North American prairie streams as systems for ecological study*

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Abstract. The Great Plains and Osage Plains of interior North America included vast prairie
regions before settlement by western man. Prairie streams that exist today are ecologically interesting
for their unstable flow regimes and harsh fluctuations in environmental conditions. How much
extant prairie streams have changed from their pre-settlement conditions is unknown, but writings
of early explorers suggest that then, as now, mainstream flows were highly variable. Although
historically, some prairie rivers were turbid, the habitats of others has increased with agricultural
expansions, and many prairie streams (fifths) are known to have disappeared. Small streams in
these regions have probably changed even more; although they were clear 100 years ago, many are
now highly turbid. Differences in ecological conditions among streams of the prairie region may
be as great in those between prairie and nearby upland streams. For example, species of the southern
plains are characterized by irregular flow and substrates of small particle size, whereas streams of
the northern plains are more consistent in flow and many have cobble substrates. For some prairie
streams, published studies exist of many ecological features, such as hydrologic regimes, produc-
tivity, respiration, organic matter processing, and composition of the biota; however, such basic
features are unknown for most streams of the interior plains. Limited investigations suggest that
typical central or southern prairie streams differ from streams of nearby uplands or northern forested
regions in functional properties and biotic composition. Community structure and ecological func-
tioning of prairie streams appear strongly influenced by physiographic (inclusions resulting
from irregular flow regimes and environmental habitats), site, or major disturbances due to drought
and flood. Despite the above conditions, numerous examples suggest that prairie stream features
are also influenced by biotic interactions, including those due to multi-trophic level effects. A relatively
new approach in stream ecology applies the analysis of complex hydraulic parameters to questions
concerning distributions and adaptations of the biota. This approach may be predictable in prairie
streams, but needs modification to include the continuous lengthy periods of low or non-flow in these
systems. As a result of the discussions giving rise to this paper, numerous specific topics are suggested
for future investigations. These can be generalized in four categories: (1) basic description and
comparison of biotas, processes, or rates; (2) biotic adaptations; (3) controlling mechanical; and (4)
comparisons of prairie-stream ecosystems with those of other kinds of temperate streams in North
America. Streams of the Mississippi Embayment, Upland Highlands, the Rocky and Appalachian
mountains, and the prairies of our inland plains provide a contrasting array of study sites to a
similar latitude for consideration by ecologists deterring a broad comparative or experimental ap-
proach to questions in stream ecology.

Key words: prairie streams, historical changes, hydrologic regime, productivity, microbial pro-
testing, organic matter dynamics, biotic interactions, disturbance, physicochemical limitations, stream
biota.

The region

The Great Plains and the Osage Plains, a vast

expanse of relatively flat land reaching from the

Ozarks and Ouachita uplands to the foothills of

the Rocky Mountains (Fig. 1), included the wid-

test reach of unbroken prairie that existed in

North America two centuries ago. Geologically,

the Osage Plains are part of the Central Low-

land which covers about 1,680,000 km² in the

central United States and Canada (Hunt 1974).

The Osage Plains rise toward the west to an

altitude of approximately 800 m at the 100th

meridian, which is an approximate boundary

between the Central Lowland and the Great

Plains Physiographic Province. The Great Plains

Province, including the Alberta Plain of Canada

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(Fig. 1) includes approximately 1,490,000 km² of semiarid land (Hunt 1974), rising to an altitude of about 1,075 m at the base of the Rocky Mountains. While there are details of difference in structural geology of the Great Plains and the Central Lowlands, Hunt (1974) showed that these two formations are separated mostly by the 100th meridian, the 600-m contour, the 30-cm rainfall line, a boundary between tall and short grasses, and the eastern limit of Tallgrass formations that contain sediments eroded from the Rocky Mountains and washed onto the plains.

These interior plains are not all homogeneous geologically or biologically. For example, in many places they are not flat. The Flint Hills of eastern Kansas have relatively sharp relief, with flat caprock mesa gently grading downward into gabled slopes to cottonwood-lined streams similar to gravel streams of the Ozark Upland. In Oklahoma, the Arbuckle and Wichita Mountains contrast sharply with the prairie, and generally the topography is more undulating than the words "plains" or "prairie" suggest. Large salt flats or sand dune areas exist, and the Black Mesa in the Oklahoma panhandle provides sizable vertical relief in sandstone. These local phenomena aside, however, the interior plains are united collectively by relatively low relief, highly variable rainfall, and, with the exception of stream borders, more open grassland than forests. The forested tracts that do exist, like the "crisscrossers" of southern Kansas, central Oklahoma, and north Texas, consist of a mixture of deciduous and coniferous trees, resembling their eastern counterparts.

The central plains region is dissected by major rivers like the Missouri, Platte, Kansas, Arkansas, Cimarron, Canadian, Washita, and Red that drain generally from west to east (Fig. 2). The larger of these systems have headwaters in the eastern slopes of the Rocky Mountains or the high plains of eastern Colorado or North Texas, and roughly parallel one another en route to the Mississippi River or the Gulf of Mexico. The southern Great Plains is drained by streams of the Texas west coast, including the Trinity, Brazos, Colorado, and Pecos Rivers (Fig. 2). In Canada, the upper Great Plains are drained by the vast McKenzie, Peace, and Saskatchewan River systems.

It is relatively easy with standard references to delineate geographically this interior plains or prairie region and the major drainages thereof. Much more difficult is the task of defining a "prairie stream" as a unique type that can be discussed in the context of modern aquatic ecology. For example, cool and warm water rivers of the northern Great Plains may have higher gradient, coarse substrates, and more persistent flow than similar-sized streams farther south in Kansas, Oklahoma, or Texas (J. A. Gore, personal communication). Because of the difficulty of generalizing about prairie streams from Canada to the United States, much of this paper focuses upon streams of the central and southern plains with which I am more familiar, and which were the subject of most discussion in the Prairie Streams Workshop.

Existing conditions

Another difficulty is knowing whether or not the prairie streams that we perceive today are reasonable facsimiles of those a traveler would have found 200 years ago, or if they are mere remnants of the former systems, having been ravaged by pump, plow, and pollution. Prairie streams of the vast interior plains range in size from the large river mainstreams to tens of thousands of kilometers of intermittent or ephemeral streams that flow only during part of the year. A few years ago, I collected minnows in streams of numbers of fish is a small river in the summit another cell mouthless to some 300 species. The titi streams slightly full of water. Even this 1 ha tailed fish Great Bend, Kansas, to waist deep, 30 m at bank of streams, flows over a few red shiners mid other southwesterner and the Canadian mid course downstream, gaiters of rainfall but or Municipal water pipe aquifer. Despite tremendous streams of the plains even more unproductive: "you haven't been here a whole year", and ed by "five years of certainty among day to by normal other streams. "Stream flowing streams in riparian in late spring the moisture loss. In Marshall County, creeks seem fairly well-graveled basins, its coast are fragmented clean water is in the entire county cly. wetter well spot (Powell and Manfred creeks) lose surface. Despite the well." central and south-some generally if large stream in crenatation, a not limited in an and south most differ and terminates the note
Many prairie mainstreams, defying the popular concept that they are muddy, are actually rather clear except immediately after rains. Rivers flowing over sand, like the Niobrara or the Chippewa Rivers of southern Kansas, can be very clear, and even the North and South Canadian Rivers of Oklahoma are relatively clear at low flow. However, a few kilometers away, e.g., in the Walnut River at Winfield, Kansas, or the Washita River in southern Oklahoma, turbidity levels are very high. The Washita River, which drains erodible red soils of southwestern Oklahoma, is the most turbid river I have encountered. Similar differences in turbidity are apparent in northern prairie rivers in Montana, Wyoming, and South Dakota: the Yellowstone, Big Horn, and Tongue Rivers are clear, whereas the Powder and Cheyenne Rivers are highly turbid with quicksand bottoms (Green, personal communication).

Prairie mainstreams and creeks do not differ greatly in transparency. Dissolved solids may differ dramatically across short distances. The Red River flows in western Oklahoma across deep Permian salt deposits from which ions are leached to the surface by numerous springs and
small creeks. As a result, its salinity is higher than that of neighboring rivers, with conductivity approaching that of sea water. In these conditions only two native fish species are able to survive (Jelliffe et al. 1972). Near the town of Oscar, Oklahoma, a small creek flows with clear water about 1.8 km from its salt-springs source to the Red River. The salinity of this beautiful little creek exceeds that of sea water much of the year, and the ichthyofauna is dominated by salt-tolerant killifish. When species at high water displace the stream, fishes temporarily invade from the river, but disappear from the creek as salt concentrations return to normal (C. Hubbard, University of Texas and D. Eddy, B. Wagner, Oklahoma State University, unpublished data).

HISTORICAL PERSPECTIVE

To have a frame of reference for considering prairie streams as natural, potentially revivified systems, we need to know how much these streams now differ from their prairie state. We know that vast differences in the prairies followed settlement: fires no longer burn back encroachments of trees in some areas (Leopold 1949): agricultural activities deepened the soils and introduced many artificial chemicals into watersheds; cattle replaced the native bison as dominant grazing; and gallery forests were cut to provide firewood to lumber. In the face of such alterations, how different are present-day prairie streams in 1988 compared with those in 1879?

Metcalf (1966), reviewing studies by historians and anthropologists, suggested that depredations sufficient to depopulate the plains occurred repeatedly in prehistoric times. As early as 1800, considerable variation existed in current or depth of streams in the Kansas River basin, as suggested by Journals of Lewis and Clark (Metcalf 1966). Turbidity appears to have been quite variable. Thomas Day reported the gallery forest of the Kansas River "about a half-mile wide, but not entirely uninterrupted". Fremont found the lower Blue River in Kansas to be "a clear and handsome stream ... running with rapid current" (Metcalf 1966). Fremont also found some creeks in the region had clear water and sandy beds, but that others were dry. Metcalf (1966) noted that none of the early explorers in the Kansas River basin reported salty bottoms, although several mentioned sand or quicksand. Metcalf summarized that "the Kansas River and its larger tributaries have long been subject to fluctuation in amount of discharge. There seems also to have been considerable fluctuation in the past, as now, in the degree of turbidity, especially in the larger streams". Metcalf noted that observations by the naturalist O. P. Hay in 1883 suggested that stream turbidity was notable only in eastern parts of streams of northwest Kansas, but that in the 1900s siltation progressed farther upstream, owing to erosion attributed to agriculture. Metcalf (1966) noted depletion of numerous fish species since the time of Hay, and that certain gasteropods have become extinct in the Kansas River system in this century. Cross and Moss (1987) documented negative change in fish fauna of the Kansas prairie streams, noting that small-stream fish faunas disappeared or suffered declines first, and that in the last 30 yr even fishes generally tolerant of "big-river" conditions have declined markedly.

Isaac Cooper was a member of the Fremont expedition as it traveled across Kansas to Colorado, south through the yement Rancho Pasa of New Mexico, then eastward along the South Canadian River to Ft. Gibson, Oklahoma (Mower and Russell 1972). Of streams in the Kansas River basin (June 1845) he wrote: "we found pretty good water---there exist some fast springs along these streams and the fiercest water I ever drank was out of the spring called Big John. For the most part however, travelers have to drink rain water ... though this stream (Arkansas River) be a mountain torrent and flows from snow covered peaks, yet owing to its wide channel at this place and loose, sandy bed, there was barely sufficient water in it to flow. The sun's rays had full control over it and it was warmer than fresh milk during the day". One cannot help being impressed that this description gains much of the mainstream Arkansas River today, upriver of its conversion to the Kerr-McClellan irrigation channel by the U.S. Army Engineers.

The Smoky Hill River (Kansas) was described by Cooper as a "broad channel filled with mud and thick water ...", and, "its water is of a dusky and smoky color being well impregnated with clay & sand" (Mower and Russell 1972). In contrast, in field notes of 14 June 1978 I described the Smoky Hill River as "Clear to slightly turbid", over a boman of sand, and small gravel. Thus, in 1845, before plowing or grazing in the western plains, Smoky Hill were spart-alternately during season.

In the upper South C, the gypsum deposits are several small creeks were being springful. The River he found 'imping red clay & sand' [for much of it existed in the towns of the the other & when a surfacing the whole of the river channels of the South Canadian to Cooper reported ('the channels') upward a great of this space a small quantity of water, deeper than 2 or 3 the 'peculiarity of the the mountain streams of water that the bed of water from the mountain terrace vast beds of sand and west Oklahoma) (Mower and Russell 1972). On 3 August 1932 Lt. the Canadian River, with Arkansas, was desc. man 1941). "The whole of the stream's "whitish color, nearly clear deep". Smaller streams on 16 August 1845, 43.5 miles through a gravelly bed showed water only in prairie creeks (50 cm). Oklahoma. Whis springs (none of which to exist). On 25 August 1845, tributaries of Washita (Oklahoma, as "Many watered in the branches, whose clear rizzlies of fishes ..." No day is as clear as the then. On 27 August 1853, whirlpool of Deer Creek, which was covered with numerous trees". In 1978 I record turbid, red. On 5 December the South Canadian.

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in the western plains, some streams like the Smoky Hill were apparently highly turbid or still-laden during some periods. In the upper South Canadian River valley of the present-day Texas panhandle, Cooper found "several small creeks of good water," and "a beautiful spring." The waters of the Canadian River he found "intregnated ... strongly with red clay & sand" (Mower and Russell 1972), much as it exists today. He also wrote: "the course of the Rojo (=Canadian) is too variable; alternately windings like a serpant from one side to the other & when elevated by feshets ... overrunning the whole basin." This description of the river-channel applies very well now to the South Canadian River. At another location, Cooper reported the South Canadian River channel "upwards of a mile in width, and over the whole of this space, there was flowing but a small quantity of water in the southern side, nor deeper than 2 or 3 inches". He described the "peculiarity" of the Canadian and most of the mountain streams that flow across the prairie as the bed was well-supplied with water from the mountains, but that upon entering vast beds of sand (east Texas panhandle and west Oklahoma) it is "swallowed up" (Mower and Russell 1972).

On 3 August 1853, Lt. A. K. Whipple found the South Canadian River, 40 km above its junction with Arkansas, was about 120 m broad (Foreman 1941), "the water flows sluggishly; is of whitish color, nearly clear, and less than knee-deep". Smaller streams described by Whipple on 16 August 1853, were "but a thread, windings through a gravelly bed thirty feet in width ... showed water only in pools", much like many prairie creeks today. Slightly southwest of Purcell, Oklahoma, Whipple found numerous springs (none of which are now known to me to be active) in August 1853. Whipple described tributaries of Walnut Creek south of Purcell, Oklahoma, as "many rivulets, with crystal waters dancing in the sunlight ... several branches, whose clear depths afforded new varieties of fish...". None of Walnut Creek today is as clear as the stream Whipple described. On 27 August 1853, Whipple found "the lovely valley of Deer Creek, which bears the clear sweet waters of several tributaries to the Canadian". In 1978 I recorded this creek as "highly turbid, red". On 9 September 1853 Whipple found the South Canadian River in Roger Mills Co. (west edge of Oklahoma) not a "noble stream", but flowing in various small channels over a bed about 150 m wide, and "red with mud".

Cpt. R. D. Marcy visited the Little Wichita River (Clay Co., Texas) in May 1852 (Foreman 1937), stating that "The stream at fifteen miles above its confluence with Red River is twenty feet wide and ten inches deep, with a rapid current, the water clear and sweet". In June 1851, I described the same stream as mod- dy, with high turbidity, and a bottom of slimy mud. On 9 May 1852 Match found the Big Wichita River (Clay Co., Texas) deep, sluggish, about 50 m wide, and the water at high stage very turbid, being "heavily charged with red sedimentary matter". The Red River was 120 m wide, 2 m deep at high stage, "highly charged with a dull-red sedimentary matter, and slightly brackish to the taste". In west Oklahoma, near North Fork of River, Marcy's party often found clear springs of "cold, limpid water" (Foreman 1937), which are rare or absent in that region now.

The writings of the early explorers, describing streams in Kansas, Oklahoma, or Texas before any substantial settlement, provide us with information on physiographic characteristics of the prairie streams before the advance of agriculture and watershed modification. My overall impression is that the pre-settlement main- stream prairie rivers, like the Kansas, Canadian, or Red were in many characteristics much as they are now, with irregular or breaded flow over wide beds, and periods of high turbidity. Silt apparently increased with advent of agri- culture (Menzel et al. 1964, Metcalf 1966) and there is no doubt that changes in river main- streams have negatively affected fish faunas (Cross and Moss 1987). However, we should also consider the possibility that large-scale spates in prairie rivers with low relief and un- consolidated substrates may have frequently changed meander patterns, bedload, erosion, and suspended load conditions, both in historic and pre-historic time. Even a single 100+ yr event might result in significant changes in channel geometry, with resulting differences in suspended load or water chemistry.

The greatest discrepancy between the streams described by the early explorers and those of today seem to be in the tributaries. In the journals of Marcy, Whipple, and others,
many creeks described in the 1850s as clear or free-flowing, are today turbid, intermittent streams. The prairie streams probably show more overall impact of post-settlement alterations than do streams of surrounding uplands. However, even in rugged parts of the Ozark upland, streams have not been immune to changes in basic hydraulic regimes due to cultural modifications of watersheds. Black (1954) vividly described how clearing and conversion of Ozark hillsides to pasture can change clear perennial streams to ones flowing only half the year, and subject to extremely high discharge after rains. We can only speculate about the degree to which the biota and ecological processes in prairie streams now resemble those of the last century, but should be alert to the possibility that "adaptations" of biotic to prairie stream may have evolved in systems with characteristics or flow schedules somewhat different from those of today. It, for example, one used salinity of flow or physicochemical conditions to explain direct or fish life cycles in an explicit prairie stream, how might conclusions be altered if we knew that two centuries ago the physical characteristics or the hydrologic regime of the stream were vastly different from present?

Ecological characteristics of prairie streams

Hydrologic regimes

One important feature of streams throughout the central and southern plains is their general seasonality of flow due to common patterns in climate and geology. Although the Chaos Plains to the east are wetter than the more western Great Plains, this entire prairie region in season in rainfall and evapotranspiration and, therefore, in stream flow. Northern Great Plains rivers probably have a very different hydrograph and flow more continually than do prairie rivers in Kansas or Oklahoma (Gore, personal communication). Many other parts of North America have essentially flowing streams. The hydrograph in the west (and the Northern Great Plains rivers) is strongly correlated to snow and depth of the montane snowpack. In the north, winter precipitation is retained as snow and released to swell streams with spring thaw. In the desert Southwest, stream flows are highly seasonal; some exist only as flash floods during the late spring "monsoon" (e.g., in southern Arizona). In the Upper Highlands (Robison, 1986), streams fluctuate less than those of the prairie, but most Ozark or Cherokee streams show some seasonality, with high flows in spring-early summer.

Streams of the southern prairies have seasonal features that are somewhat like those of low tropics of both hemispheres. In lowland tropics of Panama (Zane and Rand, 1971) and southeast Asia approximately half the year is extremely wet and half very dry. In the southern plains of Vietnam slightly north of the Mekong delta, a dry period from approximately August to January desiccates small streams. Early in the new year rains begin, typically with heavy downpours late each afternoon. The previously dry countryside becomes a quagmire, and streams run full (Matthews, personal observations). In spite of the generality of tropical wet-dry season, streams of the low tropics have flow patterns that vary considerably and unpredictably among years, thus it may be difficult for stream organisms to adapt to any specific temporal pattern (B. Stangen, personal communication). Does similar low predictability apply for streams and organisms of the American plains?

Streams of the central and southern prairies of North America have a distinct wet-dry cycle, with heavy rains in spring and early summer. After mid-summer, evaporation is rapid and many prairie streams are subject to annual desiccation from late summer through winter. Much of the prairie receives rain in late summer that on average almost equals that of spring or early summer. In Tula, Oklahoma (969W latitude) all months from March to October average 7.5 cm of rainfall (U.S. Department of Agriculture, 1941). Weatherford, Oklahoma (999W latitude) averages >5 cm of precipitation April to October. For all of Oklahoma, mean precipitation for 1886 to 1958 averaged >7.6 cm monthly from April through September, with only November through February having <5 (U.S. Department of Agriculture 1941). Desiccation of prairie streams during late summer probably relates more to transpiration and evaporation due to summer heating and isolation than to actual lack of precipitation. By

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late summer, prairie soils are very dry, and little of the rain that does fall actually reaches a stream bed.

G. R. Marxolz (personal communication) suggested that understanding movement and distribution of water is the requisite first step in any synthesis of a prairie ecosystem. He envisioned the driving variables as (1) the mid-continent hydrologic regime, (2) solution processes in soil and groundwater, and (3) riparian vegetation. Elucidation of these complicated interrelationships is one of the goals of the Long Term Ecological Research (LTER) studies at Konza Prairie (Kansas). Marxolz noted that the location of tallgrass prairie coincides with the dividing line between positive and negative mean annual precipitation to evaporation values. To the east, in tallgrass prairie, there is enough water to support tree growth, but perhaps prairie wildfire was sufficiently frequent to prevent establishment of trees.

In the prairie studied by Marxolz most streams are intermittent, and water flux depends upon lateral versus downward movement of groundwater. Konza prairie has an annual water budget of 820 mm, with approximate outputs of 180 mm lost to groundwater, 450 mm evapotranspiration, and 190 mm for streamflow (Marxolz, personal communication). In the Konza Prairie four gauging weirs and many precipitation gauges facilitate an ongoing study of water flux in unburned prairies, versus those burned at varying intervals, and will soon permit assessment of effects of native bison (Marxolz, personal communication).

Advis from local vagaries in climate and streamflow, the central and southern plains are characterized by streams that are water-limited at least part of the year. The biota must be able to survive potentially harsh conditions related to highly seasonal cycles in flow, punctuated by occasional brief but extreme spates that can occur at any time of the year. Although many prairie mainstreams now have flow partially regulated by impoundments, there is still much evidence of strong seasonality of flows. In Table 5, streams relatively unaffected by any obvious disturbance include the Smoky Hill River, Walnut Creek (Kansas), Walnut Creek (Oklahoma), Beaver River in the Oklahoma panhandle, and the Canadian River. Flow differs markedly among these selected streams owing to their east-west location and overall stream size, but all show substantial increases in discharge in May-July, and decreases from August through winter.

In contrast, note flow patterns (Table 1) at three stations on the Arkansas River in west Kansas from Lakin (westernmost) to Great Bend (easternmost). At Lakin, flow is modest in the stream channel year-round. At Dodge City, the Arkansas River is essentially dry. But at Great Bend a few kilometers downstream with inputs from small tributaries it becomes a substantial stream with year-round regulated flow. The U.S. Geological Survey notes that for the Arkansas River at Dodge City, "natural flow of stream affected by transmountain diversions, storage reservoirs, power developments, groundwater withdrawals and diversions for irrigation, and return flow from irrigated areas." Clearly, in planning any studies of prairie mainstreams, investigators must take into account a myriad of cultural factors in addition to natural climate and geomorphology.

Substrate-water interactions and deep interstitial biofilm

Southern and central prairie streams may differ from stony-bottomed upland streams in the extent of soil-water interactions, or the degree to which flowing water is exchanged with deep substrate. Many prairie streams can be separated into two classes those with a primary sand substrate versus those with clay soil as the bed. Both types of substrate differ markedly from that typical of stony upland streams, although in some uplands e.g., the Ozarks, streams may trend toward sandy bottoms. (Many northern Great Plains rivers also have cobble substrates over most of their length, and thus may have more water exchange with the stream bed.) In clay-bottomed prairie streams, water has long residence time in individual pools as stream flow decreases in late summer. In isolated pools or in pools minimally connected by small trickles, a long residence time probably allows water and soil to come to chemical equilibrium. Such pools become in effect small ponds, with sharp thermal differences as much as 9-10°C from surface to bottom (Matthews, personal observation) and perhaps more lentic than lotic characteristics. Soil-water interaction
is also increased as many over highly erodible soil carry large loads of soil water column, these pass dissolved ions, and also increase their precipitant um. Thus, 1 pondulate prairie stream is a system impermeable substratum change to deep sediment streams is effectively real deep sediments, there is evidence of water and soil deeper strata. The active important in the role (Breteschno and Klement in their analysis) is the importance of virtual bottomed streams of the "Ert" no studies addressing it. In prairie streams with or in any northern peat be exchanged existent itum, and an aureus deep. Alternatively, if sand is well-packed, or if the peat is usually a sand-mud mix River, water might flow in the substratum for long opportunity for water an aureus small prairie streams in water flowing from one pass mostly through substrate of rills, algal reactions with those in water with gravel, this be an important part of that, depending upon the importance in regulating the system. (1988). Brian H. Hill (petent) Stewart's hypol lack of phosphorous from half but permitted live mean el (i.e., without dying, to live). The gravel run phosphorus from water will have more contributable to an initial than in intermittent

Productivity and nutrient

Comparing productivity and nutrient uptake, differences in

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is also increased as many prairie streams flow over highly erodible soils, and at elevated flows carry large loads of soil particles. Within the water column, these particles can interact with dissolved ions, and also adsorb algal cells and increase their phototropism from the water col-

umn. Thus, I postulate that a clay-bottomed prairie stream is a system in which a relatively impermeable substrate minimizes water ex-

tinction to deep sediments. If the water in these streams is effectively sealed from exchange with deep sediments, there is less potential impor-
tance of water and biotic exchange with the deeper strata. The active biofilms that may be important deep in substrates of stony streams (Breznick and Klemens 1986) may be of min-

imal importance or virtually nonexistent in clay-

bottomed streams of the prairies, but I know of no
studies addressing this question.

In prairie streams with shifting sand substrata or in stony northern prairie streams, water might be exchanged extensively through the substrat-

um, and an active deep peat moss layer could exist. Alternatively, if sand particles are small and well-packed, or if the substratum is character-

istically a sand-mud mixture, as in the Canadian Prairies, water might flow only minimally through the substratum for long distances. One other opportunity for water-substrate interaction in small prairie streams is the situation in which water flowing from one perchpool to another passes mostly through gravel or gravel-hend substrata of riffles, allowing time for chemical reactions with those substrata. Interaction of water with gravel, particularly in riffles, may be an important part of complex interactions that, depending upon temperature, can be im-

portant in regulating stream algal diversity (Gwynne 1988). Becky H. Hill (personal communication) noted Stewart's hypothesis that gravel can "absolutely remove significant quantities of phycophorous from hard-water prairie streams", but permitted live microorganisms on the gravel-

de (i.e., without drying, thus allowing microbes to live). The gravel received up to 62% of phos-

phorus from water with a higher percent re-
moved attributable to microorganisms in peren-
nual than in intermittent streams.

Productivity and nutrients

Comparing productivity among systems is dif-

ficult, as differences in methods, time of day or

year, etc. complicate interpretations. However,

prairie streams for which net or gross primary productivity measurements exist appear to be relatively highly productive systems, or to have high rates of community metabolism. Rott et al. (1985) found high rates of primary production in streams of the southern Creek Plains, ap-

proaching that of desert streams. Hill and Gend-

ner (1987a) found two prairie systems of north

Texas with summer gross primary productivity
(CP) ranging from 0.7 to 7.1 g O₂ m⁻² d⁻¹, while

24-hr community respiration was 0.6-5.3 g O₂ m⁻² d⁻¹, and commented that these rates of community metabolism approached those for highly

productive desert streams. Noel (1985) found in a northern prairie stream that occasional

irrigation diminished (negative balance) were

near. In a Kansas prairie stream, Geleuth and

Martin (1978) found the CFP and 24-hr res-

piration ranged 0.5-1.2 and 0.5-1.8 g O₂ m⁻² d⁻¹,

respectively. My extrapolation of values from

Stewart (1987) (by multiplying by 14 assumed

hours of daylight) suggests net primary pro-

duction on algal-colonized tiles in Brier Creek,

Oklahoma of 0.7-1.7 g O₂ m⁻² d⁻¹ in midsum-

mer. In a reach of stream where our earlier stud-

ies (Power et al. 1985) had suggested rapid in-

creases in standing crop of Witches' elage, Frances Gwynne (University of Oklahoma, per-

sonal communication) found an average net primary productivity of 0.4 g O₂ m⁻² h⁻¹ at midday in full sunlight in April. For Brier Creek eelgrass covered by dense growths of Elkhorn-

um.

I am aware of little work documenting pri-

mary productivity in upland streams of the In-

terior Highlands. In one Osage stream (Benton

Park, Oklahoma), Stewart (in Matthews et al.

1985) reported that stream bottom dominated

by "flexis" of blue-green algae were highly pro-

ductive (0.6 g O₂ m⁻² h⁻¹), with productivity likely enhanced by the grazing of flocks. Very

high productivity values were found in Blue

River, Oklahoma, an upland stream of the Ar-

nuckle Mountains, but these high values re-

ported by Duft and Dornis (1966) may have

been very patchy. Overall, it is premature to
generalize about the productivity or rates of

community metabolism in prairie streams rel-

ative to those of streams at the same latitude in

the Osage or Ouachita uplands, or the Rocky

Mountains. Carefully coordinated simulta-

neous comparisons of this basic property of
stream ecosystems are needed to provide a start-
ing point for evaluation of similarities and dif-
ferences between and within such systems. Factors limiting primary productivity in prai-
rice stream systems are not well-understood. Stewart (1987) found that nutrient enrichment (N+P+K) markedly increased primary produc-
tivity in Brier Creek, Oklahoma, and that graz-
ing by fish (Campostoma anomalum) increased bio-
mass-specific primary productivity of pe-
riphyton (but reduced standing crop and pro-
ducitivity on an area basis). In central prairie
streams (Iowa), Burkholder-Creeco and Rich-
mann (1979) found that nutrient concentration
was not the factor limiting densities of sus-
pended algae. In turbid prairie streams insuff-
cient light may limit algal growth, and the shifting nature of fine-textured substrates (sands, silts) in some mainstreams probably inhibits growth of attached algae, but I know of no doc-
umentation of the latter. At low flow in the
South Canadian River (central Oklahoma), I
found dense mats of blue-green algae covering
the sand substrates, but this typically occurred
in autumn when the stream was relatively clear. I
know of no measurements of productivity from
such mats in prairie rivers. Interestingly, Campostoma anomalum, an herbivorous minnow whose diet is predominantly algae, thrives in some turbid prairie streams. For example, I have collected large numbers of this species from the Solomons River near Logan, Kansas, but I know of no one who has determined the diet of in-
dividuals from such turbid waters.

The River Contaminant Concept (Naizian et al. 1987, Yancey et al. 1980) depicts many streams as allochthonous in canopied headwaters, with coarse particulate organic matter (CPOM) in-
puts largely as leaf fall. Farther downstream, those streams become more autochthonous, as they widen and the canopy recedes, then still farther downstream the systems become het-
erotrophic if turbidity or depth inhibits pho-
synthesis. Prairie streams likely differ from
this picture in at least two ways. First, many
small hardwater prairie streams are sunlit due
to a lack of forest, while farther downstream
where flow is more commonly perennial gal-
ery forests and closed canopy prevail (or pre-
val; before settlement by western man). How-
ever, even now most prairie streams have at
least some gallery forest along their lower
reaches, largely because of the impracticality
of farming to the edge of stream banks. Secondly,
for prairie streams that depend on allochthon-
ous inputs for energy subsidies, the material
often originates from grasses rather than trees. Corte et al. (1982) showed that grasses com-
posed 57% of the direct littoral leaf input (al-
though total particulate organic matter (POM)
input was much greater in stream reaches with
gallery forests). Many prairie streams are in close
association with the tall or short grass species
of original prairie, or with pasture grasses. Grasslands rapidly accumulate detritus if they
are protected from fires, and this detritus can
affect nutrients and POM carried to the stream
by overland flow during rainstorms. Small prairie streams are probably autoch-
thonous in many cases. In Brier Creek and other small streams of south Oklahoma I have often
observed large standing crops of Spirogyra that assume a floating "rope" growth form, with in-
ternevred strands sometimes accumulating to
lengths of a meter or more. Such growths are
usually associated with shallows, attached to
cobbles or gravel of shallow pools or riffles, and
are most common in late summer or autumn when
stream flows are low. Agricultural activ-
ities such as fertilizer additions may stimulate
this condition. However, I have also seen sim-
ilar massive standing crops of attached algae in
Tennington Creek, Bryan County, Oklahoma,
which is a clear-water upland stream of the rugg-
ed Tishomingo Granite formation where ag-
icultural inputs are low relative to row-crop
areas. Autochthonous production coupled with
input of POM from grasses could form the basis
for a food web in these streams, and might min-
imize the importance of leaf litter relative to its
role in forested upland areas of North America.

Prairie streams may differ from wooded
streams in fundamental ways with respect to
nutrient inputs or recycling. Nitrogen fixation
by cyanobacteria, for example, is energy-inten-
sive and so could proceed more readily in well-
lighted streams than in streams where light is
less intense owing to canopy cover. Cultural
nutrient subsidies should not be overlooked in
assessing nutrient budgets for prairie streams,
and such subsidies probably exceed those of
more upland regions. Vast areas of former prai-
rie are now irrigated and fertilized extensively.
Additionally, a large percentage of native prai-
rie is now pasture, and pasturesl and are often
fertilized to increase growth of forage. The cal-

Microwave processing and surface
water dynamics

Microwave processing of
streamwater has been adapted
uniquely in the Great Lakes to
study contaminant transport.
For example, in the Upper Great
Lakes, numerous studies have
been conducted to assess the
transport of contaminants using
microwave processing. Recent
studies have investigated the
effects of microwave processing
on the transport of dissolved
organic carbon (DOC) in surface
waters. The research has shed
light on the complex interac-
tions between microwave pro-
cessing and surface water
properties. In summary, these
studies have demonstrated that
microwave processing can
significantly alter the composi-
tion of dissolved organic car-
bon in surface waters, which
could have implications for
contaminant transport and
biogeochemical cycling. The
results of these studies sug-
gest that microwave processing
may be a useful tool for
studying contaminant transport
in surface waters.
Microbial processing and organic matter dynamics

Microbial processing of materials may also be uniquely adapted in grasslands (Marzolf, personal communication). The research group at the Konza Prairie reserve in Kansas found bacteria of streams specialized for the kinds of substrates they most often find in nature. In laboratory experiments (Marzolf, personal communication, McArthur et al., 1995), bacteria isolated from streams within gallery forest grew well on leachate from bur oak leaves, and also on leachate from bluegrass grass. In contrast, bacteria isolated from grassland streams grew well on big bluestem leachates, but poorly upon bur oak leachates. Marzolf concluded that bacteria from forested stream reaches are exposed not only to tree leachates, but also to grass leachates, because grasses dominate the slopes above the gallery forest. However, bacteria from streams on grassy upland slopes would have no occasion to be adapted to grow on products from the oak trees. Furthermore, components of some bur oak leachates were toxic to some grassland bacteria. The bacteria in the grassy uplands may be adapted to quickly process monosaccharides, which may be the most available for short periods of time just after stormflows (Marzolf, personal communication). This line of investigation suggests that microbial populations of prairie streams may offer opportunities for research on highly specialized adaptations.

Little is known about functional responses of streams to intermittency, which is common in Great Plains (Hill and Gardner 1987b). Theoretically, system dynamics (e.g., amounts, transports, rates of processing of CPOM) will differ in intermittent streams, in which shredder organisms are likely less numerous than in perennial streams (Hill, personal communication). Recently, Hill and co-workers compared system dynamics in two intermittent Texas prairie streams. For both streams, retention was slight, as there was less than one debris dam per kilometer, and total system concentration was significantly related to discharge. Hill and Gardner (1987b) hypothesized that a lack of retention devices distinguishes prairie systems from forested upland streams which have more debris retention dams and filter-feeding macro-invertebrates, and might account for the overall higher level of system transport in prairie than in forested streams. Hooker and Marzolf (1987) and Tate and Curta (1986) found shredder insects low in abundance in prairie stream leaf-pack experiments, and that some leaves decay faster in a perennial than in intermittent prairie streams. Brown and Ricker (1962) also found low abundance of shredders in leaf-packs in an upland Ozark stream that is near the plains. Seston in the Texas and Kansas prairie streams was dominated by ultradine POM (Curta et al., 1982, Hill and Gardner 1987b). Hill (personal communication) concluded that prairie streams appear overall to be dominated by POM of smaller size classes than POM in forested streams of upland regions. Presumably, much of the processing in intermittent streams in the presence of fewer shredders is microbial, leading to small particulate size. The dominance of fine particulate organic matter (FPOM) in prairie streams may also result from FPOM inputs by bank erosion, wind deposition, and overland runoff (Curta et al., 1982, Hill and Gardner 1987b). Hill and Gardner (1987b) also reported that periphyton is a dominant source of POM in some prairie streams. Hill (1980) found in small tributaries of a fourth-order, intermittent Texas stream that litter from grasses and leaves dominated the POM, whereas farther downstream tree leaves were the primary POM source. However, these allochthonous sources influenced POM dynamics rather briefly (4 mo) after which periphyton production supported the stream ecosystem. Hill et al. (1980) also examined rates of leaf decomposition in Texas prairie streams, finding slightly lower breakdown rates at intermittent than at perennial sites. Also, within the perennial stream, breakdown rates were higher at third- and fourth-order sites than at a second-order site. Hill (1988) experimented with models derived from classic stream hydraulic parameters, designed to predict organic matter dynamics for a prairie stream; based on various studies by his group in prairie streams, he concludes (personal communication) that intermittent streams have
a lower ecological stability than perennial streams.

**Biota of prairie streams**

The biota of prairie streams is relatively well described, but the degree of coverage varies with taxonomic group and among stream types. Fishes are likely the best-explored and best-known group. Early detailed investigations of fishes in prairie streams were the U.S. Army "railroad surveys" conducted in the 1850s as part of surveys from Missouri to Arkansas to the west coast, which led to major taxonomic advances (and some false paths) in the 1860s. For example, the Expedition led by Capt. Robert Merri criss west Oklahoma and Texas, en route to the west coast in 1853. Surgeons attached to these expeditions collected large numbers of plants, fishes, and vertebrates which were later described and classified by scientists at the U.S. National Museum. Exceptional summaries of zoogeography of prairie fishes are by Cross et al. (1986) and Conner and Suttkus (1986), and historic alterations of the fish fauna of the central prairies are documented by Cross and Moss (1987) and Pilger and Coase (1987). Matthews (1989) offers a more detailed comparison of habitats of numerous common prairie-stream fishes, and trout states in the region have a good to excellent book on fishes by a skilled ichthyologist. Fishes generally are more diverse in the eastern prairies, with greater species richness in streams with both upland and lowland characteristics, stony bottoms in part, and complex structural features. Richness of fish faunas is low in the western plains, where salinity (Fichet et al. 1972), lack of water (Cross 1968), or other physicochemical harshness (Matthews 1986) may exclude many fish species. Although the fishes of the prairies have been well explored and described taxonomically, there is a dearth of ecological knowledge for many prairie-stream fish communities. Some common prairie fishes offer interesting enigmas. Do Neotropical gouramy really spawn only in the midst of rapids, as suggested by Moore (1942)? Are some of the small prairie fish annuals, hatching in early summer and themselves spawning in late summer or early autumn? Cyprinella lutrensis, for example, appears to breed successfully in late summer, and general patterns in length-frequency of populations in the Canadian River suggested that these spawning individuals were young-of-year (Matthews, personal observation). Why were some C. lutrensis in this stream only 14 to 16 mm long (basal post-larvae) in January 1976? Were they in fact spawned in late autumn, just before cold weather? It is known about life-history tactics of most prairie fishes. Some of the biggest gaps in knowledge about prairie-stream fishes are in the large rivers. The fish fauna of many large, deep prairie river mainstreams needs better quantification, and the effect of impoundments upon those faunas are poorly understood. The invertebrates of many prairie streams have been described in detail (Davis 1980, Gore 1980, Weyra 1986, Morris and Maddon 1978), but the degree to which a typical prairie stream fauna differs from, say, that of upland Creek streams (Brown and Ricker 1982, Cather and Harp 1975), awaits better detail on more streams in both regions. Neel (1985) provides a highly detailed account of seasonal and annual variation in invertebrates of a small northern prairie stream. He found lower diversity of invertebrates (133 taxa) than exists in streams at lower latitudes. Prairie streams, particularly those that are intermittent, may have limited aquatic insect faunas. Brian Hill (personal communication) found only about 1-2% of the abundance of benthic invertebrates in an intermittent prairie stream relative to the number that could be expected in a perennial stream of the same size. The same factors that limit species richness of fish communities likely limit richness of invertebrate communities: lack of water, unpredictable flows, homogenous substrata, and possibly even more critical, invertebrates a predation by mud or sand bottoms in many prairie streams. Conversely a relatively rich benthos may be found in riffles of prairie streams. Finally, the invertebrate fauna of a special class of prairie streams—springs or springs—can be as rich in species as those of more upland, moist, or forested regions. In a two-year survey of 50 springs through Oklahoma, J. J. Hoover and W. B. Millground found substantial invertebrate faunas associated with springs in prairie streams (Matthews et al. 1993). Although invertebrates in prairie streams have in general been reasonably well-documented, many areas remain unexplored. New studies have focused on deep infaunal of prairie streams, or invertebrate biota (paramount) at any depth. If, as posited above, clay substrata in-
hibit water-substratum exchange, in-fact in many prairie streams may be less than in storm
upland streams (Wilmot and Hynes 1974), but
streams with unstable sand beds might be fruitful
sites for investigations of a micro-obiota.
Whitman (1979) investigated the gastropod
community of a Texas creek, and Whitman and
Clark (1982) found 2-3 ppm dissolved oxygen
as deep as 30 cm in the sand substratum of the
stream bed throughout most of the year.
Zooplankton may be abundant in prairie riv-
er mainstreams. Reppy and Roger (1982) found
relatively high densities of microcrustacea in
the Missouri River from late autumn to spring.
While drift-netting for fish eggs in the main
channel of the Red River above Lake Texoma
in April, I hoped large numbers of cladocerans in
samples. However, these collections were
made during high discharge, when some zoo-
 plankton found in river mainstreams may ac-
tually be predated in ponds or backwaters and
washed into the mainstream. William B. Rich-
tonson and Beet C. Harvey (University of Okla-
homa, personal communication) found substan-
tial numbers of microcrustacea in pools of
small prairie streams, including several taxa of
benthic microcrustacea such as Eucyclops and
Daphnia that were formerly considered to be
obligate plankton. A benthic microcrustacean
assemblage can be common both in prairie
streams (Brier Creek) and in nearly streams in
the Arbuckle or Wichita mountain ranges (W.
Richardson and B. C. Harvey, University of Okla-
homa, personal communication).
Attached algae of prairie streams are histo-
ically less well known than are fish or inver-
brates. For example, in one study of periph-
yon of eastern Oklahoma streams, Pfister et al.
(1979) reported 344 taxa, 115 of which were new
for Oklahoma. Power and Stewart (1985) found
that Cladophora and Ruppia dominat-
ed the periphyton of a south Oklahoma stream,
with attached diatoms and bluegreen algae al-
most ubiquitous as an understory. Power and
Stewart (1987) described the resistance to scour
and recolonization of the periphyton community
from spates, In this stream (Brier Creek), algae largely
recovered in three to four weeks after a major
scouring event. Matthews (personal observa-
tion) found that a similar period of time was
required for re-establishment of blue-green al-
gae from spores of dominant algae. After flood
scour, Roeder (1977) found in the Skunk River, Iowa, that planktonic algae origi-
nate primarily from the substratum, with the
dominant taxa being both benthic and
planktony assemblages, but that there is much
exchange between the two. Neel (1985) found
a substantial riffle periphyton assemblage domi-
nated by Cladophora and diatoms in a northern
prairie stream. Even primary descriptions of the
algal assemblage seem to be lacking in many
prairie streams, and temporal-spatial dynamics
of the flora of these streams is very poorly
known.

Biotic interactions
Peckarsky (1985), Stutzer (1987), and nu-
merous others have contested the importance
of abiotic and biotic dominance in stream com-
munity regulation. Stutzer et al. (1988) suggest
that biotic phenomena may dominate in pool
environments where hydraulic stress is low,
whereas abiotic factors may play a more im-
portant role in riffles (high hydraulic stress) en-
vironments. As important as abiotic phenom-
enon clearly are in many prairie streams, there
is ample evidence that biotic interactions (the
algorythm, predator-prey interactions, or com-
petition influence structure of prairie stream
communities, and strong multi-level cascading
effects among components at various trophic
levels have been documented. Power and Mat-
ches (1983), Power et al. (1985), and Matthew
et al. (1987) showed in Brier Creek that algae-
grazing minnows (Campostoma) could regulate
distribution and amount of attached algae in stream
pools. Further, piscivorous fishes (Micropterus)
strongly influenced habitat use by Campostoma,
and thus directly affected dynamics of the-stream
algae. Stewart (1987) showed that grazing by
Campostoma increased the rate of primary pro-
duction by algae per unit biomass, although
scouring of the algae by these fishes powered
net productivity per unit area. Stewart (1987)
also showed that even when algal growth was
enhanced by fertilizer additions, grazing by
Campostoma played a major role in regulating
algae production. Few studies, if any, of grazing
effects due to stream invertebrates have been
carried out in prairie streams, but I have in pro-
gress a two-year study that will include
this comparison. Further, this study will ex-
iminate effects of algae-grazing inverte-
brates, and upon a variety of system-level pro-
cesses or phenomena such as productivity,
transport of particulate organic matter, and nitrogen fixation in prairie upland streams. We have already found (Matthews et al. 1987) that some of the effects of age-grazing minnows differ between Brier Creek and upland streams of the Ozark Mountains, and suspect that differences in the dominant piscivore are involved (Harvey et al. 1988).

Harvey (1987) showed another example of cascading effects among multi-trophic levels in Brier Creek. In observational and manipulative experimental studies, he found that many larval fish in the stream are eaten by "medium-sized" fish: minnows and juvenile sunfish. However, largemouth bass in the creek prey upon the medium-sized fish at bay (i.e., forced them to inhabit shallow stream pool margins), larval fish were provided refuge in which they survived in greatest numbers. The bass also protected the larval fish by eliminating the threat from the fish that preyed on them. Algal growth and predator-prey control are most important in Brier Creek during relatively stable environmental conditions, and become less important during or immediately after floods or other disturbances. The Working Group at Flathead Lake discussing biotic-abiotic interactions pointed out the importance of time-scale considerations where biotic interactions are concerned. How do effects of species of droughts compare or interact with biotic interactions to determine the ultimate community structure or dynamics of community structure of prairie streams?

I know of no clear demonstrations of competition in controlled experiments in prairie streams. However, there is circumstantial evidence that interspecific competition can and may have a substantial role in producing the biotic communities we find in prairie creeks or rivers. Historically, the Arkansas River Shiner, Notropis gilardi, was restricted to the Arkansas River drainage, and the very closely related Red River Shiner, Notropis hondi, was restricted to the drainage whose name it bears. In the mid-1970s, N. hondi first appeared, apparently by accidental transnet. In the native range of N. gilardi, during the next decade, N. hondi spread rapidly through all of the range of the formerly abundant N. gilardi, which virtually disappeared from major portions of the system as N. hondi continued its invasion (Pigg 1987). The decline of N. gilardi has been so drastic that the fish has now been listed by Oklahoma as a "species of special concern." and it is rare in some parts of Kansas. While such circumstantial evidence does not "prove" that competition is rampant, and N. gilardi is disappearing in some areas not yet invaded by N. hondi (B. F. Cross, personal communication), it suggests investigations of common resource sites by these species would be useful. For all the "roughness" that we attribute to prairie-stream organisms, lack of variation and harmony with an environment to which they are adapted, and highly vulnerable to change.

Physicochemical limitations on the benthos

The biota and biotic processes of many prairie streams are regulated at least in part by physicochemical stress. Water limitations and desiccation set absolute limits of existence for fish, but some invertebrates and many algae and microbes can survive periods of drying of the stream bed. Matthews (1987) found that fish recognized a rewatered prairie stream within the spring or early summer of one year by movement from permanent pools, and that positive correlation existed between oxygen tension and depth of silts. Gies (1982) followed colonization of fish and benthic invertebrates in a new channel of the Tongue River, and Smith and Dittler (1981) evaluated time of recovery of riffle areas after a chemical discharge into a sand fall prairie stream. Many aquatic invertebrates arrive rapidly by flight, and algae and microbes may reappear in a rewatered stream by virtue of air transport as well as hydronomic resistance structures.

Prairie streams may also be stressful environments with respect to temperatures and dissolved oxygen concentrations (Matthews 1987, Matthews and Hill 1980). In the South Cana- dian River mainstem near Norman, Okla- homa, I found midsummer water temperatures up to 38°C, which appeared to restrict fish to cooler microhabitats. Matthews and Mansell (1979) showed a direct relationship between thermal and oxygen tolerance of four minnow species.
In prairie streams of the central and southern plains, physicochemical extremes are generally predictable over annual cycles based on meteorological data. If hot, low-oxygen conditions occur every year in drying stream channels, the organisms might become adapted so that these apparently stressful events are not really a disturbance. On a shorter time scale, a predictable diel cycle of stress in many prairie mainstreams and tributaries results in lowest oxygen in early morning hours, and highest temperatures in midafternoon. Again, aquatic organisms are more likely to adapt to such predictable episodes than to events that occur erratically. Leahy et al. (1989) stressed that aquatic biota of the prairies are likely adapted to allow for a certain variability about some mean measure of potential stress. Events that fall within the expected range would not constitute a disturbance, but events outside the expected range (perhaps determined by mean ± 1 SD, or some such convention) might constitute a disturbance.

Duration as well as intensity plays an important role in determining whether a short event is a "disturbance." Overall, disturbance would be an event that alters community organization or function, and for the structuring of the community. Parameters important in evaluation of a potential disturbance include intensity, frequency, duration, predictability, season, and the geomorphological setting. Measurements of the disturbance would be accomplished by evaluating recovery time for stability in levels of productivity, or stability in (or similarity to) diversity of the previous community. Although numerous authors, e.g., Ross et al. (1983) and Power and Stow (1987) have evaluated particular disturbances in prairie streams, no single study has exhaustively examined all of the parameters above with respect to a given disturbance event in a prairie stream. Ross et al. (1983) did find that recovery of a stream fish community (Brier Creek, Oklahoma) was rapid (within a year) following extreme drought.

Droughts may be a more acute disturbance in prairie streams than floods, if the droughts are prolonged. In the 1950s three to four years of extreme drought throughout the southern Great Plains were coincident with changes in some fish communities (Hubbs and Hettler 1958). Matthews (1987) noted the destruction of a number of fish species in the upper Ogallala Aquifer region of Kansas.
of a headwater fish community in two successive years due to drought. Spates, in contrast, seem to be have somewhat short-lived effects in prairie streams. I have documented (unpublished) the composition of the Brier Creek fish assemblage by snorkeling a 1-km reach eight times, year-round. Within days following a severe spate in June 1983, the distribution of adult fishes in this stream reached was similar to that before the spate, despite the physical severity of the event (which was documented by Power and Stewart 1987). Harvey (1988) made a detailed study of washout of larval fish during high discharge in Brier Creek in early summer. While flooding virtually eliminated minnow and sunfish larvae <10 mm long, adults resumed reproductive activity rapidly after the spate. In a small upland stream not far from the prairies, Gelwick (1987) found adult fish little affected by a severe autumn spate, and that recovery of fish assemblages from high-discharge effects was rapid. The macroinvertebrates may be more severely disrupted by spates. Neal (1985) found macroinvertebrates of a prairie stream largely removed by spring spates, resulting in low population densities in late spring. The critical variables are likely event duration and mobility of organisms. Fish may find short-term hydralatic refugia during spates, but have no analogous refuge in drought. Invertebrates, less mobile than fish, may lack the ability to move to hydralatic refugia during substratum-moving spates. Clearly, adaptation of life cycles of invertebrates and fish and their life-history tactics in intermittent prairie streams need to be better understood with respect to flood and drought and the physical and chemical changes during these events.

Not all phenomena that constitute disturbance are predictable. During one late summer episode of droughting, I marked for identification more than 700 sunfish, minnows, and bass that were crowding into two deep pools in a headwater reach of Brier Creek. Unfortunately, rains were delayed, the pools dried up, and all the fish died. If rain had fallen a week or two earlier than it did, many of these fish would have survived and been potential colonists for that reach of stream. Perhaps the term "stochastic" applies to some aspects of ecology of prairie streams, and perhaps not. Overall, it may be difficult in prairie streams to answer a question like, "are droughts or spates worse disturbances?" However, my overall impression is that although high discharge displaces adult fish, destroys algae and invertebrate communities, and harms immature fishes, recolonization proceeds rapidly when peak discharge passes. Drought, however, kills more individuals (at least of fish) and even after droughtwashing, reestablishment of a biota must await colonization or regrowth from dehydrated propagules. Further, drought or dewatering seems more likely to eliminate critical components of the system, such as microbes, than does high discharge. However, after even extremely severe spates in which the entire substratum moved, I have found viable algae upon gravel (e.g., within rugosities) which can rapidly re-establish (within weeks) an active flora.

Other disturbances that need consideration in prairie stream systems are human disturbance related to impoundments, agriculture, lumbering, urbanization, mining, and so forth. The impacts of agriculture (Menzel et al. 1984) are likely to be the single most prominent feature of the western culture in prairies. Slizsicki et al. (1982) describe the wide variety of hydrological control measures that have been applied to one major prairie river mainstream (Missouri River), certainly representing major disturbance from the pristine state. Effects of impoundments and other cultural perturbations upon prairie stream invertebrates are beginning to be understood (Gore 1977, 1980, 1982, Gore and Bryant 1986, Morris and Madden 1978), but in many cases changes in a given system cannot be known precisely owing to lack of pre-alteration surveys. Prairie stream impoundments may have less effect upon streams than reservoirs in montane regions. Where there are steep valleys, dams are tall, reservoirs are deep, and ephemeral releases are cold. Cold-water releases in many regions have altered stream-channels of the biota of the tailwater streams (Craig and Kemper 1987, Hoffman and Kiliambi 1971, Lillhammer and Salveste 1984, Ward and Stanford 1979). This phenomenon has occurred in some prairie regions, with effects on the biota. For example, cold-water releases from Possum Kingdom Dam in north Texas have clearly altered the nature of the typically warm Brazos River, and have created riffle habitats below the dam that unlike riffles in rivers of the Ozark uplands. Interestingly, thermal tolerance and the enzyme systems of fishes below this dam have actually changed in the stricture of the dam (Kerman and Richmond 1982). The Great Plains, numerous hypollimnetic releases have upon tailwater biota (Gore, 1982, 1987). Many stream flows are not typically not markedly altered throughout a river. Additionally, acid may regulate flow for years, many streams (for example) do not thaw the impoundment for a dam. Southwestern prairies are influenced by infiltration of stream beds, by evapotranspiration, and by cont. km 50 distance river stream reservoirs that have little impact from the hypothesis is true, is in contrast in upland rivers like the where flow is regular, and differences in the rivers in the flow from dam in the rivers of the mo. not is persistent (Gore, pers. un. Fire is a disturbance more frequent, and was historically in prairie streams. Prairie fires were to prevent encroachment of prairie. Burning of prairie as a form of disturbance is warming of soil by in- teractional surface warming. As soils are more productive or personal communication affe. inputs of water and PO4 into prairie, acidification of rivers and perturb prairie stream ecosys tem perturbations have both pro- and cons. In severe winters, ice b. event in southw. Ice accumulation in abiotic, ice cover and ice mortality of fish is. ice is complete, ice cover mortality of fish is. ice is not depleted under the ice. Gore, personal observation ed thicker ice cover on.
have actually changed in the 40 years since con-
struction of the dam. (King et al., 1985, Zim-
merman and Schickmich 1981). In the northern
Great Plains, numerous reservoirs with deep
hypolimnial releases have had dramatic effects
on shallow water biota (Gore 1977, 1980). How-
ever, many reservoirs on southern prairie
streams are not typically so deep, and thus may
not markedly alter thermal characteristics of a
dstream. Additionally, although prairie reservoirs
may regulate flow for some distance down
stream, many streams (the South Canadian River
for example) do show some effect of the
impermeable flat downstream from the dam.
Southwestern prairie rivers are so influ-
enated by irrigation water into their sandy
stream beds, by evaporation, by local agricul-
ture withdrawals, and depots of water, that
100 km downstream from a typical southern prai-
ie stream reservoir the mainstream probably
has little impact from the impoundment. If this
hypothesis is true, it contrasts with conditions in
upland rivers like the White River (Arkansas)
where flow is regular, and there are detectable
differences in the river for many miles down
stream from dams in the Ozark region, or with
rivers of the more northern prairies where flow
is less persistent (Gore, personal communication).
Fire is a disturbance to streams that may be
more frequent, or was more frequent prob-
ably in prairie streams, than in many up-
lands. Prairie fires were once frequent enough
to prevent encroachment of forest onto the
prairie. Burning of prairie grass alters canopy
coverage: of streams (Gilliam et al., 1987), re-
move accumulated plant litter, enhances
weathering of soil by respiration, stimulates bac-
teria, releases soils microelements, and increases pri-
mary productivity on the burned site (Marzolf,
personal communication). All the results above
deficit the input of water, nutrients, leaves, and
other materials into prairie streams. Hence, fires
perturb prairie stream ecosystems, but the per-
turbation has both positive and negative effects.
In severe winters, ice is probably a distur-
bance even in southern prairie stream systems.
In shallow, intermittent prairie streams, com-
plete freezing eliminates fish. Even if the freeze
is incomplete, ice cover can cause substantial
mortality of fish or invertebrates as oxygen is
deployed under the ice (Johnson et al. 1982, Mat-
thew's, personal observations). Neel (1985) not-
ed thicker ice cover on northern prairie streams
at winter with frequent thaw and refreezing.
J. A. Gore (personal communication) and stu-
dents have recorded ice to thick as 0.75 m on a
Wyoming prairie creek, and developed models
to predict habitat availability under these con-
ditions.
In all the disturbance in prairie streams, the
perennial versus intermittent nature of flow in the
system needs to be taken into account, as well as
the fact that many large prairie streams (like the
Arkansas River) arise in mountains. These montane-prairie systems might be
be different from systems that arise on the
prairie. The geomorphology of the stream-chan-
nel and the print along a stream at which an
event occurs may also determine the degree of
effect, or whether an event can be called a dis-
turbance. Finally, it may be extremely impor-
tant to know whether disturbances in prairie
streams act as reset mechanisms, or if they main-
tain prairie stream communities in a more or-
less perennial state of climax.

Hydraulic approaches

Until recently, hydraulic approaches were
given very little emphasis in studies of stream
organisms and their functional responses
(Stastner and Higler 1985, 1986). Stastner et al.
(1988—see this issue) summarize many recent
advances in application of hydraulics in stream
ecology; thus, details need not be repeated here.
How well do hydraulic-based approaches to the
study of stream processes or biota relate to prai-
iej streams of the southern Great Plains? Much
of the applicability of hydraulics to ecology of
stream organisms must assume that at least dur-
ing much of the year, or in critical periods of
their life cycles. Flow is variable and poten-
tially influential. In a typical small prairie stream
with only a very small percent of total area
consisting of riffles, many organisms might be
adapted to factors other than hydraulic phe-
nomena. On the other hand, flow can be pe-
riodically dramatic in these streams (flash floods
[spurs], rapid stage rise), such that to persist,
organisms may need to be highly flow-adapted
as organisms are in perennial streams.
Stastner suggested (personal communication)
that the hydraulic patterns that we are critical
to understand (form or fish) in streams with sub-
stantial flow might be of key importance in many
streams of the North American prairies, de-
pending upon whether they are permanent, in-
termittent (but flowing more than 20% of the
time), or ephemeral (with flow rare, i.e., less
than 20% of the time). In streams with only
occasional flow, or very low flow rates like many
central or southern prairie streams, hydraulic
patterns may be critical during relatively little
of the year. In many prairie streams, particu-
larly in pools, other hydraulic patterns and/or
non-hydraulic phenomena may regulate stand-
ing crops of invertebrates and fish or their use
of microhabitats.

I suspect that "minimum flow" may not apply
in small streams of the prairie that normally
cese to flow for a significant portion of the
year. A critical factor may be length of time
between flows, as pools shrink and animals are
forced together spatially, or as quantity of habitat
fails: temperatures rise and oxygen declines.

What about animals normally in riffles, like
darters, forced into pools with predators? We
have no idea how this affects them. We also
have no idea how decreased flow, zero flow,
drought, etc. affect phenomena such as com-
petition between species. For example, in Brier
Creek how do interactions among minnow or
swirllfish species change from early spring when
flow is substantial to late summer when much
less water is available?

What kinds of models make best predictions
about hydraulic effects in prairie streams? Pred-
dictions for bends include shift distance models
(McLay 1970), benthic denny-hydraulic en-
vironment models like the Gorte-Judy habitat
models (Gorte and Judy 1981), and Stutzer's
hydraulic system models (Stutzer 1981). For
fish, at least two approaches include optimum
swim speed models and stream position-exten-
se energy gain models (Fausch 1984, Fausch
and White 1981, Trump and Legisl 1980). The
degree to which these models apply to intermit-
tent prairie streams remains unknown.

Areas for investigation

Some of the specific questions about prairie
streams that were raised during the workshop
are outlined in the preceding sections. Other
questions that were suggested by workshop
participants included the following:

(1) How different are stream biota and pro-
cesses in perennial prairie streams. In in-
termittent streams that flow 20 to 80% of
the time, and in ephemeral or "interrupt-
ed" streams that flow less than 20% of the
time, and during much of the year are dry
or exist as a series of pools?

(2) How do washout rates and retention times
differ in upland and typical prairie streams,
where debris dams are largely lacking?

(3) Does the retention time of water in prairie
stream pools (by virtue of low flows or cessation of flow) play a major role in
nutrient transfer and all organic matter
processing?

(4) How variable are nutrient inputs from
rainwater (e.g., nitrate) throughout the
Great Plains? Significant concentrations of
nitrate seem to be in free-falling rainwater
at the Konza Prairie site, but concentra-
tions are less in parts of Oklahoma; com-
parative studies seem needed.

(5) Can hydraulic parameters, geomorphol-
ogy, and physicochemical measurements be
incorporated into a useful hierarchic
of prairie stream classification that includes
variables like slope, channel morphome-
try, stream density, etc., to facilitate broad
comparisons within and among regions?

(6) Can expanded use of some of the U.S. Fish
and Wildlife, Environmental Protection
Agency, or U.S. Geological Survey systems
be helpful? How effective is a classification
based solely on mean annual discharge per
unit of drainage area, perhaps with infor-
mation on geology or rock type included?

(7) How should hydraulic parameters be in-
cluded in stream classification schemes?

(8) How do precipitation-dominated versus
rock-dominated systems (e.g., in Rocky
Mountains, with nutrient limitations) dif-
er?

(9) How do biogeographic phenomena con-
trol taxonomic and functional composition
of prairie stream communities? Do bioge-
ographic influences upon distributions need
to be incorporated in schemes that seek to
classify stream communities?

(10) How important are considerations of
species diversity in prairie streams, not only
taxonomically, but from the perspective of
functional groups? What are appropriate
categories of "functional groups" for prai-
rise stream invertebrates, or fishes?

(11) Do droughts increase heterogeneity in

1988
Prairie stream systems (e.g., as goals become isolated), whereas high discharge integrates or homogenizes the whole watershed?

How do bacteria make a living in prairie streams? What regulates microbial metabolism in prairie streams?

What are the dynamics of the degradation side of metabolism in prairie streams? What are the overall dynamics of the dissolved organic carbon (DOC) component in prairie streams?

How do root exudates contribute to nutrient inputs? How do dissolved materials from roots of streamside vegetation get into stream waters?

To what extent do animals and biolimns penetrate into sediments of prairie streams, and how important are they ecologically in these systems? Do spates that scour stream beds and carry sediments result in destruction of algae and bacterial films?

The preceding view of prairie stream ecology and the Prairie Streams Workshop suggest many questions about these systems or about their role in studies of stream ecology that can be summarized in four categories: (1) basic description and comparison of biotic processes, or rates; (2) adaptations of the biota to prairie stream conditions; (3) controlling mechanisms; and (4) comparative or experimental studies of stream ecosystems within the same latitude, including streams of prairies, lowlands, and uplands.

Especially at lower trophic levels, the biota of prairie streams is poorly known. Many basic rate measurements such as input and output of nutrients or POM, productivity, or materials processing are lacking for most prairie stream systems. Therefore, within North American prairie streams much research has yet to be done at the level of initial ecological exploration. Careful documentation of community composition and of system-level rates and processes is needed if prairie streams are to be computed accurately among themselves or with streams of forested uplands. Little is known about adaptation of the biota to the harsh, fluctuating conditions that characterize many prairie streams. Numerous phenomena such as adaptation of insect life cycles or life-history traits of many fishes are virtually unstudied in prairie streams. I suggest, therefore, that many volume studies could be devoted to basic ecological description and comparison among prairie streams, or between prairie and nearby upland streams. For example, how do ecological rates and processes, or generalism of times of insects differ from sand-bounded streams of the southern Great Plains, to streams of the Ozark upland, to cold rivers of the northern prairies?

As studies in prairie streams progress beyond description or documentation, an increased focus will likely be upon mechanisms. In many cases mechanisms will not be immediately apparent from comparative studies, no matter how detailed, and experimental approaches will help clarify mechanisms that underlie community structure or system processes. There will clearly be room both for controlled laboratory research and for well-designed manipulations in the field. The strongest experiments will be those that permit clarification or quantification across several treatment levels, or that detect thresholds, interactions, or indirect effects.

Finally, although much information on prairie streams is lacking, the information that does exist supports the observation that the high degree of diversity of stream types within northern temperate latitudes rivals that seen in latitudes. Teams of investigators working at carefully selected field sites within a given temperate latitude could profitably address many of the large questions in stream ecology on a comparative measure. We can see, for example, regardless of the elevations of sites that are chosen, locations at one latitude will have many similarities in light regime, and studies that require simultaneous differences in day length would not be possible. However, for other studies in stream ecology, investigators might find it desirable to hold effects of day length at nearly similar as possible, while varying elevation, rainfall regimes, canopy cover, stream gradient, stream discharge, and the like. Such studies could include a series of field sites at one latitude in North America: streams of the coastal plains, upland streams in the Appalachians and the Ozarks, low-gradient streams of the Mississippi delta, very high-gradient streams of the Rocky Mountains or the Sierra Nevada, and streams of the prairies and plains of the North American Midwest. An array of stream types, in which investigators could attack major questions in
stream ecology, would be available and valuable.

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