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Transport, retention, and ecological significance of woody debris within a large ephemeral river

PETER J. JACOBSON[1] AND KATHRYN M. JACOBSON
Department of Biology, Grinnell College, P.O. Box 805, Grinnell, Iowa 50112 USA

PAUL L. ANGERMEIER
United States Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

DON S. CHERRY
Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

Abstract. The spatiotemporal patterns and ecological significance of the retention of coarse particulate organic matter and large woody debris have been intensively studied in perennial rivers and streams but are virtually unknown in ephemeral systems. We examined the influence of 2 features characteristic of ephemeral systems, downstream hydrologic decay and in-channel tree growth, on the distribution, transport, and retention of woody debris following a flood having a ~2.6-y recurrence interval in the ephemeral Kuiseb River in southwestern Africa. A total of 2105 pieces of wood were painted at 8 sites along the river channel to measure retention patterns. The flood had a peak discharge of 159 m^3/s at the upper end of the study area, decaying to <1 m^3/s by 200 km downstream. Downstream export of wood from marking sites totaled 59.5% ($n = 1253$). Transport distances ranged from 1 to 124 km, and 34.8% ($n = 436$) of the exported wood was recovered. Marked wood retained within marking sites was significantly longer than exported wood ($p < 0.001$, *t*-test). Once in transport, there was little correlation between wood length and distance traveled ($r = 0.11$, correlation analysis, $n = 369$). Length influenced the site of retention; material retained on debris piles was significantly longer than that stranded on channel sediments ($p < 0.001$, *t*-test). In-channel growth of *Faidherbia* trees significantly influenced wood retention; 83.7% of marked wood not moved by the flood was associated with debris piles on *Faidherbia* trees. Similarly, 65% of the exported wood retained within downstream debris piles was associated with *Faidherbia* trees. In contrast to many perennial systems, we observed a general increase in wood retention downstream, peaking in the river's lower reaches in response to hydrologic decay. Debris piles induced sediment deposition and the formation of in-channel islands. Following flood recession, debris piles and their associated sediments provided moist, organic-rich microhabitats, which were focal points for decomposition and secondary production, mimicking patterns reported from the channels of perennial streams and rivers. The ecological significance of retentive obstacles and associated organic debris is a feature common to all fluvial ecosystems, irrespective of their hydrologic regime.

Key words: wood, organic matter, hydrology, coarse particulate organic matter, fine particulate organic mater, Namibia, Namib Desert, geomorphology, sediment.

Wood is an important component of fluvial ecosystems, creating structures that have many ecological roles (Harmon et al. 1986, Maser and Sedell 1994). Accumulations of wood create habitat for aquatic and terrestrial organisms; they influence the composition of fish and invertebrate communities (Angermeier and Karr 1984, Mason 1989, Smock et al. 1989, Prochzaka et al. 1991); they create localized hotspots of energy flow and nutrient cycling (Bilby and Likens 1980, Smock et al. 1989, Hedin 1990); they influence the stability of stream channels through their effect on hydraulic resistance (Keller and Swanson 1979, Abbe and Montgomery 1996); and they provide a source of fine particulate organic matter (FPOM) to fluvial ecosystems (Ward and Aumen 1986). In sand-bed rivers, debris accumulations may provide the only stable substrates, supporting most invertebrate biomass (Benke et al. 1985).

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[1] E-mail address: jacobsop@grinnell.edu

Despite extensive research on wood accumulations, available data are strongly skewed towards small systems. The dynamics of woody debris in large rivers are little known, although several authors suggest that wood is less important in such systems (Minshall et al. 1983, Naiman et al. 1987). It is likely, however, that the low levels of wood found in most large rivers reflect extensive alterations rather than intrinsic properties (Benke 1990, Dynesius and Nilsson 1994), an assertion supported by historic accounts (Sedell and Froggatt 1984, Triska 1984, Whitney 1994).

Our understanding of wood dynamics in fluvial systems also reflects a focus on perennial systems in temperate climates. Little is known of wood dynamics within dryland rivers and streams. Minckley and Rinne (1985) provide one of the few accounts, reviewing historical observations of woody debris in the streams and rivers of the American southwest. They present evidence that, although wood was formerly abundant, extensive hydrologic alterations and intensive land-use practices (i.e., wood cutting and agricultural activity) have significantly reduced inputs of wood to desert streams. Perhaps least known of all fluvial systems are the ephemeral rivers of the world's drylands. To our knowledge, Dunkerley (1992) and Graeme and Dunkerley (1993) provide the only published information on wood in ephemeral systems, reporting on the influence of in-channel accumulations on hydraulic characteristics within streams draining the Barrier Range in western New South Wales, Australia. This lack of attention to dryland systems in general, and ephemeral rivers in particular, is remarkable considering they drain roughly 1/3 of the earth's land surface (Jacobson 1997).

Two characteristics common to ephemeral rivers are likely to determine patterns of wood transport and retention. First, ephemeral rivers experience downstream hydrologic decay because of infiltration and evaporation (Graf 1988). Retention of organic matter in ephemeral stream channels must obviously increase downstream, in direct response to decreased stream power associated with hydrologic decay. Second, ephemeral rivers and streams often have extensive growth of trees and shrubs within the active channel (Graf 1988). For example, large river red gum trees, *Eucalyptus camaldulensis*, grow within ephemeral stream channels of the Barrier Range (Graeme and Dunkerley 1993). Similarly, large ana-trees, *Faidherbia albida*, grow within ephemeral river channels of the Namib Desert in western Namibia (Jacobson et al. 1995). Stem diameters may exceed 1.5 m at breast height, and both species of trees commonly exhibit a cespitose growth form (closely spaced [<2 m] groupings of ≥2 trunks) that retains significant quantities of organic matter during floods. Such trees also provide litterfall to the channel, including leaves, fruits, and wood, which accumulate between floods.

The objective of our study was to examine transport and retention patterns of wood associated with flooding in the lower reaches of the Kuiseb River, a large ephemeral river in the Namib Desert. Our approach was 1) to determine the influence of in-channel *F. albida* and downstream hydrologic decay on the pre- and post-flood distribution of wood, 2) to determine the relative importance of specific retention mechanisms (i.e., retention on debris piles versus stranding on channel sediments), and 3) to compare and contrast the geomorphologic and ecological significance of woody debris piles in ephemeral relative to perennial river systems.

Study Site

The study site was the lower 260 km of the ~560-km-long Kuiseb River, which drains a catchment of ~14,700 km^2 in west-central Namibia, the driest country in southern Africa (Fig. 1). Mean annual rainfall exceeds 350 mm in the Kuiseb's headwaters and declines westward to near 0 at the coast. Evaporation exceeds rainfall by 7 to 200 times (Lancaster et al. 1984). As a result, surface flow occurs only in direct response to strong, summer convective storms and rapidly ends after the cessation of localized rains.

From the headwaters westward, the river has eroded a shallow, sinuous valley into Late Precambrian metasediments, largely composed of schists and quartzites, which weather to provide a large proportion of the sandy bedload transported within the lower river (Ward 1987). In its middle reaches, the river is highly confined within a deeply incised canyon, often flowing over bedrock with no alluviation because of the steep gradient (0.003–0.004 m/m) and narrow channel. This canyon broadens ~65 km from the coast. Within 20 km of the coast, low crescentic

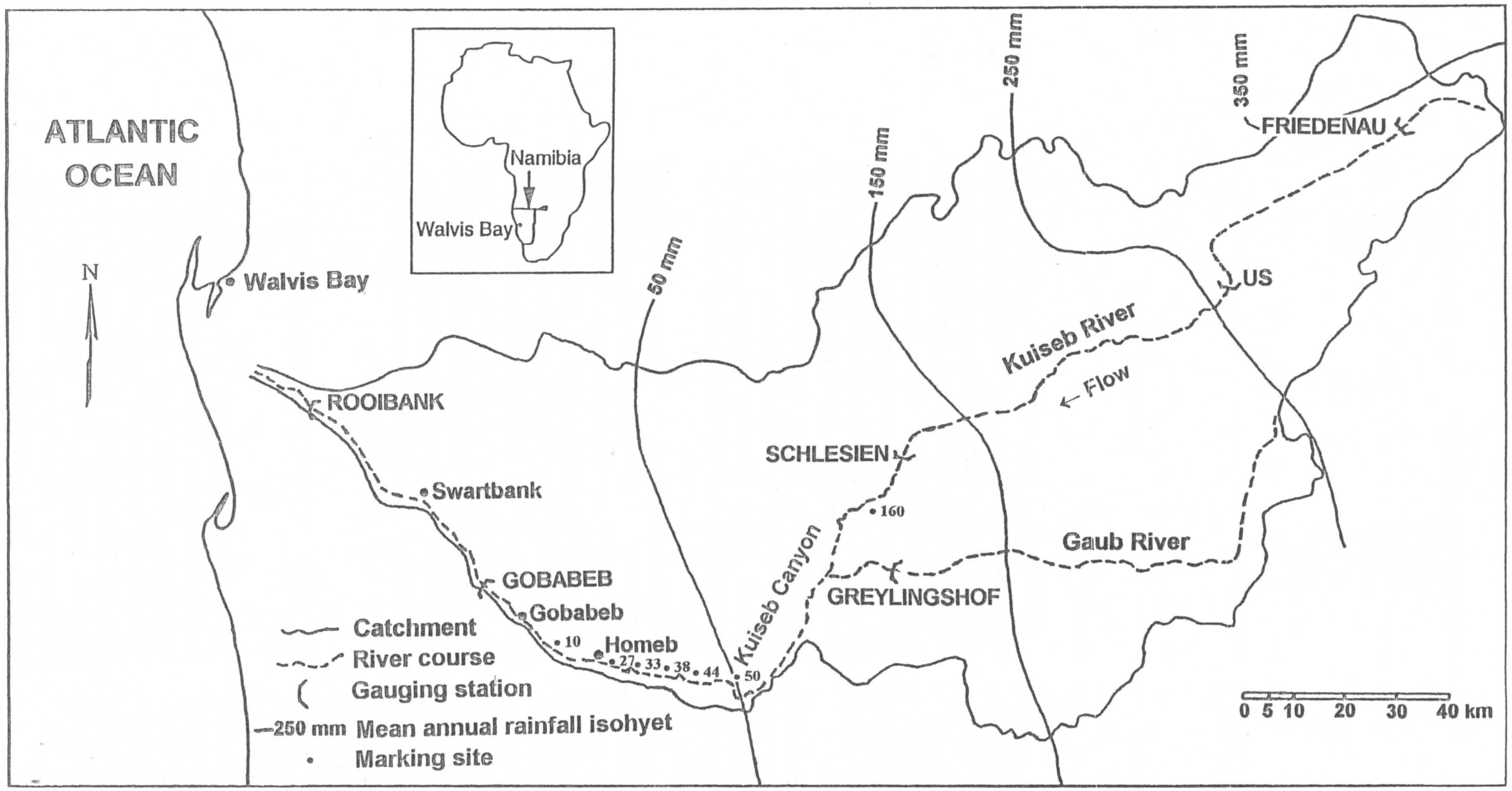

FIG. 1. Gauging stations, key geographic features, and mean annual rainfall isohyets within the Kuiseb River catchment in western Namibia. Numbers indicate wood-marking zones (km above Gobabeb).

TABLE 1. Hydrologic gauging stations within the study area and their mean annual runoff volume (MAR_V) and mean annual peak discharge (MAPD).

Station	Catchment area (km²)	Elevation (m)	Gradient (m/m)	MAR_V ($m^3 \times 10^6$)	MAPD (m^3/s)
Schlesien	6520	760	0.0040	6.59	71.9
Greylingshof	2490	720	0.0055	2.77	68.0
Confluence[a]	~9500	620	0.0035	9.51	—
Gobabeb	11,700	360	0.0030	4.65	31.9
Rooibank	14,700	120	0.0039	0.64	7.4

[a] Mean of annual sums of Schlesien and Greylingshof.

dunes cross the river, resulting in a series of poorly defined channels terminating on the coastal flats in the vicinity of Walvis Bay. Gradients below the canyon average 0.001–0.002 m/m, increasing again to >0.004 m/m within 60 km of the coast, resulting in a slightly convex longitudinal profile in the lower river. When in flood, the river's lower reaches transport a sandy bedload and a suspended load high in silt. The sandy channel sediment within the lower 150 km is largely devoid of cobble or bedrock.

The Namibian Department of Water Affairs maintains 5 automatic gauging stations along the mainstem of the Kuiseb River, and a 6th on the Kuiseb's main tributary, the Gaub River. Distinct longitudinal trends are evident among the hydrologic records from these stations (Jacobson 1997, Table 1). Mean annual runoff volume (m³) and mean annual peak discharge (m³/s) exhibit a strong curvilinear relationship with distance downstream, increasing from the headwaters to the base of the escarpment and declining westward. The study reach extends from the base of the escarpment westward to the coast. Most floods dissipate before reaching the coast.

The lower Kuiseb River has comparatively lush riparian forest, offset by the adjacent sand and rock desert (Theron et al. 1980, Seely and Griffin 1986). *Faidherbia albida* is the dominant woody species, contributing organic matter to the channel and floodplain in the form of wood and leaves, as well as dry fruits (seed pods) dropped prior to summer rains (Seely et al. 1979/80–1980/81). The tree occurs only sporadically within the escarpment and canyon reaches but extensively on downstream alluvial deposits associated with the broader channel and floodplain (Theron et al. 1980).

Methods

Discharge

Surface flow into the study reach was monitored from Schlesien and Greylingshof gauges (Fig. 1). Flow within the study reach was measured at the Gobabeb gauge, and the Rooibank gauge recorded flow at the lower end. These gauges provided a record of peak discharge (m³/s) and total flow volume (m³) for each flood event. Flow velocity (m/s) was measured during floods by timing the travel of neutrally bouyant particles. The average recurrence interval was calculated using the annual peak discharge series and the Weibull plotting formula (Gordon et al. 1992).

Annual records ($n = 14$) from the 4 gauges were analyzed to estimate the average hydrologic decay over the study reach. The mean of the sums from the annual flow volumes at the Schlesien and Greylingshof gauges was used as an estimate of the mean annual flow volume at the Kuiseb-Gaub confluence. This figure was then combined with records from the Gobabeb and Rooibank gauges to approximate the transmission loss over the study reach, expressed as a total % for the reach or %/km.

Distribution, transport, and retention of woody debris

The relative abundance and distribution of woody debris piles within the active channel were surveyed over a 95-km reach of the lower Kuiseb River, including 70 km upstream of Gobabeb and 25 km below. The number of debris piles/km were counted and each retentive structure was identified (i.e., tree stem, rock, sediment). The approximate width of active channel was measured, and valley width and channel slope were estimated at ~3-km intervals using 1:50,000 topographic maps.

Transport and retention of wood during riverflow was estimated by labeling wood with waterproof acrylic paints. Wood was marked in seven 1-km-long zones, located 10, 27, 33, 38, 44, 50, and 160 km above Gobabeb (Fig. 1). Sites were chosen for ease of access and abundance of material. All pieces within a zone were painted with a specific pattern and color without being moved. A total of 1940 pieces were marked among the 7 zones. In addition, 165 logs (>3 m long and >20 cm diameter) were selected at random from throughout the study area and individually numbered, yielding a study total of 2105 marked pieces. Marking was restricted to wood within the active channel (~2-y flood). Approximately equal numbers of stranded wood (lying free within or along the active channel) and wood retained by debris piles were marked.

Following a single ~2-d flood in January 1994, the entire channel was searched from the marking zones to the flood's end. Distance traveled from the marking zone, final position (stranded or debris pile), and the identity of the retentive structure were recorded. No search was conducted within the Kuiseb Canyon (~70–140 km upstream of Gobabeb) because of difficult access. Wood retained within the original marking site was also recorded.

Data analysis

Retention curves (sensu Speaker at al. 1984) of the material exported from 6 of the marking zones (not including 160 km) were used to calculate mean retention rates within selected sections of the study reach. Two-sample *t*-tests were used to assess differences in length (m) and transport distance (km) between retained and exported material from each of the 6 groups. The validity of assumptions of normality and equal variance between samples was assessed. Generally, data departed from normality and sample groups exhibited unequal variance. Thus, the groups were compared using the Kolmogorov-Smirnov test (Sokal and Rohlf 1995). When data were non-normal but exhibited equal variance between groups, they were compared using the Mann-Whitney U test. One-way analysis of variance (ANOVA), followed by the Tukey-Kramer multiple comparison procedure, was used to examine differences among marking zones and individual reaches within the study area (Sokal and Rohlf 1995). The relationship between particle length and transport distance was examined by simple correlation analysis. All tests were considered significant at $p < 0.05$.

Results

Discharge

The initial floodwave originated in the Gaub River catchment, and a peak of 159 m^3/s was recorded at the Greylingshof gauge, with a total flow volume of ~2.75 Mm^3 (million cubic meters). A 2nd floodwave originating within the Kuiseb catchment above the Schlesien gauge was not recorded because of instrument failure. Our observations suggested that the flood peaked at ~20 m^3/s at the Schlesien gauge, with an estimated flow volume of ~2 Mm^3. The combined flow volume estimated for the Kuiseb-Gaub confluence is thus ~4.75 Mm^3. A total of ~2.3 Mm^3 was measured at the Gobabeb gauge, representing a transmission loss of ~52% (~0.37%/km).

Transmission losses increased significantly from the Gobabeb gauge to Rooibank, where the total flow dropped to <50,000 m^3, a ~98% reduction (~1.7%/km). Peak discharge decayed similarly, dropping from 159 m^3/s at Greylingshof to 52 m^3/s at Gobabeb, a 67% reduction (~0.48%/km). The recurrence interval was ~2.6 y. From Gobabeb to Rooibank, peak discharge dropped from 52 m^3/s to ~1 m^3/s, a 98% reduction (~1.7%/km). An analysis of the annual flow record ($n = 14$) for the 3 stations revealed a similar pattern, with transmission losses from the Kuiseb-Gaub confluence to the Gobabeb gauge averaging ~52% (SD = 21%), and ~86% (SD = 12%) between the Gobabeb and Rooibank gauges. From Greylingshof to Homeb (~110 km), flow velocity at peak discharge dropped from 2.22 m/s to 1.98 m/s. From Homeb to Rooibank (~90 km), peak flow velocity dropped to 0.76 m/s.

Pre-flood wood distribution and channel morphology

The number of in-channel debris piles varied from 0 to 30 per km along the study reach (Fig.

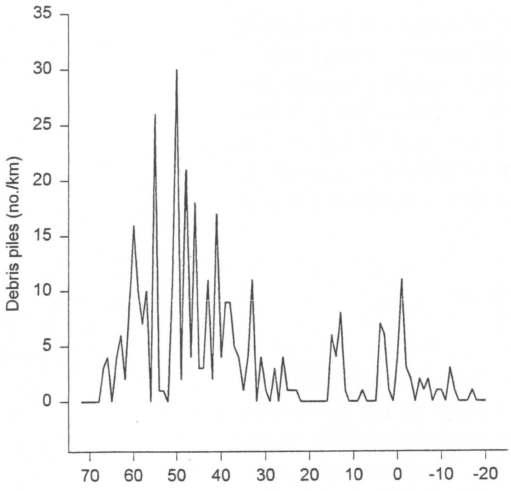

FIG. 2. The number of woody debris piles (/km) within the lower Kuiseb River.

2). Their cross-sectional area when viewed downstream ranged from <1 m² to >10 m², creating significant obstacles to transport. The distribution of debris piles was strongly influenced by the density of in-channel trees, and reaches devoid of debris piles (e.g., 16 to 22 km above Gobabeb) typically lacked in-channel trees. In contrast, peaks in debris pile abundance 12–15 km above Gobabeb and immediately above and below Gobabeb were associated with an increased tree density, relative to adjacent reaches. A total of 99% ($n = 335$) of all debris piles was retained on in-channel trees; the remaining 1% were retained on bankside rock outcrops. *Faidherbia albida* retained 97% of all debris piles, and *Tamarix usneoides* retained 2%.

Channel width ranged from <20 m in the canyon to >130 m below the Gobabeb gauge (Fig. 3). Channel width in the upper study reach is constrained within the narrow canyon (<100 m), but ~45 km above Gobabeb the valley broadens. Floodplain width increases to >1000 m ~30 km below the Gobabeb gauge. Small floods flow through a narrow (<50 m), shallow (<0.5 m) channel, but high-magnitude discharg-

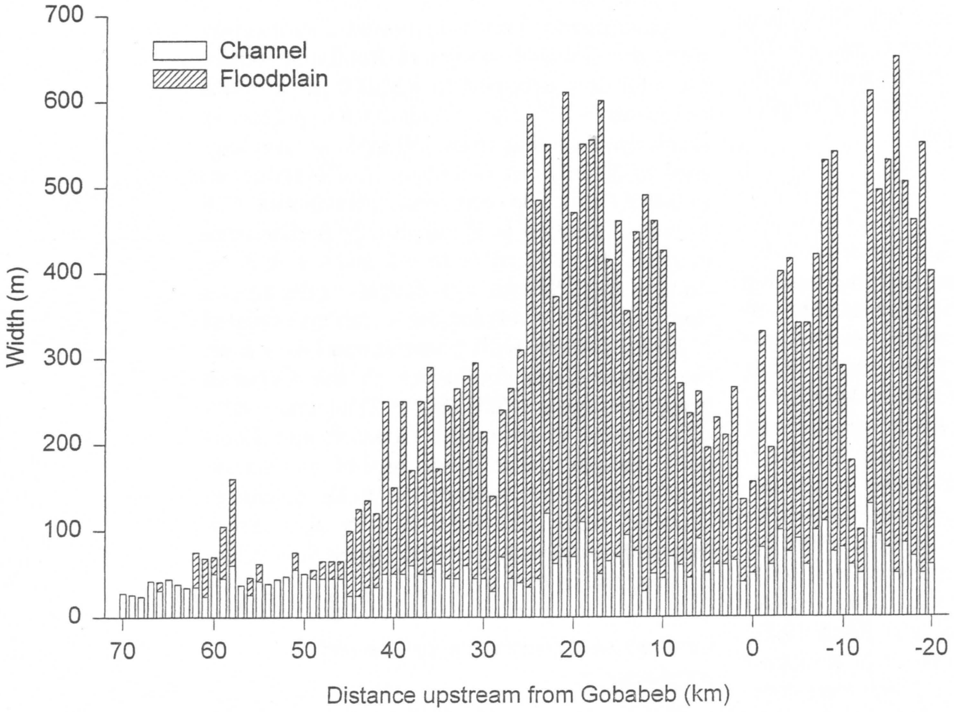

FIG. 3. Channel and floodplain width (m) downstream of the Kuiseb River canyon.

TABLE 2. Total numbers (% of total in parentheses) and positions of wood and logs marked within the study area, and the number of pieces retained or exported in response to the flood.

Zone	Marked			Retained			Exported		
Wood (km)	Total	Debris pile	Stranded	Total	Debris pile	Stranded	Total	Debris pile	Stranded
160	253	152	101	64	60	4	189	92	97
		(60.1)	(39.9)	(25.3)	(39.5)	(4.0)	(74.7)	(60.5)	(96.0)
50–10	1687	913	774	698	478	220	989	435	554
		(54.1)	(45.9)	(41.4)	(52.4)	(28.4)	(58.6)	(47.6)	(71.6)
Logs	165	70	95	90	56	34	75	14	61
		(42.4)	(57.6)	(54.5)	(80.0)	(35.8)	(45.5)	(20.0)	(64.2)
Totals	2105	1135	970	852	594	258	1253	541	712
		(53.9)	(46.1)	(40.5)	(52.3)	(26.6)	(59.5)	(47.7)	(73.4)

es expand to a width of hundreds of meters, with little increase in depth. Retention may not decrease, however, because the large woody grass *Cladoraphis spinosa* and the shrub *Pechuel-loeschea leubnitziae* are common in the channel and floodplain, and retain surficial accumulations of wood. Wood was stranded individually within the shallow channel or on the floodplain, racked up against grass or shrubs forming shallow mats.

Transport and retention of wood

Similar numbers of pile-retained (53.9%) and stranded wood (46.1%) were marked out of the total of 2105 pieces. Of this number, 1253 (59.5%) pieces were transported from the marking areas, of which 436 (34.8%) were recovered downstream (Tables 2, 3). Recovery of transported wood varied from 2.65% for material marked above the Kuiseb Canyon to 82.7% for

TABLE 3. Mean transport distances of wood and logs, and number and final position after transport for recovered wood.

Zone	Distance (km)	Total recoveries (% of total exported)	Debris pile (% of total recovered)	Stranded (% of total recovered)
Wood (km)				
160	120	5	5	0
		(2.65)	(100)	(0)
50	32	42	23	19
		(50.0)	(54.8)	(45.2)
44	27	63	33	30
		(35.4)	(52.4)	(47.6)
38	32	49	22	27
		(35.8)	(55.1)	(44.9)
33	29	83	38	45
		(33.5)	(45.8)	(54.2)
27	23	77	27	50
		(39.9)	(35.1)	(64.9)
10	13	55	27	28
		(36.9)	(49.1)	(50.9)
Logs	18	62	41	21
		(82.7)	(66.1)	(33.9)
Total		436	216	220
		(34.8)	(49.5)	(50.5)

TABLE 4. Mean length (m) of retained and exported wood and logs. Values in a row followed by different letters are statistically different at the $p < 0.05$ level.

Marking zone	Retained	Exported
Wood (km)		
160	2.8 a	1.4 b
50	2.0 a	1.7 a
44	2.4 a	1.5 b
38	2.2 a	1.4 b
33	2.3 a	1.5 b
27	2.4 a	1.3 b
10	1.6 a	1.6 a
Logs	4.7 a	4.0 b

TABLE 5. Mean length (m) of wood exported from each zone retained in a debris pile relative to that stranded on sediments. Values in a row followed by different letters are statistically different at the $p < 0.05$ level.

Marking zone (km)	Debris pile	Stranded
50	2.17 a	1.16 b
44	1.81 a	1.07 b
38	1.49 a	1.32 a
33	1.55 a	1.37 a
27	1.28 a	1.24 a
10	1.31 a	1.78 a

marked logs. Recovery averaged ~37% for the 6 zones below the canyon.

Total wood retention within the 6 zones in the 50 km above Gobabeb was 41.4%, most of which was associated with debris piles prior to the flood. Of the 698 pieces retained within the 6 zones, 68.5% were held within debris piles, reflecting their retention efficiency (Table 2). Of 913 pieces marked within debris piles, only 435 (47.6%) were exported, compared to 554 pieces (71.6%) of the stranded material. Similar patterns were observed for the zone 160 km above Gobabeb and for marked logs. Only 60.5% and 20.0% of material marked within debris piles was exported from the 160-km zone and the log sites, respectively, compared to 96.0% and 64.2% of stranded material (Table 2).

Piece length significantly influenced the probability of export. Exported wood was significantly shorter than retained wood for logs and all marking zones, excluding the 50-km and 10-km zones ($p < 0.001$) (Table 4). The lack of significance associated with the 50-km and 10-km zones may be attributable to the inadvertent marking of a large amount of stranded wood above the level reached by the 1994 flood. This bias was also reflected in the lower export of material from these 2 zones, relative to the other 4 zones.

In general, transported wood from all 6 zones below the canyon appeared to have an equal chance of being retained by a debris pile or stranding on sediment. Of the 369 pieces recovered, 46% were in piles and 54% were stranded (Table 3). Transported logs were more frequently retained in debris piles (66%) than stranded on sediment (34%). The significant difference ($p < 0.001$) in the mean length of exported logs (4.0 m) relative to woody debris (1.5 m) explains the increased log retention within debris piles (Table 4).

Wood pieces exported from the 50-km and 44-km zones and retained in debris piles were longer than those stranded on sediment ($p < 0.001$) (Table 5). However, the length of material transported from the 4 lower zones was similar in debris piles and stranded ($p > 0.05$). This difference in zones is likely a function of the significantly higher density of trees within the channel above the 38-km marking zone, relative to downstream ($p < 0.001$) (Table 6). In contrast, the mean length of material exported from the 10-km zone and stranding downstream was 1.78 m, compared to 1.31 m for material retained within debris piles. Although this difference was not statistically significant ($p > 0.05$), we would expect that the increasing influence of a broader and shallower channel combined with a decreasing discharge because of hydrologic

TABLE 6. Mean slope of the retention curves, and channel characteristics within 5 reaches of the lower Kuiseb River study area.

Reach (km)	Slope	Debris piles (/km)	Channel trees (/km)	Channel width (m)
50–36	−3.25	9.5	15.7	45
36–16	−1.14	1.6	4.2	59
16–−3	−2.63	2.7	3.2	64
−3–−10	−0.51	1.0	1.7	84
−10–−16	−3.33	0	0	78

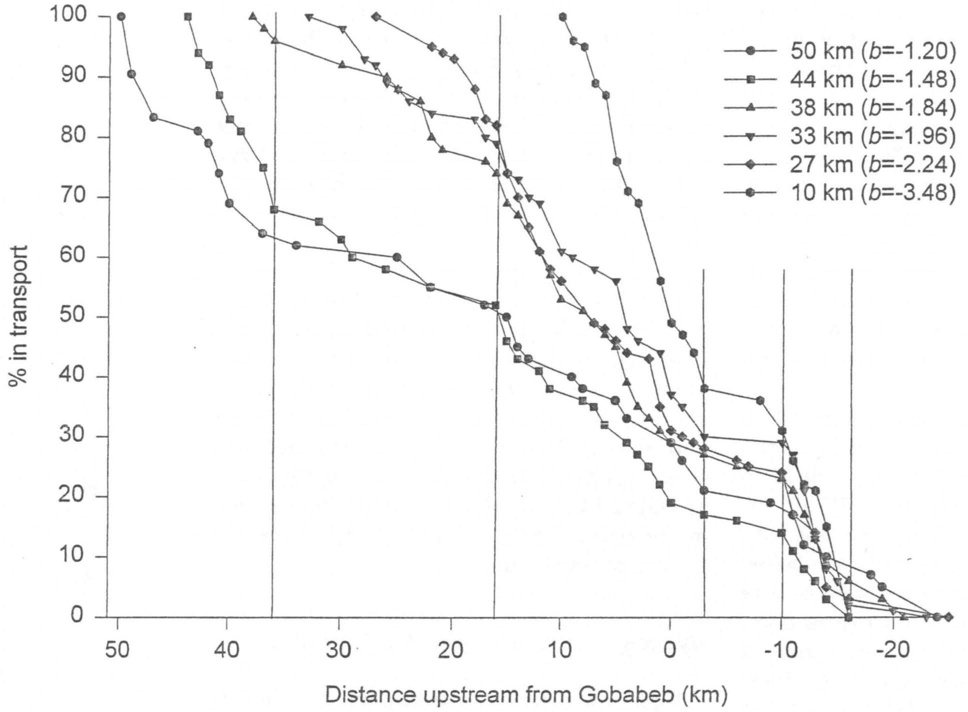

FIG. 4. Retention curves for marked wood exported from the 6 marking zones within the lower Kuiseb River (b = slope). Vertical lines delineate 5 reaches in which the slopes of individual retention curves are similar (see Table 6).

decay would increase the probability of larger pieces stranding downstream.

Transport distances for marked wood ranged from 1 to 75 km, with a median of 25 km (n = 369). Mean values for each zone ranged from 13 to 32 km, with a trend of decreasing transport distance in the lower 3 zones (Table 3). These differences were not statistically different, with the exception of the mean transport distance of wood exported from the 10-km zone, which was significantly less than that of wood exported from the 5 upstream zones ($p < 0.001$) (Table 3). Of the 62 logs recovered, transport distance averaged 18 km. The greatest distances were for 5 pieces exported from the marking zone 160 km above Gobabeb, which traveled an average of 120 km before being retained downstream of the canyon. Although piece length influenced the probability of export, once in transport there was little correlation between piece length and distance traveled ($r = 0.11$, $n = 369$).

Retention was not uniform over the length of transport for wood exported from the 6 marking zones below the canyon. Distinct variations were present in the slope of each retention curve proceeding downstream from the end of each marking zone. A comparison of the 6 retention curves revealed 5 distinct reaches in which the individual retention curves exhibited similar slopes (Fig. 4). The mean slope of the retention curves within each reach differed among the 5 reaches (ANOVA, $p < 0.001$; Table 6). However, the overall trend of all curves was a negative linear relationship between the % of wood in transport and distance downstream (r^2 = 0.95–0.98, n = 6). A downstream increase in the overall slope of the individual retention curves was also evident, increasing from −1.20 %/km for wood exported from the 50-km marking zone, to −3.48 %/km for the 10-km zone. The flood waters reached >60 km downstream of the Gobabeb gauge, but no marked wood was recovered beyond 12 km downstream of the gauge.

Several factors likely contributed to the reach-specific variation in retention. First, peak discharge dropped ~50% over the 62 km from the 50-km marking zone to the Gobabeb gauge, decreasing from ~99 m^3/s to 52 m^3/s. This decrease, combined with a gradual increase in channel width, would increase retention. Second, the density of in-channel trees and associated debris piles varied significantly ($p < 0.001$) among the 5 reaches (Table 6). The sharp drop in retention below 36 km occurred in conjunction with a significant decrease in abundance of trees and debris piles. Last, in-channel growth of *Cladoraphis spinosa* and *Pechuel-loeschea leubnitziae,* largely absent upstream, increased dramatically 10 km downstream of Gobabeb, coincident with a significant increase in retention (Table 6).

Proportions of transported wood retained on debris piles and stranded on sediment varied with distance downstream (Fig. 5). From 22 to 50 km above Gobabeb, 82% (n = 51) of the transported wood recovered was retained on debris piles. From 22 km above to 10 km below Gobabeb, the relative proportions were 44% (n = 94) of the recovered wood on debris piles, and 56% (n = 120) stranded. In the vicinity of the Gobabeb gauge, however, from 10 to 25 km downstream of Gobabeb, only 27% (n = 25) of the recovered wood was retained on debris piles, whereas 73% (n = 68) was stranded. Stranding typically occurred on the outer edges of bends and along the gently sloping banks of broad, shallow reaches.

Faidherbia albida trees were the most important retentive structure. Of 594 pieces of wood retained on debris piles within the marking zones, 83.7% (n = 497) were retained by in-channel *F. albida* trees (Table 7). Of these, 62% were retained on cespitose stems. *Faidherbia* trees retained 65% of wood exported from marking zones and cespitose stems retained 55% of this total. *Tamarix usneoides* trees retained 5.1% of the wood within the marking zones, and 19% of the exported wood. Dense thickets of the grass *C. spinosa* retained 9.9% of the wood retained on piles within the marking zones, and 8% on piles downstream. The remaining wood held within debris piles was associated with rocks, exotic plants, other trees, or the shrub *P.-l. leubnitziae* (Table 7).

Discussion

A major issue regarding the organic matter dynamics of fluvial ecosystems is the extent of within-reach processing versus export. Processing is directly linked to a stream's ability to temporarily store organic carbon within its channel, (i.e., retentiveness). Ephemeral systems provide an extreme case in which retentive structures, in combination with hydrologic decay, may eliminate export from a reach. Continued sporadic inputs may thus fuel the heterotrophic community and increase the pool of stored carbon.

Wood within the lower Kuiseb River enters the reach via upstream transport or from trees growing within it. The annual litterfall from trees within the channel and floodplain provides a regular input of organic material, including fruits, which accumulate between floods. Occasional blowdowns, combined with scour and mass wasting of banks during floods, provide additional, albeit sporadic, inputs. Once in the active channel, floods transport material to sites of retention.

Hydrologic control of transport and retention

Most wood debris in transport is carried by flotation, although several species contribute dense wood transported as bedload. The buoyancy of dry wood contributes to long transport distances. Benke and Wallace (1990) and Jones and Smock (1991) reported longer movements of wood on floodplains of low-gradient coastal streams, relative to that of in-channel material, because of drying between floods.

The most retentive sections of the study reach had either a high density of in-channel trees or a low peak discharge. Wood is efficiently retained within the lower Kuiseb River on in-channel trees and existing debris piles, or by stranding on sediment. These observations are similar to those from small streams, in which coarse particulate organic matter (CPOM) retention is related to the amount of wood present (Bilby and Likens 1980, Jones and Smock 1991, Webster et al. 1994). Jones and Smock (1991) reported that low-discharge retention in low-gradient headwater streams in coastal Virginia was characterized by passive settling onto the sediment, whereas high-discharge retention was characterized by snagging on debris dams. In-channel trees and associated debris piles are the most important retentive structures within the lower Kuiseb River. Further downstream, where both the abundance of in-channel trees and dis-

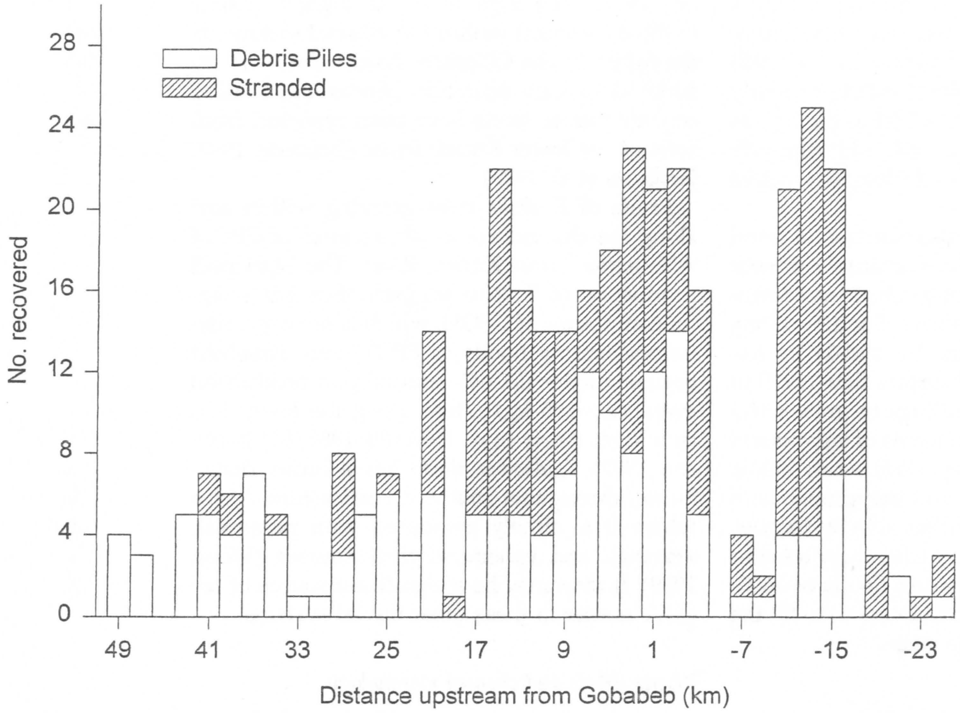

FIG. 5. Location and amount of marked wood recovered on debris piles versus channel sediments.

charge decrease markedly, stranding dominates retention.

The reach of river extending some 60 km above and 20 km below Gobabeb appears to function as a sink for woody debris. The annual flux of wood from the upstream catchment is unlikely to be transported beyond this ~80-km reach during floods of the magnitude examined in our study (~1.6-y return interval).

The decrease in abundance of in-channel trees and associated debris piles in the lower Kuiseb River is offset by an increasingly wide and shallow channel, increasing retention. However, reach retentiveness may be overwhelmed during infrequent, high-magnitude discharges (>100 m^3/s), transporting large amounts of CPOM to the lower river. Relict strand lines of CPOM occur along the lower Kuiseb River, far beyond the lateral reach of recent floods. Two such margins can be associated with the floods of 1934 and 1963, reflecting both the longitudinal and lateral extent of deposition associated with high discharge. Although we observed no large logs (>3 m) in transport at the Gobabeb gauge in the 1994 flood, >100 logs, probably associated with the 1934 and 1963 floods, are

TABLE 7. Obstacles retaining marked wood recovered from debris piles.

	Obstacles				
Recoveries	*Faidherbia*	*Faidherbia*[a]	*Tamarix*	*Cladoraphis*	Other[b]
Marking zone (n = 594)	191 (32.2%)	306 (51.5%)	30 (5.1%)	59 (9.9%)	8 (1.3%)
Downstream (n = 216)	63 (29.0%)	78 (36.0%)	41 (19.0%)	18 (8.0%)	18 (8.0%)

[a] Cespitose (≥2 stems).

[b] Includes *Pechuel-loeschea, Ficus, Acacia, Nicotiana, Datura,* and rocks.

stranded on the numerous granitic outcrops near the gauge. Observations of the magnitude and movement of woody debris in the 1963 flood are recorded in Stengel (1964). Sufficiently high discharge will export CPOM to the sea, as occurred on the Kuiseb in 1934, and regularly occurs on several more hydrologically active rivers to the north.

Alternatively, a temporary reduction in flood frequency and magnitude can favor recruitment of in-channel trees, increasing subsequent retentiveness. A period of extensive flooding along the lower Kuiseb River in the mid-1970s followed by a 4-y absence of surface flow (1979 to 1983) allowed *F. albida* seedlings to grow sufficiently to resist the erosive forces of subsequent floods. Today, the formerly wide reach below Gobabeb is split by an island overgrown with *Faidherbia* trees, lined on either side by narrow, entrenched channels. This reach is now a major retention site for CPOM during floods of sufficient magnitude (~2-y return interval) to fill the channels and flow onto the island.

Canyons, fruits, and FPOM

Our initial hypothesis regarding the retentiveness of the canyon reach was that its confined course and bedrock channel would efficiently export any introduced material, linking the upper catchment with the lower river. The recovery data demonstrated that a single flood of low magnitude (~1.3-y return interval) can export wood a distance of 120 km, nearly twice the maximum recorded in the lower river. Nonetheless, low recovery (2.7%) of wood exported from the marking site did not support our hypothesis. Inaccessibility prevented us from directly assessing retention within the canyon, and restricted our searches to the lower reach of the river.

Low recovery may also be attributable to abrasion rendering marked wood unrecognizable. The 5 pieces exported through the canyon from the 160-km zone exhibited numerous deep (≤1 cm) abrasions of the painted surfaces. This observation lends credence to the hypothesis of Sykes (1937) that the 'molar action' within narrow canyons is an important source of FPOM in desert rivers. During floods on the Colorado River, wood was physically processed to fine particles in canyon-bound reaches, prior to downstream deposition or export to the sea (Sykes 1937). The high levels of organic matter (~8% by weight) within the alluvial sediments deposited in the Colorado River delta were attributed to such upstream processing. Similar organic matter levels have been reported from soils of the lower Kuiseb River (Jacobson 1997, Jacobson et al. 1999).

Fruits of *F. albida* trees growing within and along the channel are another source of FPOM within the lower Kuiseb River. The high pod production of *F. albida* suggests that it is a significant source of CPOM, which is rapidly transformed during floods to FPOM and dissolved organic matter (DOM). Annual pod production averages ~185 kg/y/tree along the lower Kuiseb River (Seely et al. 1979/80–1980/81, Jacobson 1997). *Faidherbia albida* has a broad distribution throughout southern and eastern Africa where it is closely associated with perennial, seasonal, and ephemeral river courses (Wood 1989). It thus may be a significant source of organic matter in these other fluvial systems.

Woody debris and channel morphology

The importance of in-channel trees to wood retention is clear from the typical structure of a debris pile. Debris dams within the lower Kuiseb River typically consist of several large elements lodged against 1 or more trees within the channel, upon which successive wood is retained. Wood accumulations on in-channel trunks present a significant obstacle to flowing water, and as successively smaller pieces of wood are retained, finer material, including FPOM and sediment, accumulate within and downstream of the pile. Shields and Smith (1992) reported similar patterns from perennial streams.

Because of increased hydraulic resistance, long drapes of deposited sediment often develop downstream from debris piles. Fine-grained soils in combination with shade provided by the retaining trees create a moist microhabitat following flood recession. These drapes function as *nursery bars*, and are important sites of root sprouting by *Faidherbia* trees. If these structures are not destroyed by a high-discharge flood, they may develop into elongate islands, dividing the river course into the multiple channels commonly observed between the canyon and Gobabeb. Similar patterns have been reported from ephemeral stream channels in the Barrier

Range in Australia where *E. camaldulensis* grow along the banks and within the active channel (Dunkerley 1992, Graeme and Dunkerley 1993). These patterns also mimic the effects of the stranding of large organic debris in perennial channels where the debris may alter bank stability and initiate mid-channel bars and channel braids (Keller and Swanson 1979).

Abbe and Montgomery (1996) detailed the influence of woody debris piles on channel morphology in large alluvial (perennial) rivers, noting that woody debris jams controlled reach-level habitat diversity. Distinct jam types initiated and accelerated the formation of bars, islands, and side channels, affecting both in-channel and riparian habitat. The principal jam types paralleled patterns recorded in our study. Abbe and Montgomery (1996) observed that 'bar top jams', characterized by loose mats of woody material deposited on channel bars during recession, although common, had little effect on channel morphology, being rapidly mobilized in subsequent floods. Such unstable accumulations are abundant along the lower Kuiseb River on low banks, channel islands, and bars within the active channel. Abbe and Montgomery (1996) noted that the more stable bar apex and meander jams had the greatest effect on channel morphology. Bar apex jams reportedly formed when a large tree lodged within the channel and additional woody debris racked up against the obstruction, diverting flow to either side. Such structures created sites of sediment deposition, providing refugia for forest development in the sediment drape downstream of the structure, similar to the patterns reported here.

A reversed retention pattern

A general increase in wood retention downstream contrasts with observations in smaller, perennial systems. Lienkaemper and Swanson (1987) observed that stability of large woody debris decreased in larger channels because of increased channel width and discharge. Other researchers have noted similar trends (Minshall et al. 1983, Naiman et al. 1987). Webster et al. (1994) observed that CPOM retention in small streams depends on the probability that a piece of wood encounters an obstruction such as a rock, log, or debris pile. This probability typically decreases with increased discharge and depth downstream.

This relationship of retention to increasing downstream width, depth, and discharge does not apply in large ephemeral channels where in-channel tree growth and downstream hydrologic decay may reverse the pattern. In ephemeral rivers, hydrologic decay results in a downstream decrease in stream power, and increasing alluviation (Bull 1979). As floods travel down ephemeral rivers, increased channel width combined with decreased discharge decrease depth and increase the probability of wood retention. Alluviation may even cause convexity in the longitudinal profile of ephemeral systems. Vogel (1989) has reported convex patterns in the Namib's ephemeral rivers, and the lower Kuiseb River exhibits a convex profile (Jacobson 1997).

Reversed patterns of organic matter retention have been reported from other fluvial systems, in contrast to predictions of the river continuum concept (Vannote et al. 1980). A downstream increase in wood abundance has been reported from the Ogeechee River, a perennial blackwater system in the Coastal Plain of the southeastern United States, which has insufficient power to move wood along the channel (Benke and Wallace 1990). Historically, such patterns may have been more common prior to a century of extensive alteration to which most large, low-gradient rivers have been subjected (Sedell and Froggatt 1984, Triska 1984, Whitney 1994).

Retention and biological processing

The term 'spiraling' was introduced to describe the processing (retention, ingestion, egestion, oxidation, reingestion) of particulate organic carbon as it moved downstream (Webster and Patten 1979). In perennial rivers turnover length, the rate at which the system uses carbon relative to downstream transport, typically increases downstream in response to decreased retention efficiency (Newbold et al. 1982). Thus, headwater reaches are most important for the retention and oxidation of terrestrially fixed carbon transported into the fluvial environment. In contrast, ephemeral rivers exhibit retention peaks in the middle to lower reaches in response to hydrologic decay. In addition, spiraling is not continuous in an ephemeral river such as the Kuiseb where transport occurs in distinct pulses associated with the highly variable hydrologic regime (Jacobson 1997), and biological processing occurs between floods within a terrestrial environment. Because of water limitations that typify ephemeral river ecosystems, processing is pulsed as well. Microbial and invertebrate communities are activated by flood pulses and cease activity in response to desiccation (Shelley and Crawford 1996, Jacobson et al. 1999).

The abundance of debris piles may also influence the structure and function of biotic assemblages. For example, Bilby and Likens (1980) found that debris dams contained 75% of the standing stock of organic matter in 1st-order perennial streams, 58% in 2nd-order streams, and only 20% in 3rd-order streams. They attributed this pattern to the downstream increase in discharge, which decreased retention. Nonetheless, they reported that debris dams effectively accumulated organic material, facilitating its biological processing. These accumulations formed localized hotspots of heterotrophic activity distributed throughout the channel (e.g., Hedin 1990). Debris piles serve a similar function in ephemeral rivers where their water-retentive properties and high organic matter content support biological activity long after it has ceased in the adjacent, desiccated, bed sediment (Shelley and Crawford 1996, Jacobson et al. 1999). Although retention structures may influence decomposition and secondary production in both perennial and ephemeral rivers, their importance in creating moist microhabitats within a water-limited environment is certainly unique to ephemeral systems.

The heterogeneous distribution of wood within the Kuiseb River therefore likely influences spatial patterns of invertebrate and macrofungal richness and abundance. Such an influence is well known for the biotic assemblages within perennial rivers and streams (e.g., Benke et al. 1985, Smock et al. 1989). Similar biotic patterns occur in fungal and invertebrate communities associated with debris piles in the Namib's ephemeral rivers. For example, >80% of macrofungi (41 species) fruiting following floods in the lower Kuiseb River occur in association with woody debris piles (K. M. Jacobson, unpublished data). Polydesmid millipedes and terrestrial isopods are abundant after floods, feeding and reproducing within the moist microhabitats associated with woody debris piles, but they are typically absent from adjacent channel sediment (P. J. Jacobson, unpublished data). Although the principal abiotic constraints affecting production and community composition may differ markedly between perennial (largely aquatic) and ephemeral (largely terrestrial) systems, wood appears to play a similar role in each as both food resource and critical habitat.

Woody debris piles also influence vertebrate communities within and along river channels. Mason (1989) observed that wood deposited along rivers not only provided cover for small mammals but also retained food particles, including seeds and animal carcasses. Debris piles also served as nesting sites, providing a more moderate microclimate relative to adjacent habitats. Debris piles serve a similar function in the Kuiseb River, and we frequently observed activity of small mammals in close association with debris piles.

We believe that the frequency and magnitude of flood pulses are key determinants of decomposition and secondary production within the riparian ecosystem of the lower Kuiseb River. The retention patterns of wood and its association with in-channel trees creates a longitudinal gradient of habitat complexity within the lower 200 km of the river. Given the significance of debris piles to secondary production and community composition within other fluvial systems, we expect that further research will reveal similar patterns within the Kuiseb and other ephemeral rivers. Last, changes in the hydrologic regime of ephemeral rivers, particularly decreases in the frequency and magnitude of flooding, will have a severe negative impact on the biotic communities within these water-limited fluvial ecosystems. Such changes will not only alter organic matter transport and retention patterns, shifting the distribution and availability of key resources (i.e., food and habitat), but will also disrupt the biological and physical processing of organic matter.

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