lower perennial reaches during base flow. Note the reduced abundance of Campostoma following the major flood in May 1995 and the appearance and disappearance of either Phoxinus or Semotilus, in most instances coincident with a flood.

example, the fish assemblage in a spring-fed pool at Konza is separated from the downstream perennial reach by more than 6 kilometers of dry stream channel during dry periods. The arrival and disappearance of some species in this pool coincide with floods and drying, respectively (figure 6). Whereas all colonization attempts by southern redbelly dace (Phoxinus erythrogaster) failed, creek chub (Semotilus atromaculatus) colonized the site in February 1999 and August 1999 during high flows and maintained a population for the next 2 years. Although central stonerollers (Campostoma anomalum) were persistent between May 1995 and November 2002, catch rates were quite low during some sampling periods, and it is likely that colonization from other sources also allowed maintenance of these populations. Although this reach is not consistently colonized after spates, heightened flow increases the probability that fishes can colonize this habitat and is probably essential for maintaining the isolated populations that occur higher up in prairie watersheds. Metapopulation studies that included the degree of genetic isolation of source and sink populations would allow for better characterization of connectance of fish populations in intermittent stream systems.

The distribution of fishes after floods is most likely a tradeoff between resource quality and species interactions. Intermittent stream reaches are rapidly colonized by fishes seeking new resources (e.g., algae and invertebrates), perhaps as a result of a strategy to avoid competitive interactions in more densely populated permanent reaches, but also potentially as a result of random movement. Labbe and Fausch (2000) found that, although adult Arkansas darters (Etheostoma cragini) were more abundant in a permanent spring pool in an intermittent Colorado plains stream, juveniles grew faster and were relatively more abundant in warmer downstream pools. In Kings Creek, minnow species are commonly found in intermittent stream reaches in early summer after a series of floods. It is not clear whether these fishes disperse from downstream reaches or are washed down from upstream spring habitats. Regardless, these small fishes occupy reaches in the absence, or at least reduced abundance, of adult fishes. As the summer progresses and rainstorms become less frequent, these fishes often find themselves stranded in shrinking pools and sometimes become easy meals for raccoons, herons, or frogs.

The effects of drought on stream fish assemblages were recently reviewed by Matthews and Marsh-Matthews (2003). Their review pointed to gaps in current knowledge about drought effects at large spatial and temporal scales (e.g., entire river basins over decades) and about the influence of drought on ecosystem effects of fishes. Most studies have evaluated the short-term effect of drying in stream reaches, but these observations may underestimate the effects of drought, particularly if species abundances are presented as density and if reductions in habitat across larger spatial scales are not considered. Thus, to track the effects of drought or flooding, it is necessary to track abundance over time and at the appropriate scale (Fausch et al. 2002).

Studies that compare the population densities of fishes at baseflow conditions before and after drying can be used to evaluate the long-term impacts of drought on stream fishes. Long-term studies in Oklahoma suggest that most droughts have little lasting impact on the existing fish fauna and that recovery from drying by fish populations or assemblages in the region is rapid (Matthews and Marsh-Matthews 2003). Consecutive years of drought conditions may cause longer-lasting changes in fish assemblages (e.g., Deacon 1961, Matthews and Marsh-Matthews 2003), but these changes have yet to be determined.

Great Plains stream fishes are highly adapted to harsh conditions and can migrate to areas of permanent water, reproduce quickly, or withstand poor water quality in isolated pools (Matthews 1987, Labbe and Fausch 2000). Nevertheless, water withdrawals in a number of semiarid regions, including the Great Plains, have exacerbated stream drying and eliminated many spring refugia, while impoundments have restricted the movement of fishes and further fragmented populations. These alterations to prairie streams have had profound effects on the otherwise tolerant fish communities. Perhaps the most heavily affected guild of fishes consists of the large-river minnows that release semibuoyant eggs during turbid storm events (e.g., *Hybognathus, Macrhybopsis,* and several *Notropis* spp.; Cross and Moss 1987). This is regrettable, because these fishes have historically defined Great Plains river vertebrate communities.

The future of Great Plains streams

Prairie streams are under numerous pressures. It was noted more than a century ago that water abstraction from prairie rivers for irrigation affected stream organisms (Mead 1896), as did sediment runoff from cropland and oil spills (Jewell 1927). Many of the streams that once meandered through the tallgrass prairie regions of the Great Plains now are straight channels through drainage-tiled, repeatedly tilled cropland. These streams may retain sparse riparian vegetation and have sunlit headwater reaches, as did historical prairie streams (Wiley et al. 1990). However, such streams may be heavily sedimented and have very high nutrient concentrations; grassland watersheds retain sediments and nutrients much more efficiently than plowed and fertilized cropland. Fertilizers and pesticides applied in the watershed further stress what were once prairie streams with good water quality. Urbanized Great Plains streams receive treated sewage and nonpoint runoff containing oil and pesticides.

As a result of these impacts, homogeneous substrata and channelized streams no longer provide refugia from flood and drying. It may be possible to protect parts of watersheds and conserve characteristic terrestrial prairie remnants, but it is more difficult to protect entire watersheds encompassing healthy prairie streams or the aquifers that supply them. For example, a watershed that is dominated by row-crop agriculture may cause substantial sedimentation and eutrophication of downstream reaches. Given the importance of downstream refugia in permanent reaches and in small upstream spring-fed pools, particularly for resistance and recovery from drying, it may be necessary to protect entire watersheds containing up to fourth- or fifth-order stream channels, where perennial waters are most abundant. However, drainage basin area increases exponentially with stream order in prairie landscapes, and the future of prairie streams seems bleak, given the difficulties associated with protecting such large tracts of land. Research is necessary to determine how much and what parts of the watershed should be restored or protected to maintain natural stream assemblages and functions.

Humans have modified most prairie rivers and streams with dams, channelization, pollution, water abstraction, vast increases of impermeable surfaces in urbanized areas, and other watershed modifications. These alterations have had a substantial negative impact on a diverse fish fauna (Cross et al. 1985, Rabeni 1996). They disrupt the connectivity of river systems, alter flooding regimes, increase or decrease sediment loads, decrease connection with riparian flood zones, and alter the food webs of the Great Plains rivers. Preservation of fish assemblages associated with these rivers will require not only that watersheds be linked to in-stream conditions but also that managers, scientists, and policymakers "regard a stream as an interconnected system with component parts of channel, riparian, headwaters, and floodplain and strive to achieve a measure of conservation of all these elements" (Rabeni 1996).

Great Plains streams are often in areas where agriculture appropriates all the water from the stream and river channels. For example, heavy use of the Ogallala–High Plains aquifer in the Great Plains has moved the water table down deep enough that many streams that used to flow are now dry much of the year (i.e., they have switched from gaining stream channels to losing stream channels). The Arkansas River in Kansas provides a good example; since the 1970s, water use has led to a mostly dry channel as the river passes through watersheds that lie above the Ogallala-High Plains aquifer (figure 7). This leads to a situation in which the sewage effluent from the small city of Great Bend, Kansas, often forms the headwaters of the lower Arkansas River, and smaller side streams exist only during very wet periods. Abstraction of this kind is a common feature of grassland ecosystems of the world.

The watersheds of Great Plains streams that are not influenced by row-crop agriculture or urbanization are often maintained for cattle grazing. Unfortunately, this leads not only to the direct impacts of cattle on streams but also to the potentially greater impacts of farm ponds. These ponds provide water for cattle and mitigate flooding downstream, but they may decrease streamflow substantially by increasing evaporative losses. Furthermore, these small impoundments disrupt the connectivity of the linear landscape of streams, perhaps interfering with the natural movements of fishes and thus with the recolonization of upstream reaches after drying or flooding (Fausch and Bestgen 1997). Farm ponds are typically drained by standpipes when there is moderate

flow and by a spillway during high discharge, but they do not release water during most of the year. Thus, these ponds often make it difficult to impossible for many stream species to move upstream past the impoundments. Finally, small impoundments are often stocked with piscivorous sport fishes such as largemouth bass *(Micropterus salmoides)* that do not naturally occur in small upland stream reaches and can consume native fishes. A study of the distribution of the Topeka shiner in the Flint Hills found that the presence of small impoundments in watersheds was a major correlate with the disappearance of this federally endangered fish from streams where it once occurred (Schrank et al. 2001).

We speculate that understanding the dynamics of intermittent prairie streams will take on greater importance as the effects of global climate change take hold. Predictions of global climate change include greater variability of precipitation and streamflow, and there is no better place to study the consequences of increased hydrologic variability than in prairie streams, where hydrologic variability is a way of life. The range and extent of grasslands may also increase in the future as some forested areas, subjected to increased evapotranspirative water demands as a result of increased temperatures, are replaced by grasslands. On the opposite side of the precipitation gradient, the total amount of precipitation falling on land is predicted to increase, and some of those areas now classified as shrub or desert will receive enough precipitation to become grasslands. Finally, as more species associated with prairie streams become endangered, the ability to maintain existing natural prairie streams and to restore dysfunctional streams will assume even greater urgency.
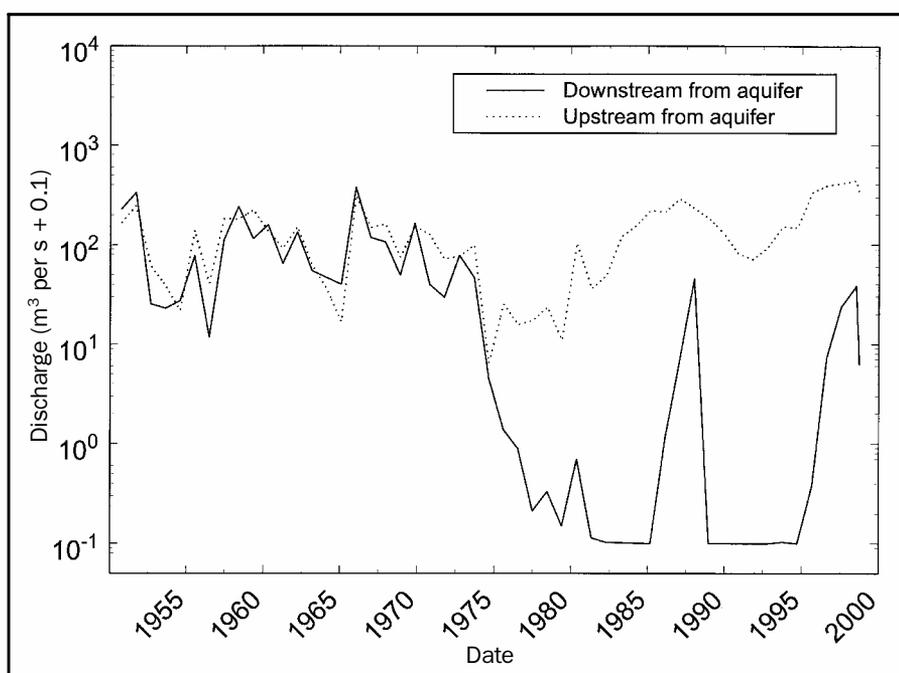
Figure 7. Discharge, in cubic meters (m³) per second, at the Arkansas River near the Kansas–Colorado border (upstream from the Ogallala–High Plains aquifer), and in central Kansas below the aquifer, since before the advent of center-pivot irrigation in the 1960s until 1999. Lowess curve-fitting (a smoothing technique in which a local regression model is fitted to each point and to the points close to it), using a 1-year moving window, was used to plot the data. A value of 0.1 m³ per second represents a dry stream channel to facilitate plotting on a logarithmic scale. Data courtesy of the US Geological Survey.

Acknowledgments

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