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Hydrologic controls of physical and ecological processes in Namib Desert ephemeral rivers: Implications for conservation and management

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A B S T R A C T

Ephemeral rivers have been largely excluded from previous attempts to classify global hydrologic regimes, or to assess the role of hydrologic characteristics in regulating ecological processes and patterns in fluvial ecosystems. The Namib Desert's ephemeral rivers are amongst the most hydrologically variable fluvial systems yet described. The coefficient of variation for mean annual runoff (CV_{MAR}) among 28 stations, representing 7 Namib rivers, averages 1.55, compared with a global mean of ~0.45. Distinct curvilinear relationships exist among hydrologic characters and longitudinal position along the rivers. In particular, peak discharge, annual flow volume, and days of flow per annum exhibit a marked decline in the lower reaches of the rivers, after a mid-catchment peak. These longitudinal gradients exert strong controls over the composition of vegetation, invertebrate, and fungal communities; the availability and structure of various micro-habitats; and the rates of ecological processes such as decomposition. Flood pulses, although variable in their timing and magnitude, play a critical role in regulating organic matter transport and deposition, and primary and secondary production. Despite the tolerance of the biota to harsh and variable abiotic conditions, these ecosystems are highly sensitive to hydrologic alterations as water is acutely limiting for many organisms and ecological processes. Accordingly, alterations to flow regimes can quickly degrade ecological integrity. Managers must seek to maintain existing hydrologic regimes, a challenge amplified by increasing human water demand and changing regional climates.

1. Introduction

Hydrologic variability is widely recognized as a key ecological organizer in fluvial ecosystems (Junk et al., 1989; Poff and Ward, 1990; Vannote et al., 1980). As a result, fluvial ecosystems have been classified based upon their hydrologic characteristics (Poff, 1996). However, such classifications exhibit a hydrologic bias towards mesic systems, typically with perennial or intermittent hydrologic regimes. Ephemeral rivers, at the driest end of the hydrologic spectrum, are usually excluded. The paucity of information on ephemeral river systems and their biota is disconcerting given their abundance. Thornes (1977) observed that approximately one third of the world is characterized by arid or semi-arid climates, and thus a large proportion of the world's fluvial systems would exhibit extreme intermittent or ephemeral flow. Such systems constitute perhaps the most abundant yet least understood types of fluvial ecosystems. Yet, while geomorphologists have assiduously applied their efforts to developing an understanding of the sediment dynamics within such systems (Baker et al., 1988; Graf, 1988; Picard and High, 1973; Tooth, 2000), their ecology is comparatively less well known.

The role of the hydrologic regime in regulating ecologically-relevant processes in more mesic fluvial ecosystems is well recognized (Poff et al., 1997; Poff and Ward, 1989). Magnitude, frequency, duration, timing and rate of change of flow events are key hydrologic components, changes in which may in turn alter the structure and functioning of riverine ecosystems (Poff et al., 1997). Thus, a river's unaltered flow regime offers a logical template for restoration and management efforts. Such efforts have again, however, predominantly focused on comparatively mesic systems, and thus the challenge for ephemeral systems is to clearly establish the links between key hydrologic components and their influence on physical and ecological processes, as well as key species.

Ephemeral rivers are characterized by their absence of flow and the episodic interruption thereof by advancing floods. The rivers and their floodplains exhibit complex longitudinal, lateral, vertical and temporal gradients of water and nutrient availability, with important implications for pattern and process in the dependant biotic communities. This four-dimensional nature of fluvial ecosystems has been well described in the context of more mesic

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systems (Ward, 1989), and ecological theory developed in such systems offers an important conceptual template to guide our understanding of the functioning of ephemeral systems.

The hydrologic regime is a key factor shaping community structure within fluvial ecosystems, strongly correlated with many important habitat characteristics (Poff and Ward, 1990; Power et al., 1988). In mesic systems, water flow is known to: regulate the movement of materials, creating longitudinal, lateral, and vertical resource and disturbance gradients; determine the spatial and temporal distribution of both aquatic and riparian habitats; affect desiccation and thermal stress, as well as population dynamics and biotic interactions; and serve as a link between aquatic and terrestrial components of the fluvial system (Junk et al., 1989; Palmer et al., 1996; Stanley et al., 1997; Vannote et al., 1980; Walker et al., 1995). Thus, as the variability of stream flow increases, so too does the variability of many physical and ecological processes.

Poff and Ward (1990) observed that the long-term regime of natural environmental heterogeneity and disturbance may be considered to constitute a physical habitat template, constraining the types of species attributes appropriate for local persistence. Understanding the inherent variability of a system and the tolerances of key biotic elements would thus provide a basic framework for evaluating ecosystem response to environmental change. Jacobson (1997) examined the hydrologic regimes of the Namib's ephemeral rivers, considering their role in shaping a characteristic 'physical habitat template,' and how such a template influences their associated biota, and their sensitivity to natural and anthropogenic disturbance.

Below we review the: 1) geographic and hydrologic characteristics which typify the Namib's ephemeral rivers, 2) influence of their ephemeral hydrologic regime on physical and ecological patterns and processes, 3) response of these systems to hydrologic alterations, and accordingly, 4) the challenges ahead for their conservation and management.

2. Regional setting

2.1. The western rivers and their catchments

The driest country in southern Africa, Namibia takes its name from the coastal Namib Desert running the length of the country and extending inland ~150 km to the base of the Great Western Escarpment. A dozen large ephemeral rivers, with catchments from 2000–30,000 km^2, drain the mountainous escarpment and flow west across the plains of the Namib Desert before entering the Atlantic Ocean or ending amongst the dunes of the Central Namib Sand Sea (Fig. 1) (Jacobson et al., 1995). In total, their catchment areas encompass ~190,000 km^2, nearly a quarter of Namibia. A strong climatic gradient extends across western Namibia, and while the inland plateau may receive more than 500 mm of rain per annum, rainfall drops to near zero at the coast. Mean annual rainfall exceeds 300 mm in the headwaters of many of the rivers, a number of which originate on the inland plateau at elevations from 1500 to 2000 m. At the eastern edge of the Namib Desert at the escarpment's base, mean annual rainfall averages ~100 mm and declines westward to near zero at the coast (Jacobson et al., 1995) (Fig. 1).

Most rain falling in the catchments originates over the Indian Ocean and falls in the form of strong, convective storms during the hot summer months. While sporadic rains may begin in October and continue through May, most falls during the months of January through April. Annual evaporative losses are high throughout the catchments, particularly in the lower desert reaches. In the Central Namib, a mean pan evaporation rate of 3168 mm y^{-1} has been recorded, with yearly rates reaching as much as 4000 mm, some 200 times the mean annual rainfall (Lancaster et al., 1984). Even in the comparatively mesic headwaters of the larger catchments, potential evaporative losses exceed 3000 mm y^{-1}, more than 7 times the maximum mean annual rainfall. As a result, surface flow is in direct response to rainfall, and flow rapidly ends after the cessation of local rains. Isolated wetlands, formed where localized groundwater discharge produces short reaches of perennial surface flow, provide the only exception. Only the upper portions of the catchments, from the escarpment inland, contribute significant runoff to the lower reaches of the rivers in most years, with the hyper-arid coastal plains contributing little runoff to mainstem rivers in all but exceptionally wet years (Jacobson et al., 1995).

While there is a great deal of geological variation among catchments, most exhibit steep topographic and climatic gradients from their inland headwaters to their coastal or Namib termini. The geology of the Kuiseb River catchment has been intensively studied and provides a general physiographic template for many of the rivers (Ward, 1987). The Kuiseb begins on the interior plateau of central Namibia at an elevation of ~2000 m and a mean annual rainfall of ~350 mm. From the headwaters westward the river has eroded a shallow, sinuous valley into schists and quartzites, which weather to provide a large proportion of the sandy bedload transported within the river's lower reaches. West of escarpment separating the inland plateau from the coastal plains, the river has incised a deep canyon (>200 m) in similar rocks. The river is highly confined herein, often flowing over bedrock with no alluviation due to the steep gradient and narrow channel. The canyon broadens 65 km from the coast, whereafter the river occupies a wide, shallow valley which finally becomes indistinct within 20 km of the coast. Within 20 km of the coast, low cresentic dunes cross the river, resulting in a series of poorly defined channels terminating on the coastal flats in the vicinity of Walvis Bay. Many of the general characteristics of this catchment are shared by other Namib rivers, including the pronounced climatic and topographic gradients, a large percentage of surficial bedrock, sparse vegetation, and shallow, poorly developed soils throughout the catchments (Jacobson et al., 1995).

Eight of the twelve major rivers have headwaters in private farmlands; ten flow through communal farmlands and all either originate in, cross or flow into proclaimed conservation and tourism areas. The rivers and their catchments support a rich assemblage of vegetation and wildlife critical to agriculture and tourism, two key sectors of the Namibian economy (Giess, 1971; Jacobson et al., 1995; NLAC, 2009), while also providing water for agriculture, tourism, and mining, as well as Namibia's most important economic centers (Swakopmund, Walvis Bay, Windhoek) (Jacobson et al., 1995).

2.2. Hydrologic characteristics of rivers within the Namib Desert

2.2.1. The ephemeral hydrologic regime

Hedman and Osterkamp (1982) defined ephemeral rivers as those systems in which measurable discharge occurs less than 10% of the year. Several well studied, albeit small, systems provide a general indication of hydrologic patterns typical of such systems. The extensive studies of Walnut Gulch, draining roughly 100 km^2 in southeastern Arizona, and the Nahal Yael watershed, draining roughly 0.6 km^2 in Israel, are two examples (Renard, 1970; Schick, 1988). Water flow in small ephemeral channels is characterized by passage of well-defined peaks, often of only a few hours duration. Downstream reductions in flow occur due to infiltration into channel and floodplain sediments, the extent of which is highly variable, and evaporative losses (Tooth, 2000; Nanson et al., 2002). This downstream attenuation in flow volume is perhaps the best known characteristic of ephemeral rivers, reported from systems ranging from <1 to more than 30,000 km^2 (Crerar et al., 1988;

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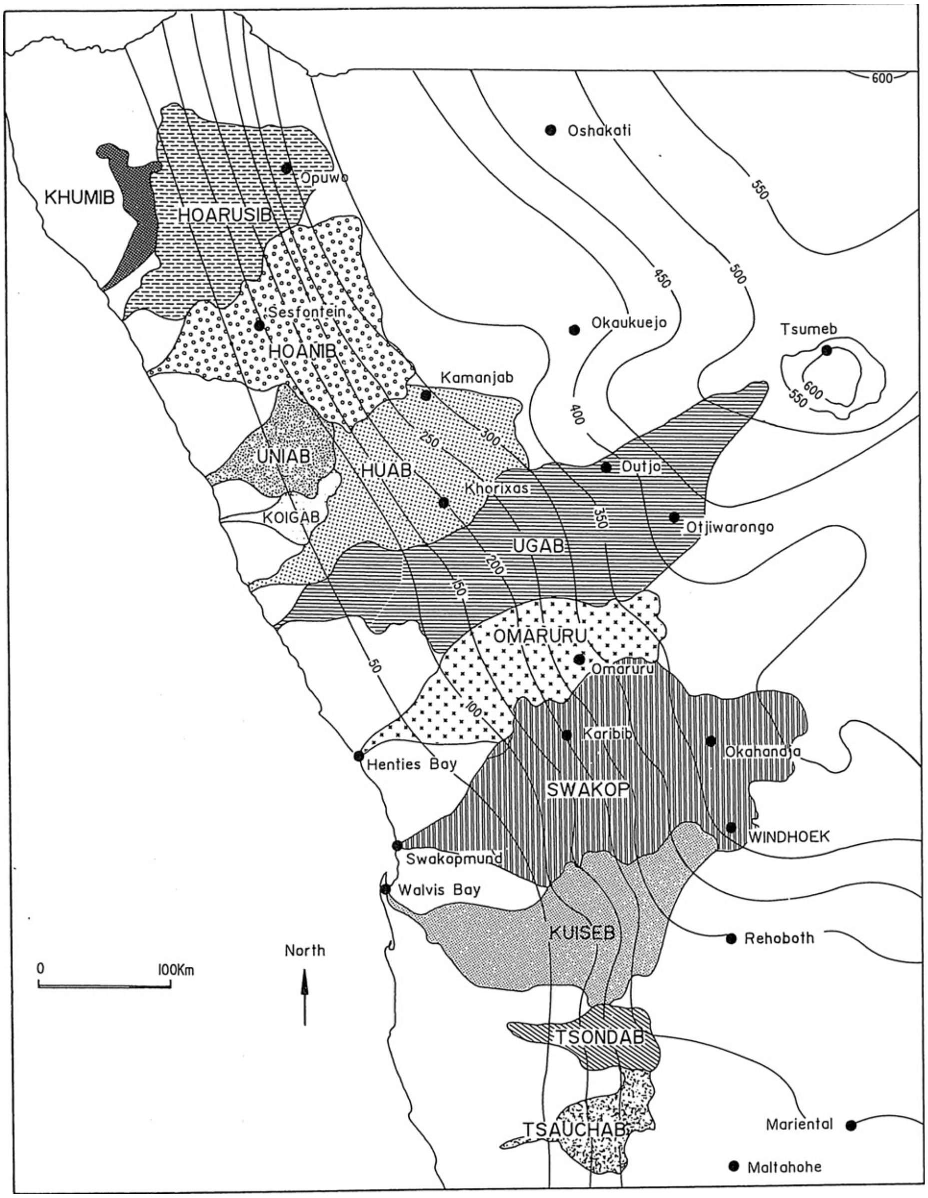

Fig. 1. Major ephemeral river catchments within the Namib Desert and mean annual rainfall (mm) isohyets (Jacobson et al., 1995).

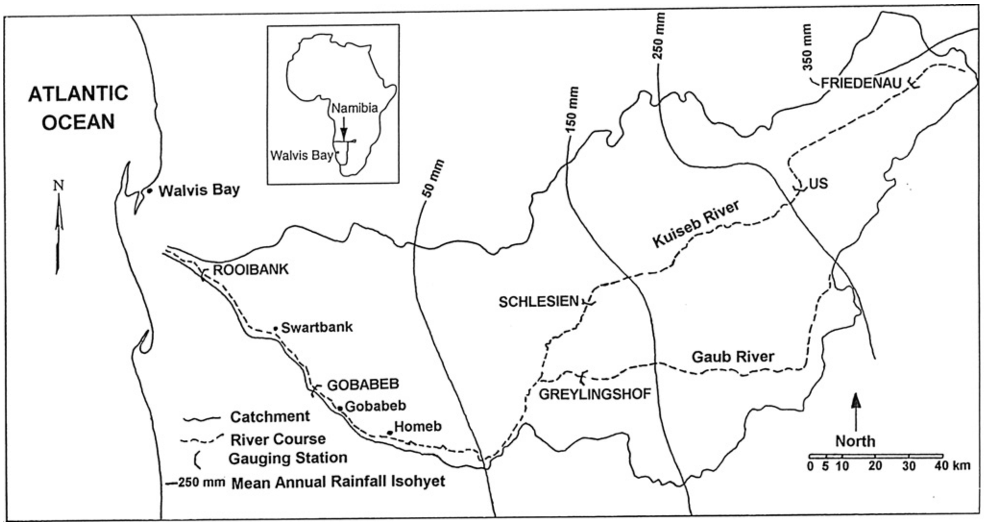

Fig. 2. Gauging stations, key geographic features, and mean annual rainfall (mm) isohyets within the Kuiseb River catchment in west central Namibia (Jacobson et al., 2000a).

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Table 1
Mean, minimum (Min), and maximum (Max) annual runoff as total volume (MAR_V) and depth over catchment (MAR_D) and coefficients of variation (CV_{MAR}) and skewness (CS_{MAR}) of the mean annual runoff volume for all stations ($n = 28$) over the length of record ($n = 20$ years) for the Tsauchab, Kuiseb, Swakop, Omaruru, Ugab, Huab and Hoanib catchments. The mean annual percent runoff (Runoff %) was calculated as the MAR_D divided by the mean annual precipitation of the catchment.

	MAR_V (Mm^3)	CV_{MAR}	CS_{MAR}	MAR_D (mm)	Runoff %	Area (km^2)
Mean	6.83	1.55	2.21	2.92	1.00	4652
Min	0.023	0.80	0.41	0.18	0.09	17.3
Max	29.62	3.32	3.94	14.9	3.82	21,800

Hughes and Sami, 1992; Leopold et al., 1966; Picard and High, 1973; Sharma et al., 1984; Walters, 1989).

2.2.2. *Namib hydrology*

The ephemeral rivers crossing the Namib Desert offer a unique opportunity for understanding the hydrologic and biotic characteristics of large ephemeral systems, unusual in that many are well-gauged and, in many cases, subjected to comparatively little anthropogenic alteration (Jacobson et al., 1995). The reports of Stengel (1964, 1966) provided the first documentation of hydrologic events in four of the Namib's major ephemeral rivers. Hydrologic records were largely anecdotal, however, as the rivers either lacked automatic gauging stations, or gauges had only recently been installed, and little ecological data were reported, other than an account of disturbance to the riparian forest associated with a major flood in the lower Kuiseb River in 1963.

Jacobson (1997) analyzed the mean annual flow statistics for 28 stations along the Namib's rivers, noting the highly variable nature of the rivers' hydrologic regimes (Table 1). Mean annual runoff (MAR_V) varied by more than three orders of magnitude among the stations. Predictably, stations recording flow from the comparatively mesic headwater regions exhibited the lowest variability in their annual runoff series, while those closest to the coast the highest. The influence of infrequent, high-magnitude events on mean values was reflected in a large positive skewness coefficient. Mean annual runoff depth (MAR_D), calculated by dividing MAR_V by catchment area, averaged 2.92 mm, and percent runoff averaged approximately 1.0% (Jacobson, 1997). Similar values were also observed among the 14 gauging stations within the Kuiseb River catchment (Table 2).

Distinct longitudinal trends were readily apparent among the rivers' mainstem stations, as illustrated by the five stations along the Kuiseb (Table 3) (Jacobson, 1997) (Fig. 2). From the headwaters towards the coast, mean annual runoff exhibited a curvilinear pattern, first increasing towards the base of the escarpment, then decreasing markedly at downstream stations within the Namib plains. A similar pattern was observed in peak discharge, which declined towards the coast, after a peak in the middle reaches of the catchment. Associated with the downstream decay in total runoff was a marked increase in the both the variation and skewness of annual runoff series, reflecting the increasingly variable nature of the hydrologic regime in the rivers' lower reaches and the influence of infrequent, high-magnitude events. There was also an increase in the occurrence of zero-flow years in the runoff series at downstream stations.

Table 2
Mean, minimum (Min), and maximum (Max) runoff as total volume (MAR_V) and depth over catchment (MAR_D) and coefficients of variation (CV_{MAR}) and skewness (CS_{MAR}) of the mean annual runoff volume (MAR_V) for all Kuiseb River stations ($n = 14$) from 1979 to 1993. The mean annual percent runoff (Runoff %) was calculated as the MAR_D divided by the mean annual precipitation of the catchment.

	MAR_V (Mm^3)	CV_{MAR}	CS_{MAR}	MAR_D (mm)	Runoff %	Area (km^2)
Mean	1.88	1.31	1.50	2.25	0.76	2796
Min	0.023	0.79	0.41	0.04	0.025	17.3
Max	6.59	2.00	2.64	7.20	2.15	14,700

In addition to the variability among years in the runoff series for each station, there was also significant variation in the characteristics of individual floods among stations (Table 4) (Jacobson, 1997). Most obvious was the marked downstream decrease in the average number of floods per year and the total number of floods recorded. The average duration of individual floods also varied among stations, peaking mid-reach and declining thereafter. A similar pattern was observed for mean annual number of flow days. Finally, the onset of flow also varied widely among stations, with downstream flow delayed by up to two months relative to upstream stations.

These statistics rank the Namib's rivers amongst the driest and most variable rivers yet described. Alexander (1985) reported mean annual runoff/rainfall ratios of 65.7% for Canada, 9.8% for Australia, and 8.6% for South Africa. In contrast, the mean value for the Namib's rivers is approximately 1.0% (Jacobson, 1997). The mean CV_{MAR} of 1.55 calculated for the 28 stations in Namibia is the highest figure yet reported for a region's rivers. McMahon (1979), in reviewing the runoff characteristics of arid regions, reported a mean CV_{MAR} ranging from a low of 0.65 for North America, to a high of 1.27 for arid inland Australia. Unquestionably, though, the most distinctive hydrologic feature of Namibia's westward-flowing rivers is the strong curvilinear relationship between many flow characteristics and distance downstream within an individual river system (Jacobson, 1997).

3. Hydrologic influences on physical and ecological patterns and processes

3.1. *Solute and sediment transport*

Downstream attenuation in both peak discharge and total flow volume are perhaps the best known characteristics of ephemeral rivers, documented across a range of systems of varying size (Jacobson et al., 2000a; Leopold and Miller, 1956; Picard and High, 1973; Schick, 1988; Sharma et al., 1984; Walters, 1989). Associated with this attenuation are a downstream decrease in stream power and a corresponding increase in alluviation (Bull, 1979). The resulting alluvial deposits are perhaps the most extensively studied aspect of ephemeral systems (Baker et al., 1988; Graf, 1988; Picard and High, 1973; Warner, 1988). While the episodic floods that form these alluvial deposits have long fascinated the desert traveler (Van Dyke, 1901), reports of their chemical composition and transport dynamics remain scarce. Fisher and Minckley (1978) were the first to document temporal variation in the chemical characteristics of a 'flash flood', sampling floodwaters in Sycamore Creek, an intermittent stream in the Sonoran Desert. The high levels of dissolved and particulate material revealed the importance of such floods, despite their brief duration, to the mass transport of materials from dryland catchments to downstream systems.

Namib Desert floodwaters transport high concentrations of total suspended sediments (TSS), and the organic proportion is commonly beyond the range typically reported from the world's rivers (Ittekkot and Laane, 1991), although similar to that observed in other dryland systems (Fisher and Minckley, 1978; Sykes, 1937). Jacobson et al. (2000a) recorded a mean of 35.3 gl^{-1} in floodwater samples collected during discharge peaks in the lower Kuiseb River, with fine particulate organic matter (FPOM) contributing an average of 11.8% to the suspended load. Similar, although slightly lower, levels have been reported from the lower Hoanib River (Leggett et al., 2005). The upstream reaches of the Namib's rivers

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Table 3
Mean annual runoff as total volume (MAR_V) and depth over catchment (MAR_D), coefficients of variation (CV_{MAR}) and skewness (CS_{MAR}) of the mean annual runoff volume (MAR_V), mean annual peak discharge (MAPD), mean annual precipitation (MAP), catchment area, and upstream channel length for mainstem stations of the Kuiseb River from 1979 to 1993. Total river length is 560 km.

Station	MAR_V (Mm^3)	Median (Mm^3)	CV_{MAR}	CS_{MAR}	MAPD (m^3/s)	MAR_D (mm)	MAP (mm)[a]	Area (km^2)	Length (km)
Friedenau	1.51	1.42	0.79	1.00	42.7	7.17	330	210	58
Us	6.22	4.78	0.88	0.69	77.7	3.27	210	1900	176
Schlesien	6.59	4.13	1.16	1.41	71.9	1.01	100	6520	304
Gobabeb	4.65	1.27	1.32	1.29	31.9	0.40	21	11,700	479
Rooibank	0.64	0	1.57	1.54	7.4	0.04	11	14,700	535

[a] Approximate mean annual precipitation at gauging station.

thus supply a large subsidy of organic matter to downstream reaches.

Jacobson et al. (2000a) sampled a flood in the lower Kuiseb River, estimating that 3338 metric tons were exported out of the escarpment into the lower river within the Namib Desert. Termination of floods within the rivers' lower reaches renders them a sink for materials exported from upstream. Vogel (1989) observed such localized deposition, noting that the Namib's rivers deposit their inorganic sediment load along a stretch of riverbed corresponding to the average reach of their floods, resulting in a convex deviation in the river's longitudinal profile near the coast. Sediment deposition patterns, both inorganic and organic, are shaped by this convexity within the lower reaches of the Kuiseb River's longitudinal profile (Jacobson et al., 2000a, 2000b). Interannual hydrologic variation alters the position of deposition zones for dissolved and particulate material, both organic and inorganic, with upstream or downstream shifts in response to changes in discharge (Jacobson et al., 2000b). The spatial and temporal extent of these accumulations within the Namib's rivers is thus directly dependent on the dynamics of the rivers' hydrologic regimes.

3.2. *Organic matter dynamics*

3.2.1. *Organic loads*

While the largest component of a river's organic load is typically in the dissolved state in more mesic watersheds (Allan, 1995; Moeller et al., 1979; Thurman, 1985), the pattern is reversed in the Namib's rivers. Values recorded in the Kuiseb River are among the highest yet reported, with particulate organic matter (POM) constituting approximately 97% of the total organic load (Jacobson et al., 2000a). Jones et al. (1997) observed a similar pattern within the Sonoran Desert, reporting that POM represented 98.3% of the total annual carbon exports. Total organic loads in the Namib's rivers are high, with mean total organic matter (TOM) levels of more than 4000 mg l^{-1} reported from the lower Kuiseb River (Jacobson et al., 2000a), similar to levels reported from Sonoran Desert streams (Jones et al., 1997). In contrast, Mulholland and Watts (1982) reported TOM concentrations for streams throughout North America averaged less than 43.4 mg l^{-1}.

Table 4
The number of zero-flow years, mean annual flood number, total flow events, mean duration of individual flow events, mean total annual flow days, and mean date of first flow for mainstem stations of the Kuiseb River from 1979 to 1993.

Station	Zero years[a]	# Floods/y	# Floods[b]	Duration (d)[c]	Flow (d/y)[d]	Julian date[e]
Friedenau	0	7.9	118	3.7	24.4	68
Us	0	4.9	73	5.0	28.9	81
Schlesien	0	2.7	40	11.1	25.7	105
Gobabeb	4	1.3	21	3.9	8.7	126
Rooibank	9	0.9	13	2.2	3.9	129

[a] Number of zero-flow years in record.
[b] Total number of floods over record.
[c] Mean duration of floods in days.
[d] Mean days of flow per annum.
[e] Mean date of first flood (October 1 = Julian 1).

Riparian vegetation can deliver large amounts of organic matter to ephemeral river channels. With low decomposition rates during interflood periods, large accumulations may accrue, yielding high POM and dissolved organic matter (DOM) levels when surface flow resumes. Fruits of *Faidherbia albida* trees growing within and along the channel are an important source of POM and DOM within the lower Kuiseb River. Annual pod production averages ~185 kg/y/tree along the lower Kuiseb River (Seely et al., 1979/80–1980/81, Jacobson, 1997). DOM levels of up to 228 mg l^{-1} have been observed in water samples collected during the first flood following the preceding dry season, which leached and flushed accumulated *Faidherbia* fruits downstream (Jacobson et al., 2000a). Leaching experiments with fresh plant litter have shown that up to 40% of the organic matter of the plant may be dissolved in 24 h (Thurman, 1985). Soluble carbohydrates and polyphenols are the principal constituents lost during leaching (Suberkropp et al., 1976), and these materials make up more than 50% of the dry mass of *Faidherbia* fruits (Wood, 1989). The DOM concentrations measured in the lower Kuiseb River are among the highest reported from any aquatic system. Averaging 82 mg l^{-1} at peak discharge, they greatly exceed the estimated global average of 10 mg l^{-1} for streams and rivers (Meybeck, 1982).

A key issue regarding the organic matter dynamics of rivers and streams concerns the extent of in-stream processing occurring relative to downstream export. Opportunities for such processing are directly linked to the stream's ability to temporarily store organic carbon within the channel (i.e., their retentiveness) (Maser and Sedell, 1994; Webster et al., 1994). The Namib's ephemeral rivers are an extreme example where retentive structures, in combination with hydrological decay, often result in little or no export from a reach or the system as a whole when floods do not reach the Atlantic or occur within endoreic basins such as the Tsondab or Tsauchab (Fig. 1).

3.2.2. *Woody debris and channel morphology*

In-channel trees contribute to the retention of both the organic and inorganic loads transported during flow events (Jacobson, et al., 1999b; Jacobson et al., 2000b). Debris dams within the lower Kuiseb River typically consist of several large logs lodged against one or more trees within the channel, upon which additional wood is retained. Such accumulations are a significant obstacle to flowing water, and as successively smaller pieces of wood are retained, finer material, including FPOM and inorganic sediment, accumulate within and downstream of the pile. This increased hydraulic resistance results in the formation of long drapes of deposited sediment downstream from debris piles. These fine-grained, nutrient-rich soils create moist micro-habitats following flood recession, functioning as nursery bars for germinating seedlings, as

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well as root sprouts from scoured *F. albida* trees (Jacobson, et al., 1999b; Jacobson et al., 2000b). If these sites are not eroded by subsequent high-discharge floods, they may develop into elongate islands, dividing the river course into multiple channels. Such patterns have been reported from ephemeral stream channels in the Barrier Range in Australia where *Eucalyptus camaldulensis* grow along the banks and within the active channel (Dunkerley, 1992; Graeme and Dunkerley, 1993).

3.2.3. 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. This pattern of decreasing downstream retention, commonly observed for wood in perennial streams (Lienkaemper and Swanson, 1987; Webster et al., 1994), does not apply in large ephemeral channels where in-channel tree growth and downstream hydrologic decay reverse the pattern. In marked 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 et al., 2000a), and biological processing occurs in pulses that follow microbial activation by floods (Jacobson et al., 1999a; Jacobson et al., 2000b). Microbial and invertebrate communities activated by flood pulses subsequently cease activity in response to desiccation (Jacobson et al., 1999a; Shelley and Crawford, 1996).

Transport and processing of organic matter in the Namib's ephemeral rivers are thus largely uncoupled. Transport occurs during flooding, when material is removed from one terrestrial environment and deposited in another. While little processing occurs in the terrestrial phase throughout the year, flood pulses trigger a significant increase in the rate of organic matter decomposition (Jacobson et al., 1995; Jacobson et al., 1999a). Thus, transport and processing are discontinuous, occurring in discrete ‘batches’ associated with flood pulses. This pattern is markedly different from that within more mesic fluvial ecosystems, where consumption of fluvially-transported organic matter and uptake of aqueous nutrients is typically a continuous, biologically-mediated process occurring within the water column (Newbold et al., 1982, 1983).

Debris piles are known to facilitate such processing, exerting a strong influence on the structure and function of the biotic assemblages and associated processes within fluvial ecosystems. Bilby and Likens (1980) found that debris dams contained 75% of the standing stock of organic matter in 1st-order perennial streams, noting that debris piles 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 an identical function within ephemeral rivers, however, where their water-retentive properties and high organic matter content support biological activity following floods, often long after it has ceased in the adjacent, desiccated channel (Jacobson et al., 1999a; Jacobson et al., 2000b; Shelley and Crawford, 1996).

The heterogeneous distribution of wood thus not only has a strong influence on spatial patterns of invertebrate and macrofungal richness and abundance within perennial rivers (e.g., Benke et al., 1985; Smock et al., 1989), but also within 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 (Jacobson et al., 1999a). Polydesmid millipedes and terrestrial isopods are abundant after floods, feeding and reproducing within the moist micro-habitats associated with woody debris piles, but they are typically absent from adjacent channel sediment (Shelley and Crawford, 1996). Large polydesmid millipedes are seldom observed in deserts (Golovatch and Kime, 2009), but *Cnemodesmus riparius* from the riparian forests of the Namib is an exception. The organic-rich silt faces and debris piles which remain moist for a month or more following floods are the critical habitat for this species, allowing its persistence in an otherwise inhospitable setting (Shelley and Crawford, 1996). 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 carbon source and critical habitat (Jacobson et al., 1999a).

3.3. Soil properties

Abrams et al. (1997) examined ecologically-relevant soil properties within the floodplain of the Kuiseb River, contrasting the relative importance of landscape position and plant community association to soil nutrient status. Flood inputs, and hence landscape position, were identified as the key factor controlling soil organic matter and nutrient accumulation. As previously noted, landscape position within the longitudinal extent of the Namib's Rivers has a strong influence on patterns of sedimentation. Vogel (1989) commented on the rivers' convex profiles towards the coast, attributing them to downstream hydrologic decay. The relative position of this deposition varies, shifting upstream or downstream in response to decreases or increases in flood magnitude, respectively. As a result, floods within ephemeral rivers create, via their regulation of transport and deposition, distinct longitudinal patterns in the characteristics of floodplain soils; in turn affecting the composition and productivity of the riparian ecosystems they support (Jacobson et al., 2000b).

3.3.1. Classification and texture

Riparian soils are in the Fluvent suborder, characterized by alternating layers of fluvially-deposited silts and sands of both fluvial and aeolian origin. These interstratified sediments exhibit irregular carbon-rich layers with depth, originating from buried O- or A-horizons, or fluvially-deposited organic matter. O- and A-horizons occur on the infrequently-flooded, alluvial terraces that border the lower reaches of the rivers. Soils are typically well-drained, although silt and clay horizons act as hydraulic barriers, limiting infiltration but also, conversely, desiccation of underlying sediments. While terrace and floodplain soils may be dry to depths below one meter for years in the absence of flooding, these same soils may remain moist at depths >30 cm for weeks to more than a year following flood inundation. Riparian soils exhibit a torric moisture regime, and are best classified as Typic Torrifluvents (Soil Survey Staff, 1992), or Fluvisols under the FAO-UNESCO soil classification system.

3.3.2. Soil salinity

Soil salinity is known to affect the distribution, morphology, and productivity of riparian trees along dryland rivers (Busch and Smith, 1995; Jolly et al., 1993), and solute-rich floodwaters do increase soluble salt concentrations at sites within the lower reaches of Namib rivers (Jacobson et al., 2000b). Floodwater samples along the lower Kuiseb River show a downstream increase in conductivity, and levels of sodium, potassium, calcium,

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magnesium, and chloride all exhibit a downstream increase within the river's lower reaches (Jacobson et al., 2000a). Nonetheless, reported levels are below those likely to influence the distribution and production patterns of plants (Singer and Munns, 1987). An exception can occur at wetland sites, however, where capillary movement of water from a shallow groundwater table to the surface, and its subsequent loss via evaporation, may result in soil salinization and visible surficial salt accumulations. This salinity may explain the absence of *F. albida* trees at some wetland sites, and their replacement by halophytic species such *Tamarix* (Jacobson et al., 2000b).

3.3.3. *The hydrology and ecology of silt*

Transmission losses in the lower reaches of the rivers are high, ranging from ~0.4–1.7% k m^{-1} in the lower Kuiseb, and result in rapid downstream decreases in stream power and capacity (Jacobson et al., 2000a). As stream power and capacity decrease, alluviation increases (Bull, 1979), and the downstream increase in silt percentage observed in the Namib's rivers thus parallels the downstream reduction in mean discharge. Accordingly, the longitudinal profile of the rivers is typically convex in their lower reaches (Fig. 3), delimiting an alluviation zone as suggested by Vogel (1989).

Silt within the western rivers has been viewed with some disdain because of its potential role in sealing river beds during flooding, thus preventing infiltration and recharge (Crerar et al., 1988). The same physical properties of silt which may give rise to such effects also have tremendous ecological significance with the Namib's riparian forests. Silt deposition patterns in ephemeral rivers exert a strong control on moisture dynamics within floodplain soils, influencing decomposition, production, and habitat suitability. Silt layers within soil horizons may act as hydraulic barriers, slowing the downward movement of moisture. Following overbank floods, moisture stored in floodplain soils may move down slope, often along sand-silt contact zones, wetting channel banks at silt-rich layers within the soil profile. These moist silt exposures along the active channel are key post-flood habitats for a diverse community of blue-green algae; fungi, including both basidio- and ascomycetes; lower plants, including mosses and liverworts; and invertebrates (Jacobson et al., 1995, 2000b; Shelley and Crawford, 1996).

Silt layers on the floodplain surface also act as hydraulic barriers, but in this case delaying the desiccation of underlying sediments. While exposed alluvial sand deposits can dry to a depth of more than 30 cm within weeks of inundation, several centimeters of silt capping can maintain subsurface moisture levels sufficient to support microbial activity for several months or more following recession (Jacobson et al., 2000b). This subsurface moisture thus drives biogeochemical cycling within an otherwise arid environment, supporting the decomposition of silt-associated organic matter by an unusual assemblage of Basidiomycetes, including the fungus *Battarrea stevenii* (Jacobson et al., 1999a). Mature *Battarrea* sporocarps may break through the silt cap from 4 to 12 months after a flood has inundated the floodplain. The large size of the sporocarps (>0.5 m) allows them to access deeper soil organic matter deposits where moisture may persist for months following floods. While the pulse of carbon and nitrogen mineralization associated with drying and rewetting cycles has been described from soils across a range of climates (Cabrera, 1993; Van Gestel et al., 1993), the effect may be particularly pronounced in the riparian soils along the Namib's ephemeral rivers.

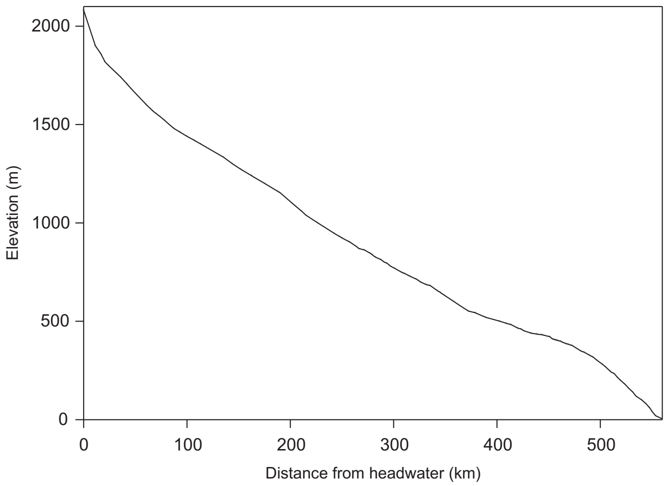

Fig. 3. Longitudinal profile of the Kuiseb River, showing the convex alluviation zone (~380–480 km) within the river's lower reaches (Jacobson et al., 2000b).

Vertical heterogeneity in moisture and nutrient availability within riparian soils also has a strong influence on rooting patterns of riparian vegetation. Fine roots of *F. albida* are abundant in buried organic matter deposits and organic-rich silt horizons, yet virtually absent from adjacent mineral soil layers. The higher root densities associated with these zones likely reflect advantageous rooting in response to the higher moisture and nutrient availability (Jacobson et al., 2000b; Wood, 1989).

The physical processing of woody debris, *F. albida* fruits, and other organic matter during floods yields large amounts of highly-labile particulate organic matter which is subsequently intercalated with silt within floodplain soils (Jacobson et al., 2000a, 2000b). More than a dozen species of fungi, including several species of lignin-decomposing fungi typically found only on logs and other woody debris, are commonly found fruiting from surficial silt deposits within one to two weeks of flood recession, and silt-associated FPOM (fine particulate organic matter) is the principal nutrition source for these fungi (Jacobson et al., 1999a; Jacobson et al., 2000b).

As silt deposits dry, they shrink and crack into large, polygonal plates up to 0.5 m across. Up to ~10 cm thick, these silt plates are separated by cracks of several centimeters or more, often curling slightly at the edges and partially separating from underlying sands. The resultant heterogeneous surfaces create unique microhabitats within the rivers' floodplains. Moist microclimates within cracks and under silt plates provide refugia for frogs (*Tomopterna delalandei*) and invertebrates. Insectivores, including scorpions (*Parabuthus villosus*) and shrews (*Crocidura cyanea*), actively forage within these habitats (Jacobson et al., 2000b).

Primary and secondary production in dryland ecosystems is typically limited by low soil water content and nutrient-poor soils (West, 1991). Accordingly, floods, providing both water and nutrients, are keystone events within ephemeral river ecosystems, and alluviation zones, with their organic- and nutrient-rich silts and increased moisture availability, are the most biologically productive reaches within the Namib's ephemeral river ecosystems (Jacobson et al., 2000b). The density of *F. albida* along the Kuiseb River reflect this, as the peak in tree density corresponds with the peak in soil silt and nutrient content within the mid-reaches of the river's alluviation zone. Thus, the hydrologic regime, through its control of soil properties, particularly nutrient and moisture availability, is the principal factor controlling both the structural and functional characteristics of ephemeral river riparian communities, including their longitudinal distribution. Accordingly, alteration of the hydrologic regime can produce a concomitant shift in the structure, productivity, and distribution of these fluvial ecosystems (Jacobson et al., 2000b).

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3.4. Riparian forests

Perhaps the most distinctive biotic feature of the rivers is the comparatively lush riparian forest along their channels (Jurgens et al., 1997), a stark contrast to the adjacent sand and rock desert and a critical resource for the region's wildlife (Seely and Griffin, 1986). *F. albida* is a key woody species in many of the rivers, contributing organic matter to the channel and floodplain in the form of wood and leaves, as well as large numbers of dry fruits (seed pods), dropped into the channel and floodplain prior to the onset of the summer rainy season (Seely et al., 1979/80–1980/81; Theron et al., 1980). While the tree occurs sporadically within the escarpment and canyon reaches of the rivers on isolated pockets of alluvium, the most expansive stands are in the rivers' lower reaches where it grows on the extensive alluvial deposits associated with broader channels and floodplains.

Forest composition varies along the length of the rivers. Many have narrow canyon reaches where flow velocity is high and floods move over a shallow alluvium or bed rock. Fig trees (*Ficus* sp.), capable of forcing their roots into rock fissures on canyon walls, may be the only trees that persist in such reaches. More protected sites with sufficient alluvium can be colonized by species such as *F. albida* and *Tamarix usneoides*, species which respond to scour and root damage with vegetative root suckering (Jacobson et al., 1995; Wood, 1989). In perennial floodplain rivers, the magnitude, frequency, and duration of floods diminish laterally from the channel, and the riparian vegetation on these surfaces reflects these gradients (Bell, 1974; Mitsch et al., 1991). In ephemeral systems, such gradients occur both laterally and longitudinally, and riparian vegetative communities vary accordingly, shifting in response to patterns of deposition, disturbance, and moisture and nutrient availability (Jacobson et al., 1995; Jacobson, 1997). These lateral and longitudinal variations represent gradients of subsidy and stress (Odum et al., 1979), and hydrologic alterations may accordingly shift their positions.

Ward and Stanford (1983) suggested that the intermediate-disturbance hypothesis of Connell (1978) provided an explanation for species diversity patterns in fluvial ecosystems, noting that diversity will peak in communities subjected to moderate levels of disturbance. Similarly, Vannote et al. (1980) observed that the middle reaches of the stream continuum, the region of greatest environmental heterogeneity, may exhibit the highest species diversity. Hydrologic control of disturbance and resource availability creates similar patterns of diversity within the Namib's ephemeral rivers, wherein intermediate reaches may exhibit the richest biotic assemblages, due to the interacting effects of moderate levels of disturbance and moisture stress, and a comparatively high level of habitat complexity (Jacobson, 1997). The observations of Shalom and Gutterman (1989), who reported that disturbance associated with flooding in constrained reaches of an ephemeral river in Israel decreased species richness relative to that in less confined reaches downstream, lends credence to this observation.

The full suite of woody species found in the Namib's riparian forests also varies with latitude and the frequency and size of flows. Small rivers with irregular flows, such as that of the Tsondab and the Tsauchab Rivers, may be dominated by hardy *Acacia* and *Parkinsonia* species. Larger systems, with more regular seasonal flows, support a greater diversity of trees, all dependent on groundwater for survival (Robinson, 1976; Ward and Breen, 1983). For example, the forests of the Kuiseb and Swakop are dominated by *F. albida*, *Euclea pseudebenus*, *T. usneoides*, *Ficus sycomorus*, *Acacia erioloba* and *Salvadora persica* (Seely et al., 1979/80–1980/81). The Omaruru and other northern rivers also support large individuals of *Combretum imberbe*. Finally, from the Ugab northward *Colophospermum mopane* may be found within the forests (Jacobson et al., 1995).

In addition to their riparian forests, many of the Namib's rivers contain wetlands at sites where groundwater is forced to the surface by shallow bedrock (Loutit, 1991). Such sites support various hydrophytic and halophytic species, including *Cyperus*, *Juncellus*, *Phragmites, Scirpus and Typha,* as well as large stands of bushy *Suaeda* and *Tamarix*.

An unwelcome contributor to the flora of nearly all western rivers is the diverse range of alien plants introduced to Namibia, many of which have become established in the rivers. All of these species are easily dispersed via floodwaters (Loutit, 1991) and some, including *Prosopis*, are also transported by domestic stock. *Argemone*, *Datura, Nicotiana, Prosopis, and Ricinus* occur within the lower Kuiseb River, and their dynamics may reflect both their utilization by humans, livestock and wildlife, as well as the river's hydrologic regime (Henschel and Parr, 2009/2010). Sections of the lower Swakop River within the Namib-Naukluft Park are virtually pure *Prosopis* forests, providing an example of how invasive such species can be, although the ecological effects of these species on the western catchments remains largely unknown (Jacobson et al., 1995; Henschel and Parr, 2009/2010).

3.4.1. Supporting regional biota: the Namib's linear oases

The water and vegetation resources within ephemeral rivers are well-recognized as key refugia for the region's biota (Kok and Nel, 1996; Loutit, 1991). Giraffe *Giraffa camelopardalis angolensis* in the northern Namib Desert prefer riparian habitats, almost to the exclusion of all other habitat types (Fennessy, 2009), similar to the preference exhibited by the region's elephant *Loxodonta africana* (Viljoen, 1989), for which *F. albida* is a key resource (Leggett, 2006). Rhinoceros *Diceros bicornis bicornis* and Hartmann's mountain zebra *Equus zebra hartmannae* make continuous use of riparian habitats throughout their range in the western rivers (Loutit, 1991). In the Kuiseb River, groundwater-dependant pools and the seed pods of *F. albida* are critical resources for gemsbok *Oryx gazella* and baboon *Papio ursinus*, particularly during drought periods (Hamilton et al., 1977). In general, riparian vegetation is preferred fodder year-round for animals such as elephant, rhino, giraffe, baboon, and kudu (Loutit, 1991; Seely and Griffin, 1986; Viljoen, 1989) whose ranges extend down from higher rainfall regions inland.

For larger and more mobile species, including elephant, the rivers serve not only as key habitats but as key links facilitating movements across comparatively inhospitable landscapes, particularly within the hyper-arid expanses of the Namib Desert in the rivers' lower reaches. Animals move not only longitudinally within the rivers but also cross north-south between them (Leggett, 2006). During such movements, rivers and springs act as rungs in a ladder, allowing successful passage across the dry landscape. Accordingly, hydrologic alterations that alter water and vegetation resources within the rivers' lower reaches will negatively impact landscape-scale connectivity among critical resources for the region's megafauna (Jacobson et al., 1995).

The rivers' significance for the region's biota extends well beyond its megafauna. For example, more than 700 species of insects have been recorded from the lower Kuiseb River (Prinsloo, 1990), including several endemic species such as the tenebrionid beetle, *Physadesmia globosa* (Crawford et al., 1990). Detritus derived from the riparian corridor's vegetation constitutes the key food resource for many such common detritivores (Hanrahan and Seely, 1990). While the interdependence of the riparian and adjacent desert food webs is largely unknown, some level of reciprocal subsidization undoubtedly occurs, analogous to that which has

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been reported from along temperate streams (Nakano and Murakami, 2001).

While the terrestrial biota is reasonably well known, comparatively little work has been done on the limnology of the Namib Desert, and the work of Day (1990) remains the most comprehensive synopsis to date. Ephemeral waters are largely dominated by crustaceans and permanent waters by insects.

3.4.2. *F. albida: a critical yet sensitive resource*

Numerous studies have highlighted the importance of *F. albida* to wildlife within the western rivers, including ungulates (Hamilton et al., 1977) and elephants (Viljoen, 1989). The foliage and seed pods are no less important to the region's farmers, however, and are widely sought and utilized as a dry season fodder for livestock (Jacobson et al., 1995; Loutit, 1991; Moser-Nørgaard and Denich, 2010). The reverse phenology of the species makes these resources particularly significant as they are present when little other forage may be available on the adjacent arid landscapes, particularly during drought years. While *F. albida* is a critical resource for livestock, however, they may also have a strong negative influence on its regeneration through the browsing of seedlings (Moser-Nørgaard and Denich, 2010).

Successful recruitment of woody seedlings in arid riparian forests is tied to the ability of their roots to maintain contact with the alluvial water table. Stave et al. (2005) observed that regeneration of *F. albida* likely depended on slow rates ($\sim$5 cm day^{-1}) of water table decline during post-flood periods. Mature *F. albida* are also known to be quite sensitive to excessive rates of decline in alluvial water tables. Ward and Breen (1983) documented the death of many large *F. albida* during a prolonged non-flood period ($\sim$4 years) on the lower Kuiseb River, during which the water table dropped by over 3 m. While young trees ($\sim$5–10 years old) were not adversely affected, mature trees experienced significant mortality. O'Connor (2001) also observed that tree size affected mortality, with young *F. albida* largely immune to the influence of small catchment dams on an ephemeral tributary of the Limpopo River in South Africa. The likelihood of dieback of mature trees was reportedly greater at higher elevations above the river channel, likely reflecting greater depth to water.

F. albida is known to be a facultative phreatophyte, able to draw on deep groundwater reserves but also able to utilize shallow soil moisture derived from precipitation or floods (Roupsard et al., 1999). A recent study of *F. albida* along the Kuiseb River highlighted the significance of floods in maintaining not only the availability of groundwater but shallow and deep reservoirs of soil moisture as well, all of which are accessed to vary degrees on a seasonal basis by the tree's roots (Schachtschneider and February, 2010). Both juvenile and adult trees utilized shallower soil water resources when available, but were predominantly dependant on groundwater during the dry season.

4. Hydrologic alteration of Namib rivers

Floods are the key ecological organizer responsible for the existence, productivity, and interactions of the main biotic elements within ephemeral river ecosystems. While the ecological significance of the 'flood pulse' was originally noted in reference to large, perennial systems such as the Amazon (Junk et al., 1989), the lateral and longitudinal linkages associated with floods in the Namib's ephemeral rivers are no less significant (Jacobson, 1997). Junk et al. (1989) suggested that the flood pulse concept was less applicable to systems where the pulse is variable noting that, "unpredictable pulses generally impede the adaptation of organisms." Walker et al. (1995) disagreed, however, observing that floods in dryland rivers are no less significant for riverine processes, despite their greater spatiotemporal variability, adding that life-history traits such as opportunism and flexibility, characteristic of many species in dryland systems, can be viewed as adaptations to unpredictability. Thus, hydrologic alterations may exert a range of negative effects on dependant biota.

Soil water and groundwater recharge along Namibia's ephemeral rivers is largely dependent on seasonal flooding (Dahan et al., 2008; Morin et al., 2009), and in its absence groundwater levels, and the health of riparian vegetation, may quickly decline (Jacobson et al., 1995). Blom and Bouwer (1985) observed falls in the water table ranging from 2 to 6 m along the lower Kuiseb River during a period of reduced river flow in the early 1980's. During this period numerous large mature *F. albida* collapsed and died along the river (Ward and Breen, 1983), and a significant increase was observed in the percentage of dead *F. albida* in the forest canopy (Theron et al., 1985). Over-extraction of alluvial groundwater can produce similar declines in groundwater tables and associated groundwater-dependant riparian ecosystems, as has been observed in the lower Kuiseb and Omaruru Rivers over the past several decades (Huntley, 1985; Jacobson et al., 1995).

Even more pronounced water table declines may be induced by upstream dams along the Namib's rivers. Surface water storage structures on ephemeral rivers can reduce the magnitude, frequency and duration of flow events, as well as delay their occurrence. The lower reaches of Namibia's ephemeral rivers are naturally characterized by a downstream decline in all of these parameters (Tables 3 and 4), and water storage developments will only serve to accentuate these existing patterns, much to the detriment of the rivers' ecological integrity. Such structures are often large relative to annual flows, ensuring continued water availability during dry periods, but also resulting in limited downstream reservoir spillage. Larger reservoir capacities ensure a stable annual yield of significant volume. McMahon and Mein (1978) suggested that reservoir storage capacity in dryland rivers should be proportional to the square of the CV of the mean annual flow. While such engineering helps buffer water resource supplies from hydroclimatic variance, it maximizes impacts downstream.

The Swakopport Dam, a large (69 Mm^3) impoundment in the upper Swakop River catchment southwest of Okahandja, was completed in 1978. It did not spill water, however, until the 1987/88 and 1988/89 water years, with a continued absence of spills up to 1995, when monitoring at the downstream Westfalenhof gauge was discontinued. A decline of 7–11 m occurred in downstream water tables during this period (NDWA, unpublished data, Fig. 4), and these low levels have been persistent due to the dam's significant reduction in downstream flow. In the fourteen years prior to damming, the 2-yr return interval peak discharge was $\sim$80 m^3 sec^{-1} with an annual runoff volume of $\sim$6 Mm^3. During the seventeen years of record following dam completion, the 2-yr peak discharge dropped to $\sim$6 m^3 sec^{-1} with an annual runoff volume of only $\sim$0.05 Mm^3 (NDWA, unpublished data, Fig. 5). As a result, there has been a pronounced decline in the *F. albida* within the river's lower reaches (Jacobson et al., 1995). The cumulative impact of many small dams may also reduce downstream flow on ephemeral rivers in southern Africa, particularly during drought years, with similar impacts on downstream water tables and associated riparian vegetation (Jacobson et al., 1995; O'Connor, 2001).

4.1. *Environmental flows in ephemeral rivers*

Determining how best to utilize available water resources within existing tight economic, social and environmental constraints presents rivers managers with an enormous challenge, even in comparatively mesic systems (Poff et al., 1997). This

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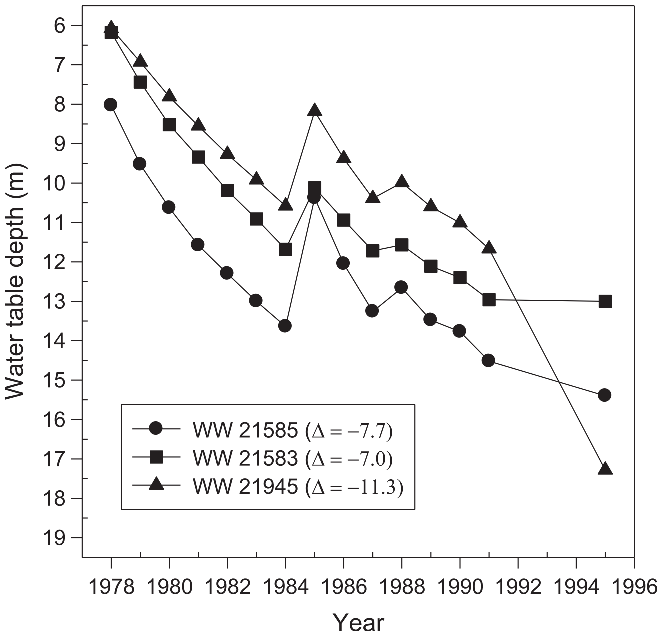

Fig. 4. The decline in alluvial water table depth (m) recorded at monitoring wells within the lower reach of the Swakop River following completion of the Swakopport Dam upstream in 1978 (Namibian Department of Water Affairs, unpublished data).

challenge becomes extreme, however, in the context of dryland rivers (Boulton et al., 2000). While a river's natural flow regime does offer a fundamental template for restoration and management (Poff et al., 1997), the answer to the question of "how much water does a river need" (Richter et al., 1997) is perhaps most extreme in the case of ephemeral river ecosystems, wherein even small changes in flow regime may trigger undesirable physical (e.g., reduced recharge and falling water tables) and biological responses (e.g., loss of wetlands and riparian vegetation) (Jacobson et al., 1995). Hence, for the Namib's rivers, the simple answer may be that they largely need what they have! The challenge for resource managers in Namibia is thus to ensure that incremental utilization of the rivers' water resources stops short of the level which would result in the cessation of key physical and biological processes within the rivers' lower reaches (Table 5).

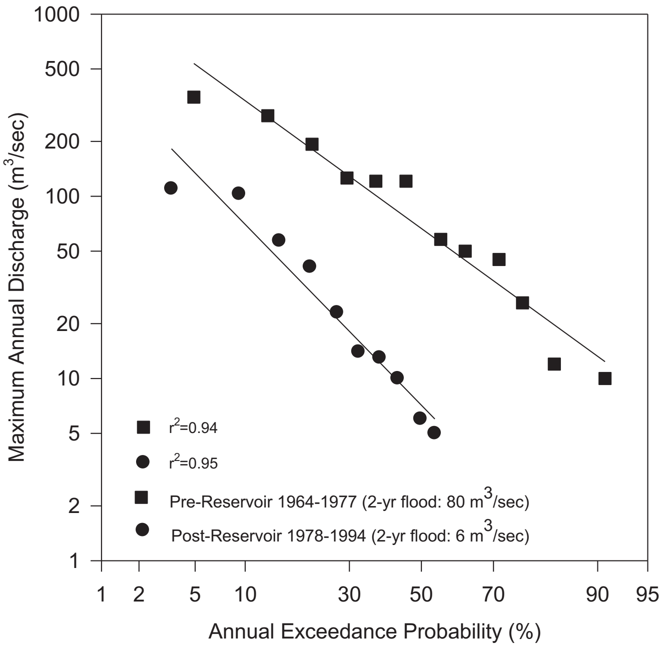

Fig. 5. Annual exceedance probability of maximum annual peak discharge recorded at the Westfalenhof gauge downstream of the Swakopport Dam pre- and post-completion of the Swakopport dam in 1978 (Namibian Department of Water Affairs, unpublished data).

The first attempt to quantify and provide environmental flows for a Namibian ephemeral river was the release of water from the Oanob Dam (Jacobson et al., 1995; Kambatuku, 1997). Recognizing the environmental effects of reducing frequency and volume of downstream runoff within ephemeral rivers, the Namibian Department of Water Affairs initiated a study in 1989 to evaluate the suitability of water releases from dams to compensate for a lack of natural flooding (Van Langenhoven and Church, 1989). This study focused upon the newly built Oanob Dam on the Oanob River at Rehoboth (one of Namibia's easterly-flowing ephemeral rivers). Concern had arisen over potential effects of the dam on one of the largest and densest stands of *A. erioloba* trees in the country. The dam was completed in 1990 and in 1993 enough water had accumulated to enable the DWA to stage a controlled flood release without jeopardizing water supply to Rehoboth. This effort sought to maintain groundwater levels within the downstream aquifer to ensure the vitality of the extensive floodplain woodland. Such artificial floods, released from upstream reservoirs, have been used elsewhere, most notably on the Colorado River, in attempts to mimic the physical and ecological patterns associated with natural flow regimes (Patten et al., 2001; Poff et al., 1997).

Although well intentioned, the release was largely ineffective for several reasons. Scaling the release to match the size of natural floods was not feasible. For the Oanob River, an average of approximately 14 Mm^3 of flood water passed the site of the Oanob Dam annually during the 52 years preceding the release. These floods had an average peak discharge in excess of 150 m^3 sec^{-1} (Jacobson et al., 1995). The artificial flood, in contrast, had a peak discharge of ~15m^3 sec^{-1} and totaled ~2.5 Mm^3. As a result, the flood traveled less than 15 km over the dry channel sediments downstream from the dam, and downstream water tables showed little or no response to the limited recharge (Kambatuku, 1997).

Table 5
Key physical and ecological processes controlled by floods in Namib Desert ephemeral rivers.

Process	References
Sediment and nutrient transport/deposition	Jacobson et al., 1999a, b; 2000a; 2000b
Soil formation/nutrient enrichment	Abrams et al., 1997; Jacobson et al., 2000b
Leaching of dissolved organic carbon	Jacobson et al., 1999b; 2000a
Leaching of wetland soil solutes	Jacobson et al., 2000b
Groundwater/soil water recharge	Dahan et al., 2008; Jacobson et al., 1999a
Waterhole formation/replenishment	Hamilton et al., 1977; Loutit, 1991
Microbial/bryophyte rehydration	Jacobson et al., 1995; Jacobson et al., 1999a
Microbially-mediated organic matter decomposition	Jacobson et al., 1999a
Organismal dispersal (natives and exotics)	Jacobson et al., 1995; Loutit, 1991
Scour/disturbance of soils and vegetation	Jacobson et al., 2000b; Loutit, 1991
Seed dispersal/germination	Loutit, 1991; Seely et al., 1979/80–1980/81
Root suckering (e.g., *F. albida*)	Jacobson et al., 1995
Invertebrate activity/reproduction	Day, 1990; Shelley and Crawford, 1996
Anuran activity/reproduction	Channing, 1976

The floodwater sediment load was also markedly different from that typically observed in natural floods. As previously noted, such floods carry a heavy load of silt and organic matter. In contrast, the artificial flood on the Oanob River carried almost no organic material and sediment levels were low (Jacobson et al., 1995). A final factor was that the sediment-free water released from the dam scoured channel sediments below the dam, redepositing them further downstream in response to hydrologic decay. The net result was a slight decrease in the river's elevation gradient below the dam. Such effects are well known as they have been frequently recorded in association with dams on perennial rivers flowing over alluvial beds (Williams and Wolman, 1984).

Ultimately, although Clause 95 of Namibian Constitution calls for "the maintenance of ecosystems, essential ecological processes and biological diversity," the Namibian Water Resources Management Act of 2004 (Government of Namibia, 2004) does not include a direct provision for maintenance of environmental flows (Bethune et al., 2005). It does, however, grant the minister authority to reserve water resources to "reasonably protect aquatic and wetland ecosystems, including their biological diversity and to maintain essential ecosystem functions." The Act also references the functions of basin management committees, including monitoring and data collection to ensure the sustainable management of water resources. To date, however, the Act has not been fully implemented, and the environmental water requirements of the Namib's rivers remain at risk (Menges, 2011).

4.2. Management of ephemeral river ecosystems

Namibia's ephemeral rivers have long provided critical water resources for Namibia's agricultural, urban and industrial development. While such development has often been distributed throughout the length of individual watersheds, large-scale hydrologic alterations have typically focused on high-volume impoundments within the upper watershed (e.g., Swakop River dams) or high-volume groundwater withdrawal from alluvial aquifers in the rivers' lower reaches (e.g., Kuiseb, Omaruru). The management of these systems is becoming increasingly complex, however, in the face of growing and competing demands for water among and along the rivers (Seely et al., 2003). Upstream benefits of dams may accrue to inland farmers and municipal residents at the expense of downstream residents and the ecosystems and aquifers upon which they depend. Such discrepancies highlight the need for integrated water resource management, as well as the conjunctive use of surface and groundwater resources (Seely et al., 2003).

Without question the greatest management challenge facing Namibia's ephemeral river ecosystems is the maintenance of hydrological connectivity within individual watersheds in the face of growing human water demands. Such connectivity includes not only the distribution and movement of water itself, but also the water-mediated transfers of matter, energy and organisms (Pringle, 2001). Managers of Namibia's proclaimed conservation areas, including the Namib-Naukluft, Dorob and Skeleton Coast National Parks, face a particularly acute challenge as these reserves occur within the hyper-arid lower reaches of the rivers. As such, they are last in line for water, especially sensitive to any upstream changes that alter patterns of downstream flow and materials transport (Jacobson et al., 1995). While desert stream ecosystems can expand and contract in response to wetting and drying cycles (Stanley et al., 1997), persistent drying of Namibia's ephemeral river ecosystems could result in their collapse (Jacobson et al., 1995). Thus, reductions in downstream flow, whether driven by climatic change or water development projects, pose a grave threat to Namibia's coastal conservation areas. The future of Africa's "super park" (Fuller, 2011) is far from secure.

Water extraction associated with mining, particularly uranium, poses perhaps the most immediate risk to some of Namibia's western ephemeral river ecosystems (Menges, 2011; Miller, 2010; NLAC, 2009). While coastal water demands have approximated the sustainable yield of the aquifers within the lower Kuiseb and Omaruru Rivers over the past several decades, increased demands associated with proposed uranium mining developments would vastly exceed sustainable supplies (Pallet, 2008). Perhaps most importantly, the economic value of water use per cubic meter in the uranium mining sector is far below that of water used in other economic sectors, with recent analyses noting that tourism is a far more efficient use of water resources than uranium mining (NLAC, 2009). Accordingly, development of coastal desalination facilities offers perhaps the best option for meeting increasing demands for domestic and industrial water while reducing reliance on the region's rivers, although the sourcing of associated energy needs remains unresolved (Pallet, 2008).

4.3. Climate change: an uncertain future

Rivers in arid or semi-arid regions are highly responsive to climatic change, and such responses may be distinctly nonlinear in arid climates (Dahm and Molles, 1992; Nemec, 1986), with slight changes in temperature and precipitation resulting in large changes in runoff. Various projections have highlighted the likelihood that southern Africa and its arid regions will experience significant warming and drying due to anthropogenic climate change (Dai, 2010), and continental-scale analyses of 20th-century records indicate that the Namib has already undergone an increase in temperature and a reduction in precipitation (Hulme et al., 2001). Regional studies across southern Africa reveal increases in occurrence of extreme hot days and dry season length, as well as increases in average rainfall intensity (New et al., 2006), although observed declines in regional precipitation are not yet statistically significant. Even optimistic projections of future emissions trajectories yield estimates of 10–20% declines in precipitation over southern Africa during the coming century (de Wit and Stankiewicz, 2006). Evidence for such changes and their potential impacts may already be emerging.

Foden et al. (2007) reported that regional warming and associated water balance constraints have led to population declines along the northern range limit of *Aloe dichotoma* in Namibia. An examination of local climatic records from *A. dichotoma's* range, including three stations within or near the headwaters of several of the westward-flowing ephemeral rivers, revealed significant increases in temperature and decreases in water balance over the past several decades. Foden et al. (2007) note that *A. dichotoma* is comparatively more robust than other plant species in its biome in the face of drought and climatic variation, providing a conservative indicator of the biotic impacts of regional warming and drying in the Namib.

Ultimately, the potential influence of projected climatic changes on downstream flow in the Namib's ephemeral rivers remains unclear. While increases in temperature combined with decreased precipitation will most certainly reduce downstream flow, changes in rainfall intensity and potential responses of catchment vegetation may also exert strong controls on downstream runoff. The palaeohydrologic record within the Namib's rivers highlights the importance of understanding the interactions between climate and hillslope processes within the catchments. Paleohydrologic changes involving periods of increased rainfall and runoff within the upper reaches of the rivers' catchments are thought to have shifted zones of aggradation along the river's lower reaches at various times during the Late Quaternary (Lancaster, 2002; Ward, 1987).

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5. Conclusions

This review of the ecological significance of hydrologic regimes within the Namib Desert's ephemeral rivers reveals the pervasive and critical influence of hydrologic controls on physical and biological processes. A clear body of evidence reveals that large shifts in the rivers' hydrology will yield undesirable alterations of their integrity, particularly within their lower reaches. Nonetheless, long-term utilization of the rivers' water resources with comparatively minor ecological impacts is possible, and has been achieved in rivers such as the Kuiseb. Without question, the most damaging hydrologic alteration for the rivers' lower reaches is large-scale impoundment within the upper catchment.

It is also clear that the future of these systems and their hydrologic regimes is uncertain. The trajectories of climate change and societal demands on the rivers' water resources are unknown, and the appropriate legislative instruments to ensure their protection are not yet in place. The challenge going forward is to thus ensure that development and utilization of water resources within the rivers stops short of the level which would result in the cessation of key physical and biological processes within the rivers' lower reaches (Table 5). Key to achieving this is the continuing maintenance and monitoring of the rivers' hydrologic gauging network, monitoring of groundwater tables where extraction is occurring, and ultimately, the use of such data in the adaptive management and conservation of the rivers' resources.

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