AN EPHEMERAL PERSPECTIVE OF FLUVIAL ECOSYSTEMS:

VIEWING EPHEMERAL RIVERS IN THE CONTEXT OF CURRENT LOTIC ECOLOGY

by

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(ABSTRACT)

Hydrologic and material dynamics of ephemeral rivers were investigated in the Namib Desert to assess how hydrologic regimes shape the physical habitat template of these river ecosystems. An analysis of long-term hydrologic records revealed that the variation in mean annual runoff and peak discharge were nearly four times higher than the global average, rendering the rivers among the most variable fluvial systems yet described. Further, a pronounced downstream hydrologic decay characterized all of the rivers. The high spatio-temporal variability in flow was reflected in patterns of material transport. Retention of woody debris increased downstream, in contrast to patterns typically reported from more mesic systems, largely attributable to hydrologic decay. Woody debris piles were the principal retentive obstacles and played an important role in channel dynamics. They were also key microhabitats for various organisms, forming 'hotspots' of heterotrophic activity analogous to patterns reported from perennial streams. Large amounts of fine particulate and dissolved organic matter (FPOM and DOM) deposited in the lower reaches of the rivers serve to fuel this heterotrophic biota. As a result of the hydrologic decay, sediment concentration (both organic and inorganic) increased downstream and the lower reaches of these rivers acted as sinks for material exported from their catchments. FPOM and DOM concentrations were among the highest reported for any aquatic system, and, contrary to patterns reported from more mesic systems, FPOM dominated the total organic load transported in these rivers. Inorganic solute concentration also increased downstream, resulting in a downstream increase in soluble salt content in floodplain soils. Soils within the river's lower reaches served as effective long-term integrators of hydrologic variability. The mean extent of floods entering the lower river was defined by an alluviation zone, evident from the convexity exhibited in the lower section of the rivers' longitudinal profiles. A downstream increase in the proportion of silt within floodplain soils is associated with increased sediment deposition. Silt deposition had a positive influence on moisture availability, plant rooting, and habitat suitability for various organisms, including fungi and invertebrates. In addition, a strong

positive correlation was observed between silt, organic matter, and macronutrients. Thus, the hydrologic control of transport and deposition patterns has important implications for the structure and function of ephemeral river ecosystems. Finally, an examination of the influence of elephants upon riverine vegetation highlighted the importance of these systems as isolated resource patches interspersed in an arid and hostile landscape. Further, it illustrated that flooding was a key ecological process and that hydrologic alterations would affect the fluvial ecosystem as well as the regional landscape they drain.

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General Introduction

Hydrologic variability is widely recognized as a key ecological organizer in fluvial ecosystems (Vannote et al. 1980, Junk et al. 1989, Poff and Ward 1990). As a result, attempts have been made to classify fluvial ecosystems based upon their hydrologic characteristics (see Poff 1996 for a recent review). However, these classifications have all exhibited a hydrologic bias towards mesic systems and none have included ephemeral rivers and streams. The paucity of information on ephemeral river systems and their biota is disconcerting when one considers their abundance. Thornes (1977) observed that approximately one third of the world is characterized by arid or semi-arid climates, and roughly another third exhibits seasonally concentrated river flow. Thus, a large proportion of the natural channels of the world exhibit intermittent or ephemeral flow. Such systems constitute the most abundant but least understood types of fluvial ecosystems. Yet, while geomorphologists have assiduously applied their efforts to developing an understanding of the sediment dynamics of these systems (Picard and High 1973, Graf 1988, Baker et al. 1988), ecologists have largely ignored them. As a result, virtually nothing is known regarding their organic matter dynamics, their biota, and the associated influences of their unique hydrologic regimes. Thus, I initiated a study of the hydrologic and material dynamics within the ephemeral rivers of Africa's Namib Desert, focusing in particular upon the Kuiseb River, a large (~560 km long, ~15,000 km^2 catchment) system that flows past the Desert Ecological Research Unit of Namibia. This facility, one of the few long-term ecological research sites on the continent, provided a convenient base from which to monitor hydrologic activity within this highly variable system.

Chapter 1 discusses an analysis of the long-term hydrologic records that were available for seven of the Namib's rivers. The spatial and temporal variability was assessed, both within and between these systems, and then compared to patterns reported from other fluvial systems the world over. These patterns are discussed in the context of their role in defining the habitat template within ephemeral river ecosystems, with reference to what is currently known regarding the biota of the Namib's ephemeral rivers.

Chapter 2 details the results of an investigation of the woody debris dynamics within the lower Kuiseb River. While the importance of woody debris to the structure and function of fluvial ecosystems has been well established for more mesic systems (Maser and Sedell 1994), no study has documented transport and retention patterns and their ecological significance within an ephemeral river. A mark-recapture approach was used to monitor the transport and retention patterns of woody debris associated with floods in the Kuiseb River. The influence of the river's hydrologic regime upon pre- and post-flood distribution of woody debris was examined, and retention mechanisms identified. Finally, observations were recorded regarding the geomorphologic and ecological significance of woody debris.

Although woody debris plays many important ecological roles in fluvial systems, the majority of the organic carbon load transported by rivers and streams consists of dissolved and fine particulate matter (Mulholland and Watts 1982), and dissolved matter is commonly the largest proportion. Patterns in ephemeral rivers are unknown. Similarly, little is known regarding the dynamics of inorganic particulates and solutes in association with floods. To my knowledge, only one study has recorded the variation in chemical characteristics of flood waters in an ephemeral river as the flood travels downstream (Sharma et al. 1984). Chapter 3 discusses the variation in chemical characteristics of floods as they travel downstream in the Kuiseb River. The composition of the organic and inorganic loads is discussed, and source and sink areas for transport materials identified.

Chapter 4 describes the alluvial soils within the lower reaches of three of the Namib's rivers, including the Kuiseb. I expected alluvial soils to be an effective long-term integrator of the hydrologic variability inherent in ephemeral systems. Thus, floodplain soils were sampled at multiple sites along the rivers to assess the influence of hydrologic variation on soil properties.

Finally, while the previous four chapters focus on the influence of floods in shaping abiotic characteristics of ephemeral river ecosystems, Chapter 5 examines the significance of the systems themselves in the broader context of the arid landscapes in which they lie. Ephemeral river courses provide a patchily distributed network of water and vegetation resources that are maintained by flood pulses and are key to the survival of many species of wildlife within the arid landscapes of the Namib Desert. The influence of the degradation or loss of individual resource patches on foraging behavior among remaining patches is discussed in the context of a population of desert elephants and the effect they are having on the vegetation of the Hoanib River. The conservation significance of flooding as a key ecological process is addressed in relation to its role in maintaining key habitat patches in arid landscapes.

I conclude with a brief discussion of some of the similarities among fluvial ecosystems that occur despite obvious differences in their hydrologic regimes. At the same time, the ecological characteristics of ephemeral rivers diverge from their more mesic counterparts in several important ways, and these are discussed in an attempt to develop a broader understanding of the influence of hydrology on the structure and function of fluvial ecosystems.

References

Baker, V.R., R.C. Kochel, and P.C. Patton, eds. 1988. *Flood geomorphology.* John Wiley & Sons, New York. 503 pp.

Graf, W.L. 1988. *Fluvial processes in dryland rivers*. Springer-Verlag, Berlin. 346 pp.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The Flood Pulse Concept in river-floodplain systems. Pages 110-127 in D. P. Dodge, ed. *Proceedings of the International Large River Symposium.* Can. Spec. Publ. Fish. Aquat. Sci.

Maser, C. and J.R. Sedell. 1994. *From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans*. St. Lucie Press, Delray Beach.

Mulholland, P. J., and J. A. Watts. 1982. Transport of organic carbon to the oceans by rivers of North America: a synthesis of existing data. *Tellus* 34: 176-186.

Picard, M.D. and L.R. High. Jr. 1973. *Sedimentary structures of ephemeral streams.* Elsevier Scientific Publishing Company, Amsterdam. 223 pp.

Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environ. Management* 14: 629-645.

Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrologic descriptors. *Freshwater Biology* 36: 71-91

Sharma, K. D., J. S. Choudhari, and N. S. Vangani. 1984. Transmission losses and quality changes along a desert stream: the Luni Basin in N.W. India. *Journal of Arid Environments* 7: 255-262.

Thornes, J.B. 1977. Channels changes in ephemeral streams: observations, problems, and models. Pages 317-335 in K.J. Gregory, ed. *River channel changes*. John Wiley & Sons, Chichester.

Vannote, R. L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Chapter 1:

Hydrologic characteristics of ephemeral rivers: implications for ecological pattern and process.

Abstract: Ephemeral rivers have been largely excluded from previous attempts to classify global hydrologic regimes or assess the role of hydrologic characteristics in regulating population and community processes and patterns in fluvial ecosystems. I examined the long-term flow records of a series of large ephemeral rivers in western Namibia to quantify their hydrologic characteristics and, in conjuction with preliminary field observations, postulate the significance of their distinctive hydrology for the structure and functioning of the associated biota. The ephemeral rivers crossing the Namib Desert are among the most hydrologically variable fluvial systems yet described. The mean annual coefficient of variation (CV_{MAR}) among 28 stations, representing 7 rivers, averaged 1.55, ranging from 0.80-3.32, compared with a global average of approximately 0.45. Distinct curvilinear relationships were observed between many hydrologic characters and longitudinal position along the mainstem river. In particular, mean peak discharge, flow volume, and days of flow per annum exhibited a marked decline in the lower reaches of the rivers, after a mid-catchment peak. Preliminary observations suggest that 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 secondary production. Despite the tolerance of the biota to harsh and variable abiotic conditions, these ecosystems are sensitive to hydrologic alterations because water is acutely limiting for many organisms and ecological processes. Understanding the biota within these systems and the role of hydrology in controlling system dynamics is a much-needed step in expanding our knowledge of the world's fluvial ecosystems.

Keywords: Namib Desert, floods, hydrology, riparian, organic matter dynamics

Introduction

The hydrologic regime is a key factor shaping the community structure of fluvial ecosystems, including both their aquatic and riparian components, as it is strongly correlated with many important habitat characteristics (Power et al. 1988, Poff and Ward 1990). The flow of water regulates the movement of materials, creating longitudinal, lateral, and vertical resource and disturbance gradients; determines the spatial and temporal distribution of both aquatic and riparian habitats, affecting desiccation and thermal stress, as well as population dynamics and biotic interactions; and serves as a link between aquatic and terrestrial components of the fluvial system (Vannote et al. 1980, Stanley et al. In Press, Palmer et al. 1996, Junk et al. 1989, Walker et al. 1995). Thus, as the variability of stream flow increases, so does the variability of many ecological processes. Because the importance of flow to pattern and process, various authors have attempted classifications of fluvial ecosystems based upon their hydrologic characteristics (Poff 1996).

Poff and Ward (1989) quantified the relative positions in 'flow space' of 78 streams from across the U.S., developing a conceptual framework to facilitate an a priori assessment of the relative importance of abiotic and biotic factors in regulating population and community processes and patterns in lotic ecosystems. 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 that constrains the types of species attributes appropriate for local persistence." Although their work excluded floodplain systems, this concept of a 'habitat template' could be extended to riparian areas as well. Thus, the abiotic characteristics (including hydrological) of a given fluvial system form the physical habitat template which influences the biota within it. Understanding the inherent variability of a system and the tolerances of key biotic elements provides a basic framework for evaluating ecosystem response to environmental change. Poff and Ward (1990) suggested that the cataloging of hydrologic and geomorphologic characteristics for a variety of representative lotic systems would provide such a framework for predicting recovery from both natural and anthropogenic disturbance across a broad geographic range.

An increasing interest in characterizing stream flow regimes has expanded the database from which inferences may be made regarding their influence on fluvial ecosystem structure and function (Poff 1996). Despite this increased interest, however, the geographic and hydrologic scope of these studies is still limited. Streamflow characterizations, whether regional (Alexander 1985, Jowett and Duncan 1990), continental (Poff and Ward 1989, Poff 1996) or global (Finlayson and McMahon 1988, Haines et al. 1988, McMahon 1979), have largely excluded systems at the xeric end of the hydrologic continuum or 'flow space.' For example, in Poff and Ward's (1989) study, the driest regime was their 'harsh-intermittent' class, exhibiting a mean of 269 days of flow per annum. In a more extensive analysis, Poff (1996) expanded the scope of this class to

include streams and rivers exhibiting an average of as few as 181.5 days of flow per annum. To date, however, no studies have quantified the hydrologic variability of ephemeral rivers or considered their role in the context of a general framework of 'habitat templates.' Thus, little is known of how the hydrologic characteristics of ephemeral rivers influence associated biota and their sensitivity to natural and anthropogenic disturbance.

Expanding the geography of fluvial ecosystems

Ephemeral rivers and streams have been excluded from the lotic classifications to date for several reasons, including the lack of hydrologic data, the lack of aquatic scientists within the world's drylands (and possibly their disinterest in systems often lacking an aquatic biota), and the comparative inaccessibility of many arid regions. For example, Haines et al. (1988), in their presentation of a world map of river regime types, noted that inadequate data were available to characterize dryland rivers. They lacked data for the vast arid expanses within northern and southern Africa, inland Australia, Asia, the Middle East, and portions of southwestern North America, most of which are drained by ephemeral systems. Ephemeral systems of South America, northern and southern Africa, the Middle East, and Asia were also largely omitted from the analyses of Finlayson and McMahon (1988). The extensive drylands of Australia were represented by only three stations located within the arid central deserts. Comin and Williams (1994) attributed the general lack of attention to dryland river systems to the fact that few limnologists live within or near dryland regions.

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 roughly another third exhibits seasonally concentrated river flow. Thus, a large proportion of the natural channels of the world exhibit intermittent or ephemeral flow. Such systems constitute the most abundant yet least understood types of fluvial ecosystems. This fact should motivate developing a better understanding of the hydrology and biota of dryland fluvial systems. Yet, hydrologic data remain scarce relative to more mesic systems. McMahon (1979) reported that in Australian arid zones (covering some 75% of the continent) there is one stream flow gauging station (with at least 15 years of data) per 350,000 km^2, in contrast with one per 3,200 km^2 in the humid regions. The hydro-climatic data network (HCDN), a U.S. Geological Survey streamflow data set comprising records from 1,659 stream-flow gauging stations, is strongly skewed towards more mesic systems (Landwehr and Slack 1992). The arid and semi-arid regions of the western U.S. contain comparatively few stations, and the majority of these are on perennial or intermittent systems.

An additional motivation for the study of these systems is the fact that in drylands around the world, current trends are towards the maximal exploitation of all available water resources. Thus, the maintenance of natural hydrologic regimes, and the biota they support, is becoming increasingly improbable as human populations, and

associated water demands, continue to grow. Many of these water-limited fluvial ecosystems may be radically altered before their characteristics are even dimly understood.

Distinctive features of ephemeral hydrologic regimes

Hydrologic regimes of ephemeral rivers are more difficult to characterize than those of more permanent rivers. Precipitation in ephemeral river catchments is highly sporadic, localized, and typically of short duration (Graf 1988). As a result, runoff is highly variable, both among years and among storms within a year; the rate of rise of hydrographs is typically very rapid, with peak discharges being reached within minutes; and runoff may be generated over small areas, so that tributary and even mainstem flow may occur while large portions of the channel system remain dry. At the same time, the number of precipitation and surface-flow measuring stations is dryland regions is too low to effectively monitor hydro-climatic activity (Graf 1988, Jacobson et al. 1995). In addition, precipitation and flow-record lengths are short and often interrupted, reliable stations are few, river cross sections in alluvial channels are frequently unstable during flow events, and surface flows are often violent and contain high levels of sediment and debris, resulting in frequent jamming of recording equipment. Thus, while the comparatively stable systems of more mesic regions have lengthy, uninterrupted records, the most spatially and temporally variable systems are characterized by the poorest records. Further, the irregularity of rainfall and associated floods, the frequency of zeros in runoff records, and the skewness of flow distributions complicate the analysis of hydrologic patterns in these systems.

Despite these difficulties, several well studied, but small, systems provide a general indication of hydrologic patterns typical of ephemeral rivers. 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 ephemeral channels is characterized by the 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. This downstream attenuation in flow volume is perhaps the best known characteristic of ephemeral rivers and has been reported from a number of systems of varying sizes, ranging from <1 km^2 to more than 30,000 km^2 (Leopold and Miller 1956, Vanney 1960, as cited in Mabbutt 1977, Leopold et al. 1966, Picard and High 1973, Sharma et al. 1984, Crerar et al. 1988, Schick 1988, Reid and Frostick 1989, Walters 1989, Hughes and Sami 1992, Sharma and Murthy 1994). However, these studies have viewed this pattern only with respect to its effects upon runoff yields for water supply, groundwater recharge, water quality, materials transport, and channel geomorphology. Little attempt has yet been made to interpret the ecological significance of these unique hydrologic patterns to the biota associated with these systems. Aquatic

ecologists have largely ignored such systems, given their limited (or nonexistent) aquatic fauna, which occur only where groundwater maintains temporary or perennial pools or streams. In a similar vein, terrestrial ecologists have examined elements of the riparian biota but have given little consideration to the influence of fluvial processes on their dynamics.

Ephemeral rivers of the Namib Desert

The ephemeral rivers crossing the Namib Desert provide a unique opportunity to investigate the hydrologic and biotic characteristics of large ephemeral systems. These rivers are unusual in that many are well-gauged and, in many cases, subjected to little alteration. Gauging stations have been in place since the mid-1960's to 1970's, accumulating a significant database managed by the Namibian Department of Water Affairs. In particular, the Kuiseb River catchment contains 14 automatic recording runoff stations, five of which are located along the mainstem river.

The reports of Stengel (1964, 1966) provided the first documentation of hydrologic events in four of the Namib's major ephemeral rivers. The studies compiled available data regarding the rivers' geology, hydrologic and sediment dynamics, and geohydrology. The hydrologic records were largely anecdotal, however, as the rivers either lacked automatic gauging stations, or individual stations had just recently been installed. Thus, no quantitative information could be provided on key hydrologic variables, and how these varied longitudinally within, as well as between systems. Similarly, little information was given regarding the biota supported by the rivers, except an account of the disturbance to the riparian forest associated with a major flood in the Kuiseb River in 1963. Nonetheless, the reports provide an important record of the historic frequency of large floods within the rivers.

My objectives in the present study were to analyze the available hydrologic data and quantify the hydrologic patterns within the large ephemeral rivers draining western Namibia; to contrast the variability of these systems to that of other rivers throughout the world; and to discuss the potential influence of the ephemeral hydrologic regime on ecological patterns and processes within the region's rivers, with reference to what is currently known of their flora and fauna.

Methods

Site Description

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 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. Twelve ephemeral rivers, with catchments from 2,000-30,000 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 (Jacobson et al. 1995). The rivers' headwaters receive from 100 mm to 400 mm of rain annually, dependent upon how far inland the catchment extends. Only the upper portions of the catchments, from the escarpment inland, contribute significant runoff to the lower reaches of the rivers in most years. The coastal desert plain contributes little runoff to the mainstem river in all but exceptionally wet years.

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 rain may begin in October and extend through May, most falls during the months of January through April, a fact reflected in the mean monthly runoff series of the gauging stations. Annual evaporative losses are high throughout the catchments, particularly in the lower desert reaches. In the Central Namib, a mean pan evaporation rate of 3,168 mm y^{-1} has been recorded, with yearly rates reaching as much as 4,000 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 3,000 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.

While their is a great deal of geological variation among catchments, all exhibit steep topographic and climatic gradients from their inland headwaters to their coastal or Namib termini. Of all the rivers, the geology of the Kuiseb River has been the most intensively studied and provides a general physiographic template for all of the rivers. Ward (1987) examined the Cenozoic geology of the Kuiseb Valley and provided a thorough review, with references to many of the other western rivers. The Kuiseb begins on the interior plateau of central Namibia at an elevation of ~2, 000 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.

Definition and use of hydrologic terms

At present, the confused state of the hydrologic lexicon complicates the classification of hydrologic regimes in dryland rivers. 'Ephemeral' has been used in various contexts and a brief review is necessary to establish some clarity in our use of the term. Mabbutt (1977) placed dryland rivers into three groups, each characterized by the source of its surface flow. Exogenous rivers arise in distant humid uplands, flowing into or across the desert. Examples include the Nile, Colorado, the Tarim of Asia, and the Murray-Darling system in Australia. All such systems are perennial, although their flow may exhibit great seasonal variability. The second group consists of those rivers rising in moister uplands within the desert itself. Mabbutt noted that such systems may, when snow- or spring-fed, be perennial, such as the Jordan, but typically are seasonal and exhibit increasing intermittency as they move onto the plains. Finally, the third and most common type of desert system Mabbutt identified was the ephemeral river, entirely dependent upon desert storms for surface flow. Such storm-fed systems contribute to, rather than draw from, local groundwater sources.

In a similar way, Boulton and Lake (1988) distinguished 'temporary' or 'intermittent' rivers, with more-or-less regular, seasonally intermittent discharge, from 'ephemeral' or 'episodic' rivers, which flow only after unpredictable rainfall. Matthews (1988) provided a definition based upon annual flow duration, distinguishing ephemeral systems, flowing <20 % of the year, from intermittent systems flowing between 20-80 % annually. This characterization is similar to that first proposed by Hedman and Osterkamp (1982) for streams in the western U.S., which focussed on both the percentage of time a system was flowing and the relative contributions of groundwater to that flow. Perennial streams were those with measurable surface discharge more than 80 % of the time, part or all of which was from groundwater discharge from adjacent upland areas into the channel. Intermittent streams were those flowing from 10 to 80 % of the time, with a channel at or near the water table surface. Discharge could be the result of discontinuous supply from either groundwater or surface water sources or both. Finally, an ephemeral stream was one flowing only in direct response to precipitation; with measurable discharge occurring less than 10 % of the time. The stream channel is above the water table at all times, and thus receives no contributions from groundwater sources. One drawback of this scheme, however, is that assessing groundwater contributions to seasonal flow is not possible given the limited data available for most dryland systems. Thus, distinguishing intermittent from ephemeral systems based upon geohydrologic characteristics is not easily accomplished for most systems.

Most recently, Comin and Williams (1994) recognized the numerous adjectives used to describe streams and rivers exhibiting temporary flow and provided a lexicon based on their literature review. Temporary systems, which are frequently dry, were divided into intermittent and episodic running waters. Intermittent systems, occurring in semi-arid as well as temperate and tropical regions, contain water or are dry at more or

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less predictable times during an annual cycle. They may be dry for <1 month and have highly predictable flows during a well-defined wet season, or they may be dry for periods considerably longer than one month and have less predictable flows during a short wet season. In contrast, episodic systems, restricted to arid and hyper-arid regions, contain water on an unpredictable basis. They discouraged the use of the term ephemeral as a synonym for episodic and the use of the term temporary as a synonym for intermittent. I find this general classification scheme unsatisfactory, however, because it hinges on a loosely defined classification of the predictability of flow and the length of intervening dry periods. It is unclear exactly where the threshold between intermittent and episodic occurs. Nonetheless, such distinctions must be viewed as arbitrary, for fluvial systems and their associated biotic characteristics span a hydrological continuum ranging from dry palaeochannels exhibiting zero annual flow to perennial channels in which annual flow is never interrupted. Herein, I will use the definition of Hedman and Osterkamp (1982), and define ephemeral rivers as those systems in which measurable discharge occurs less than 10 % of the year.

Finally, the definition of a flood as a distinct hydrologic event warrants some discussion given the unique nature of ephemeral river hydrologic regimes. Floods in alluvial channels have been defined geomorphologically as occurring whenever flow fills the channel to (or beyond) bankfull discharge, ending when discharge drops below this level (Leopold et al. 1964). In ephemeral rivers, however, floods may be said to occur whenever there is flow within the usually dry channel and are characterized by their magnitude, duration, total flow volume, and number and magnitude of discharge peaks during the flood. The flood ends when surface flow ceases. Thus, a flood in an ephemeral system is not a gradual rise in stage, causing the inundation of lateral areas, but rather a comparatively rapidly moving, longitudinal throughput.

In a similar way, the definition of a floodplain within ephemeral rivers is complicated by the unique nature of the hydrologic regime. Floodplains are traditionally defined as surfaces periodically inundated by lateral overflow from an adjacent river. While floodplains in ephemeral rivers are distinct from the active channel based upon geomorphologic criteria, in an ecological sense the channel itself may often function as a floodplain, being periodically inundated by flood pulses with or without the inundation of adjacent floodplains.

Regional Hydrologic Summary

The gauging records from the western rivers were reviewed to identify stations with the most extensive records and a minimum of missing years. Flow statistics were calculated for the individual stations and then summarized for comparison with other regional analyses. A total of 28 gauging stations, representing 7 rivers were used in the analyses. The mean record length for the 28 stations was 20 years, ranging from 13-32 years of record. In addition, the Ugab and Omaruru Rivers contained widely separated

stations along the mainstem channel, allowing an examination of the longitudinal variation in hydrologic characteristics. Although the records from individual stations may have been of longer duration, the temporal scope of this analysis was restricted to those periods for which data were available from all mainstem stations.

The following descriptive statistics were calculated from the annual runoff series for each station using NCSS 6.0 statistical software: mean annual runoff volume (m^3) (MAR_V); coefficient of variation of mean annual runoff (CV_{MAR}), calculated as the standard deviation divided by the mean; coefficient of skewness of the mean annual runoff (CS_{MAR}); mean annual peak discharge ($m^3 s^{-1}$) (MAPD), calculated from the annual peaks in the runoff series; mean annual runoff depth (mm) (MAR_D), calculated by dividing the mean annual runoff (m^3) by the station's catchment area (km^2) and dividing by 1,000; and mean percent runoff, calculated by dividing the mean annual runoff (mm) by the estimated mean annual precipitation (MAP) over the station's catchment area (MAP and catchment area were obtained from records of the Namibian Department of Water Affairs). The average of the 28 values of each statistic was then calculated to provide the summary statistics reported herein. The total river length and relative positions of the individual stations were obtained by digitizing the channel course from 1:50,000 scale topographic maps. Zero-flow years were identified from each station's annual runoff series.

Kuiseb River Analyses

A more detailed analysis was conducted on the 14 Kuiseb River stations, allowing an examination of the range of variability within a single river system. The Kuiseb River is unique among Namibia's western rivers in that it encompasses 14 gauging stations, positioned on both tributaries and the mainstem river. Five stations monitor mainstem flow from drainage areas ranging from approximately 210 to 14,700 km^2. These stations span nearly the entire length of the river (~ 560 km), the first sited 58 km from the headwater and the last at 535 km. Nine additional stations are dispersed throughout the catchment, monitoring flow from tributaries draining from 17.3 to 2,490 km^2. All of these stations occur from the base of the escarpment eastward, monitoring the source areas for the majority of the flow reaching the lower river. Although one mainstem station has a continuous record since 1963, most stations were only installed in 1977/78. Thus, a 15-year record was used in the analyses, extending from 1979 to 1993.

Summary statistics for the 14 stations were calculated as previously described. In addition, a series of statistics was calculated to characterize the variability among individual floods at the 5 mainstem stations. The mean number of floods per year was calculated for each station from an analysis of the annual runoff series. Floods were defined as distinct events, separated by a minimum of a 24 h period without flow. Although many floods contained multiple peaks in response to tributary inflow or multiple precipitation events, these fluctuations were not considered as discrete floods. The length of each flood was also derived from the runoff records, and the total number of

floods over the 15 year record was summed for each station. Finally, the mean annual date of the first flood was calculated from the annual runoff series. The hydrologic year begins October 1 and runs through September 30 of the following calendar year. Flow records were converted to Julian dates and analyzed to determine the mean date.

Results

Regional Summary

The mean annual flow statistics for the 28 stations, summarized in Table 1, reveal the highly variable nature of the rivers' hydrologic regimes. MAR_V averaged 6.8×10^6 m^3, ranging from approximately $0.023\text{-}29.6 \times 10^6$ m^3. The coefficient of variation of the mean annual runoff (CV_{MAR}) averaged 1.55, ranging from 0.80-3.32. Stations recording flow from the comparatively mesic headwater regions exhibited the lowest variability in their annual runoff series, while the two coastal stations in the database yielded the two highest CV_{MAR} values recorded. Nonetheless, there was no correlation between catchment size and the CV_{MAR} ($r^2=0.009$). The influence of infrequent, high-magnitude events on the mean values was reflected in the coefficient of skewness (CS_{MAR}), averaging 2.21 with a range from 0.41-3.94. With the exception of several small, comparatively mesic headwater stations, normality was rejected for all of the annual flow series. The average MAR_D for the 28 stations was 2.92 mm, ranging from 0.18-14.9 mm. Percent runoff averaged approximately 1.0 %, ranging from 0.09 to 3.82 %.

Distinct longitudinal trends were readily apparent among the mainstem stations on the Omaruru and Ugab rivers (Tables 2 and 3). From the headwaters towards the coast, MAR_V first increased, then decreased markedly at downstream stations in both rivers. A similar pattern was observed in the MAPD and MAR_D series, which declined towards the coast, after a peak in the upper to middle reaches of the catchments. Associated with the downstream decay in total runoff was a marked increase in the both the CV_{MAR} and the CS_{MAR} of the annual runoff series. The 2-3 fold increase in both statistics between the inland and coastal stations reflects the increasingly variable nature of the hydrologic regime in the lower reaches of the rivers. There was also an increase in the occurrence of zero-flow years in the runoff series at downstream stations. While the upper reaches of the Omaruru River flow almost annually, no flow was recorded at the Henties Bay gauging station for 10 years of a 19-year flow series. The Ugab River also exhibited a less pronounced increase in the number of zero-flow years at downstream stations, increasing from 0 in the headwaters to 3 at the coast (Table 3).

Kuiseb River Analyses

Gauged catchments within the Kuiseb River system range from $17.3\text{-}14,700$ km^2, producing a MAR_V among the fourteen stations of $\sim 1.9 \times 10^6$, with a range of 0.023×10^6 m^3 to more than 6.5×10^6 m^3 per annum. The variability among stations was high, with CV_{MAR}

values ranging from 0.79-2.00 (mean=1.31). A negative linear relationship (r^2=0.50) was present between the CV_{MAR} and the MAR_D. Few of the annual series exhibited a normal distribution, a fact reflected in the high CS_{MAR} values, ranging from 0.41-2.64 (mean=1.50). Finally, MAR_D and % runoff were low, averaging 2.25 mm (0.04-7.20) and 0.76 % (0.025-2.15), respectively.

The mainstem stations of the Kuiseb River exhibited longitudinal trends similar to those observed among the mainstem stations of the Ugab and Omaruru Rivers (Table 5). The five Kuiseb stations span 477 km of the roughly 560 km long river, and over this distance, MAP drops from roughly 330 mm at the Friedenau station, to 11 mm at Rooibank. Catchment areas monitored by the stations range from 210-14,700 km. The MAR_V exhibited a strong curvilinear relationship (r^2=0.94) with distance downstream. Runoff increased from the headwater Friedenau station ($1.5x10^6$ m^3) to the base of the escarpment, peaking at approximately $6.6x10^6$ m^3 at Schlesien. Westward from the Schlesien station, MAR_V decreased markedly, dropping to only $0.638x10^6$ m^3 at Rooibank, a seven-fold decline over some 230 km of river. Expressed in mm per annum, MAR_D exhibited a negative linear relationship (r^2=0.84) with distance from headwaters to coast, dropping from 7.17 mm to 0.04 mm over the 477 km distance. The MAPD showed a similar trend to that of MAR_V, increasing from the headwaters towards the base of the escarpment, and then rapidly declining westwards.

Associated with the downstream decay in MAR_V was a positive linear relationship between the CV_{MAR} (r^2=0.95) and distance downstream. The influence of infrequent, high-magnitude events on the mean runoff values is reflected in the downstream-increase in the CV_{MAR} and CS_{MAR} values. The CV_{MAR} ranged from 0.79 at Friedenau in the headwaters of the catchment, to 1.57 at Rooibank, 477 km downstream and roughly 25 kilometers from the coast. Of particular interest was the increasing discrepancy between the mean and median annual runoff values from the headwaters to the coast. At Friedenau, close to the headwaters, the median runoff value was 94 % of the mean. At Gobabeb, however, 421 km downstream, the median was only 27 % of the mean annual runoff value. At Rooibank, another 56 km downstream, the median had dropped to zero. The median value of zero at Rooibank is attributable to the increase in zero-flow years, from 0 at the headwater and escarpment stations, to 9 over a 15 year record at Rooibank.

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 the stations. Most obvious was the marked decrease in the average number of floods per year. While the Friedenau station recorded an average of 7.9 floods per year (CV=0.43), only 0.9 floods per year reach Rooibank (CV=1.22). Over the 15 year record, from 1979-1993, a total of 118 floods were recorded at Friedenau, dropping to only 13 at Rooibank. The average duration of individual floods also varied among stations. At Friedenau, floods lasted an average of 3.7 d, increasing to 11.1 d at Schlesien, and then declining to 2.2 d at

Rooibank. The onset of flow, expressed as the Julian date (JD), also varied widely between stations. The mean date of the first flood at Rooibank (JD=129) was delayed by two months relative to Friedenau (JD=68). The mean date for the Schlesien station of 105, equivalent to 13 January, is reflected in the mean monthly flow distribution, compiled from the 32 year annual runoff series. Finally, the mean total days of flow per annum increased slightly from Friedenau to Us (24.4-28.9 d y^{-1}), followed by a pronounced downstream decline to only 3.9 d y^{-1} at Rooibank.

Discussion

Namibia's westward-flowing ephemeral rivers exhibit extreme hydrologic characteristics, ranking them among 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 Namibia is approximately 1.0%. 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 (1983), 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. These values reflect the comparatively 'mesic' nature of the stations in McMahon's arid region database. In McMahon's study, only 11 of 68 catchments exhibited MAR_D below 10 mm, in contrast to 27 of the 28 Namibian stations. The MAR_D of the Namibian stations averaged 2.92 mm, compared to 21 mm for 16 Australian stations, the most arid group in McMahon's analysis. In contrast, on a global basis, McMahon (1992) reported a CV_{MAR} of 0.45-0.48 for world rivers with catchments ranging up to 10,000 km^2. Values for southern Africa ranged from 0.78-0.81 and for Australia, 0.59-0.88.

Downstream increases in CV_{MAR}, such as those observed among mainstem stations along Namibia's rivers, have been previously reported. In Australia, researchers noted that as catchment area increases, the variability in annual flow (CV_{MAR}) also increases, the reverse of that observed in more mesic systems (Finlayson and McMahon 1988, McMahon et al. 1991). McMahon (1992) noted that Australia was the only continent where mean CV_{MAR} increased with catchment area. This pattern was explained by the fact that many large Australian rivers enter the sea in well-watered areas, yet rise in arid interior regions exhibiting high flow variability (Finlayson and McMahon 1988). This climatic gradient is the reverse of that in western Namibia, where the headwaters of the rivers are better-watered relative to downstream reaches. In Namibia, the downstream increase in hydrologic variability can be attributed to the downstream increase in the aridity of the catchments and the associated hydrologic decay.

On a global scale, there is a strong positive relationship between annual runoff and catchment area (McMahon 1992). In contrast, although the relationship is poor (r^2=0.07), the trend among the 28 Namibian stations is a decrease in runoff with increasing catchment size. The poor correlation can be attributed to the fact that many stations in

the Namibian database, while of similar size, exhibit large differences in MAR_D dependent upon their position within the strong east-west climatic gradient across the region. Similarly, while McMahon (1983) observed a general increase in runoff variability as MAR_D decreased, I observed a poor relationship amongst the 28 Namibian stations ($r^2=0.009$). This was again attributable to the influence of the climatic gradient, inducing variation in MAP amongst catchments of similar sizes.

Unquestionably, 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. This trend is typified by the general increase in flow volume from the headwaters through the escarpment, followed by the pronounced decay in the Namib reach of the rivers. A similar relationship with distance was observed for the mean discharge, individual flood duration, and the total number of days of flow per annum. Given the importance of flow in regulating the characteristics of fluvial and riparian ecosystems, I predict that similar curvilinear patterns occur in the structure and functioning of biotic communities within the Namib's rivers.

Hydrologic Gradients - Implications for pattern and process

Given the pronounced variability and downstream decay that characterize their hydrologic regimes, I believe that ephemeral systems constitute a unique 'habitat template' among the world's river and stream ecosystems. The spatial relationships within any fluvial ecosystem can be viewed in terms of lateral (channel-floodplain), longitudinal (upstream-downstream) and vertical (surface-groundwater) linkages within the stream network, the relative importance of which vary in space and time within and between systems (Ward 1989). Flow is strongly correlated with most of the important abiotic attributes of fluvial systems, including erosive disturbance, desiccation and thermal stress, and resource availability and renewal rates. Thus, as the variability of stream flow increases, so too does the variability of many ecological processes. I predict that in ephemeral rivers, patterns of erosive disturbance, organic matter retention, soil moisture availability, habitat complexity, species richness, and the rate and duration of many ecological processes, will all reflect the linear and curvilinear relationships between runoff characteristics and position within the river network.

For example, in perennial floodplain rivers, the magnitude, frequency, and duration of floods diminishes laterally away 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 I expect riparian vegetative communities to vary accordingly, in response to shifting patterns of disturbance and moisture availability. I propose that the longitudinal variation in flood intensity (mean annual frequency, magnitude, and total flow volume) results in a subsidy-stress gradient (sensu Odum et al. 1979). Along this gradient, increases or decreases in flood intensity,

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interacting with channel physiography, can either enhance or reduce riparian productivity at a site through shifts in erosive disturbance and desiccation stress.

Peckarsky (1983) suggested that streams may be located along a gradient from harsh to benign physical conditions, with the relative control of lotic community structure by abiotic or biotic factors dependent upon a streams position along this gradient. I believe that this view can be extended to all fluvial ecosystems, including those of ephemeral river systems. My observations suggest that interactions between hydrologic characteristics and channel physiography determine the disturbance regime at any particular site within the channel network. In the lower reaches of the Namib's ephemeral rivers, erosive disturbance increases upstream in association with an increase in flow frequency, volume and discharge, combined with the effects of an increasingly confined channel cross section. While the frequency and magnitude of this disturbance decreases downstream due to hydrologic decay and a broadening channel, desiccation stress increases with the reduction in frequency and magnitude of flooding.

Ward and Stanford (1983) suggested that the intermediate-disturbance hypothesis of Connell (1978) provided an explanation for species diversity patterns in lotic ecosystems. The hypothesis predicts that species diversity will be greatest in communities subjected to moderate levels of disturbance. Diversity is enhanced by the spatio-temporal heterogeneity resulting from intermediate disturbance, which maintains the community in a non-equilibrium state. Vannote et al. (1980) observed that the middle reaches of the stream continuum, the region of greatest environmental heterogeneity, exhibit the highest species diversity values. Headwater reaches and the lower portions of rivers have lower diversity values associated with more constant environmental conditions. I expect that the hydrologic control of disturbance and moisture availability in ephemeral rivers creates a similar continuum along the river network, wherein intermediate reaches 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. This view is supported by 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.

Finally, hydrologic influences over soil characteristics in ephemeral rivers may also exert strong controls on riparian vegetation communities. A recent study revealed that high levels of nutrients and organic matter were present in the riparian soils of the Kuiseb River, relative to those in adjacent upland sites (Abrams et al. 1997). Although the study did not examine potential longitudinal patterns in soil characteristics, the pronounced downstream attenuation in both mean flood frequency and magnitude may influence soil characteristics such as salinity and organic matter content, among others.

The flood pulse in ephemeral rivers

I believe that floods are the key ecological organiser responsible for the existence, productivity, and interactions of the main biotic elements within ephemeral river ecosystems. While originally proposed in reference to large, perennial systems such as the Amazon (Junk et al. 1989), this hypothesis is equally relevant to the study of ephemeral rivers. However, interpreting the ecological significance of floods in ephemeral rivers depends upon the recognition of the importance of both lateral and longitudinal linkages. While the view of the flood pulse put forward by Junk et al. (1989) stressed the lateral interaction between the channel and river, the longitudinal linkges associated with ephemeral river floods are of equal if not greater significance.

Longitudinal transfers of water and materials are critical to the functioning of the water-limited riparian ecosystems in ephemeral rivers, where any input of moisture, irrespective of its variability, may serve to supplement available resources. In ephemeral rivers crossing the Namib Desert, where rainfall averages 20-50 mm, flood pulses not only serve to transfer materials laterally and longitudinally, but also provide a key resource (water) that limits primary and secondary production, thus triggering ecosystem processes. Flood pulses within the rivers activate a terrestrial decomposer community consisting of a diverse assemblage of invertebrates and fungi, otherwise inactive during intervening dry periods (Jacobson et al. 1995, Shelley and Crawford 1996, Jacobson et al. In Review). Ephemeral river ecosystems thus function in many respects as a 'floodplain without a river', wherein the highly variable fluvial processes support a terrestrial biota, dependent upon flooding.

Junk et al. (1989) suggested that the flood pulse concept is 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, noting that floods in dryland rivers are no less significant for riverine processes, despite their greater spatio-temporal variability. They pointed out that life-history traits such as opportunism and flexibility can be viewed as adaptations to unpredictability and are characteristic of many elements of the biota in dryland systems. My observations in the Namib's rivers lend support to this view.

While floods in dryland rivers and streams have been seen in the context of aquatic communities as a disturbance (Fisher and Grimm 1991), I suggest that it is the prolonged absence of flooding that constitutes a disturbance in ephemeral river ecosystems. Junk et al. (1989) first proposed this view in reference to large floodplain-river ecosystems, where they felt the absence of the seasonal flood pulse would constitute a disturbance rather than the pulse itself. Flood pulses in ephemeral rivers, although undoubtedly a disturbance to isolated aquatic communities, are not disturbances in the context of the catchment as a whole. At present, however, no studies have detailed faunal responses to

flood pulses other than the work of Viljoen (1989), who noted that floods influence the seasonal distribution of elephants in the northern Namib Desert.

Hydrologic variability and organic matter dynamics

Given the extended periods without surface flow, organic matter from riparian litterfall and adjacent upland sources (via aeolian inputs) accumulates in the dry channels of the Namib's ephemeral rivers. These in-channel organic matter accumulations are analogous to, although occasionally more extreme, the seasonal accumulations reported from intermittent streams. Boulton and Lake (1988) observed that in the Australian catchments of intermittent streams draining *Eucalyptus* spp. forests, peak litterfall coincided with periods of low or zero flow, resulting in the accumulations of large amounts of detritus in receding pools and the dry streambed. When flow begins, a 'pulse' of organic matter (both coarse particulate and dissolved) moves downstream, the fate of which is entirely unknown (Boulton and Suter 1986). Similar observations have been made in North American prairie streams, where it has been reported that much of this material may be reinjected into downstream riparian habitats (Gurtz et al. 1988).

Boulton and Suter (1986) recognized the aquatic bias of intermittent-stream ecology, pointing out the paucity of work done on the inhabitants of dry streambeds. In listing the common elements of the terrestrial fauna in two intermittent streams in Victoria, they noted that, "these invertebrates may be important terrestrial consumers of material originally produced or exported by the stream and provide an interesting reversal of the terrestrial to aquatic transfer." They coined the term 'terrestrial limnology' in reference to the terrestrial processing of fluvially-derived organic matter. Busch and Fisher (1981) suggested a similar fate for the 'excess' production exported from desert streams by floods, although no mention was made of the fate of fluvially-transported allochthonous organic matter.

In a similar way, little is known regarding the organic matter dynamics of ephemeral rivers, including both fluvial transport and subsequent processing. Nonetheless, several facts are clear from my preliminary observations. First, the patterns of transport and processing of organic matter in ephemeral rivers diverge from those reported from more mesic systems in that they are uncoupled from one another. Transport occurs during flooding, when material is transported from one terrestrial environment and deposited in another. Further, although some processing occurs in the terrestrial phase throughout the year, flood pulses trigger a significant increase in the rate of organic matter decomposition (unpublished data). Thus, transport, and processing to some degree, are discontinuous, occurring in discrete 'batches' associated with flood pulses. This pattern is markedly different from that in most lotic 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).

Finally, given the downstream hydrologic decay, I hypothesize that organic matter retention increases in the lower reaches of the rivers, in direct response to the decreased stream power associated with the declining discharge. Preliminary observations suggest that increasing channel complexity and an increase in riparian vegetation may also significantly influence retention (unpublished data). Although such a pattern would contrast with that reported in low- to mid-order perennial streams and rivers, it is similar to hypotheses regarding the historic patterns associated with lowland perennial rivers (Sedell and Froggatt 1984, Triska 1984). A similar pattern has been reported from intermittent prairie streams and ephemeral streams, where a downstream increase in retention has also been observed (Crocker 1993, Gurtz et al. 1988).

Hydrologic alteration and ephemeral river ecosystems

While much remains to be learned regarding these inherently variable ecosystems, and the tolerances of key elements of their biota, I believe it is clear from the preceding analysis and discussion that their hydrologic regime plays a central role in shaping and regulating their patterns and processes. At the same time, it is clear from the limited evidence to date, that changes in that hydrologic regime will be translated directly into changes in the structural and functional characteristics of the systems.

Given the extreme pressure being placed upon dryland systems around the planet by rapidly expanding human populations, there is an urgent need to develop a broader understanding of the role that hydrological processes play in structuring in maintaining the full range of fluvial ecosystems and not just those of wet-temperate or perennial-dryland rivers. While Walker et al. (1995) suggested that dryland rivers have an extraordinary capacity to absorb change, this assertion has not been tested in the context of ephemeral rivers. There are reasons to believe that such systems may be highly sensitive to certain types of disturbance. I suggest that hydrologic alterations are the greatest threat these systems face, either through anthropogenically-induced shifts in regional climate or through the construction of water control structures. The non-linear response of arid catchment runoff to changes in precipitation has been well documented, suggesting even small shifts in precipitation patterns could significantly affect runoff patterns (Dahm and Molles 1992, Rodier 1985). At the same time, the greater hydrologic variability inherent in ephemeral rivers is taken into consideration in the construction of water storage impoundments. Larger reservoir capacities are required, relative to rivers in humid regions, to ensure a stable annual yield of significant volume. For example, 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.

I believe that such alterations in the hydrologic regime of ephemeral rivers would translate into marked shifts in the longitudinal abiotic gradients which characterize these systems, affecting disturbance regimes, organic matter retention patterns, soil moisture

availability, and the rate and duration of many ecological processes. These shifts would induce significant changes in the species richness and productivity of ephemeral river ecosystems. Dewatering ephemeral rivers could in effect, result in the contraction of these ecosystems, eliminating local refugia and creating gaps in the regional landscape (Jacobson et al. 1995). For example, closure of a large (69 Mm^3) impoundment in the upper Swakop River catchment dramatically reduced the MAR in the lower river, triggering a drop in the groundwater table, a loss of perennial streamlets and associated wetlands, and a large dieback of the riparian tree, *Faidherbia (Acacia) albida*. Ward and Breen (1983) reported a large die-back of mature specimens of this tree along the lower Kuiseb River in response to the prolonged absence of surface flow (4 years) and associated groundwater declines. This event is unique in the 34 year flow record of the river. These examples serve to highlight the potential sensitivity of ephemeral river ecosystems to hydrologic alterations. At present, however, our ability to assess the impacts of hydrologic alterations on ephemeral river ecosystems is constrained by our limited knowledge of the diversity of their biota, as well as the tolerance ranges of the individual elements.

Finally, classifying all rivers flowing less than 10 % of the year as ephemeral masks the variability among individual systems. Rivers and streams with perennial flow exhibit a wide range of biologically significant variability in their hydrologic regimes, such as the seasonal patterns differentiating snow-melt from spring-fed streams (Poff and Ward 1989). In a similar way, not all ephemeral rivers are created equal. Many are allogenic, to one degree or another, draining better-watered mountains or inlands, and thus exhibiting pronounced climatological gradients from their headwaters to lower reaches. Others, with their catchments lying solely within an arid zone would not exhibit allogenic control of their hydrologic regime. Poff and Ward (1990) suggested that cataloging the hydrologic and geomorphologic characteristics for a variety of representative lotic systems would provide a framework for predicting recovery from both natural and anthropogenic disturbance across a broad geographic range. Such a catalog has been developed for the 'flow space' spanning perennial to intermittent systems. I believe that such an approach, if expanded to include the xeric end of the hydrologic continuum and encompass ephemeral rivers and streams, would be a significant contribution to the pressing challenge of managing the finite water resources and river and stream ecosystems of the world's drylands.

Acknowledgments

References

Alexander, W.J.R. 1985. Hydrology of low latitude Southern Hemisphere land masses. *Hydrobiologia* 125: 75-83.

Bell, D.T. 1974. Tree stratum composition and distribution in the streamside forest. *American Midland Naturalist* 92: 35-46.

Boulton, A.J., and P.S. Lake. 1988. Australian temporary streams - some ecological characteristics. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* 23: 1380-1383.

Busch, D.E., and S.G. Fisher. 1981. Metabolism of a desert stream. *Freshwater Biology* 11: 301-307.

Comin, F.A., and W.D. Williams. 1994. Parched continents: Our common future? Pages 473-527 in R. Margalef, ed. *Limnology now: a paradigm of planetary problems.* Elsevier, Amsterdam.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Crerar, S., R.G. Fry, P.M. Slater, G.v. Langenhove, and D. Wheeler. 1988. An unexpected factor affecting recharge from ephemeral river flows in SWA/Namibia. Pages 11-28 in I. Simmers, ed. *Estimation of natural groundwater recharge.* D. Reidel Publishing Company.

Crocker, M.T. 1993. Benthic organic matter storage response to ephemeral streamflow in a semi-arid landscape. *Bulletin of the North American Benthological Society* 10: 109.

Dahm, C.N., and M.C. Molles, Jr. 1992. Streams in semiarid regions as sensitive indicators of global climate change. Pages 250-260 in P. Firth and S.G. Fisher, eds. *Global climate change and freshwater ecosystems.* Springer-Verlag, New York.

Finlayson, B.L., and T.A. McMahon. 1988. Australia versus the world: a comparative analysis of streamflow characteristics. Pages 17-40 in R.F. Warner, ed. *Fluvial geomorphology of Australia.* Academic Press, Sydney.

Fisher, S.G., and N.B. Grimm. 1991. Streams and disturbance: are cross-ecosystem comparisons useful? Pages 196-221 in J. Cole, G. Lovett, and S. Findlay, eds. *Comparative analyses of ecosystems: patterns, mechanisms, and theories.* Springer-Verlag, New York.

Gurtz, M.E., G.R. Marzolf, K.T. Killingbeck, D.L. Smith, and J.V. McArthur. 1988. Hydrologic and riparian influences on the import and storage of coarse particulate organic matter in a prairie stream. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 655-665.

Haines, A.T., B.L. Finlayson, and T.A. McMahon. 1988. A global classification of river regimes. *Applied Geography* 8: 255-272.

Hedman, E.R., and W.R. Osterkamp. 1982. Streamflow characteristics related to channel geometry of streams in Western United States. *U.S. Geological Survey Water-Supply Paper* 2193: 1-17.

Hughes, D.A., and K. Sami. 1992. Transmission losses to alluvium and associated moisture dynamics in a semiarid ephemeral channel system in southern Africa. *Hydrological Processes* 6: 45-53.

Jacobson, P.J., K.M. Jacobson, and M.K. Seely. 1995. *Ephemeral rivers and their catchments: sustaining people and development in western Namibia*. Desert Research Foundation of Namibia, Windhoek. 160 pp.

Jacobson, K.M., P.J. Jacobson, and O.K. Miller, Jr. In Review. The autecology of *Battarrea stevenii* (Liboshitz) Fr. in ephemeral rivers of southwestern Africa. *Mycological Research*.

Jowett, I.G., and M.J. Duncan. 1990. Flow variability in New Zealand rivers and its relationship to in-stream habitat and biota. *New Zealand Journal of Marine and Freshwater Research* 24: 305-317.

Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The Flood Pulse Concept in river-floodplain systems. Pages 110-127 in D.P. Dodge, ed. *Proceedings of the International Large River Symposium*. Canadian Special Publications in Fishries and Aquatic Sciences.

Landwehr, J.M. and J.R. Slack. 1992. Hydro-Climatic Data Network: a U.S. Geological Survey streamflow data set for the United States for the study of climate fluctuations, 1874-1988. *U.S.Geological Survey Open-File Report 92-632*.

Leopold, L.B., W.W. Emmett, and R.M. Myrick. 1966. Channel and hillslope processes in a semiarid area, New Mexico. *U.S. Geological Survey Professional Paper 352-G*: 193-253.

Leopold, L.B., and J.P. Miller. 1956. Ephemeral streams - hydraulic factors and their relation to the drainage net. *U.S. Geological Survey Professional Paper 282-A*.

Mabbutt, J.A. 1977. *Desert landforms.* The MIT Press, Cambridge.

Matthews, W.J. 1988. North American prairie streams as systems for ecological study. *Journal of the North American Benthoogical Society* 7: 387-409.

McMahon, T.A. 1979. Hydrological characteristics of arid zones. Pages 105-123. *The hydrology of areas of low precipitation.* International Association of Hydrological Sciences, Canberra.

McMahon, T.A. and R.G. Mein. 1978. *Reservoir capacity and yield*. Developments in Water Science, No. 9, Elsevier, Amsterdam.

Mitsch, W.J., J.R. Taylor, and K.B. Benson. 1991. Estimating primary productivity of forested wetland communities in different hydrologic landscapes. *Landscape Ecology* 5: 75-92.

Newbold, J.D., J.W. Elwood, R.V. O'Neill, and A.L. Sheldon. 1983. Phosphorous dynamics in a woodland stream ecosystem: a study of nutrient spiralling. *Ecology* 64: 1249-1265.

Newbold, J.D., P.J. Mulholland, J.W. Elwood, and R.V. O'Neill. 1982. Organic carbon spiralling in stream ecosystems. *Oikos* 38: 266-272.

Odum, E.P., J.T. Finn, and E.H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. *BioScience* 29: 349-352.

Palmer, M.A., P. Arensburger, A.P. Martin, and D.W. Denman. 1996. Disturbance and patch-specific responses: the interactive effects of woody debris and floods on lotic invertebrates. *Oecologia* 105: 247-257.

Picard, M.D., and L.R. High, Jr. 1973. *Sedimentary structures of ephemeral streams.* Elsevier Scientific Publishing Company, Amsterdam.

Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology* 36: 71-91.

Poff, N.L., and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1805-1818.

Poff, N.L., and J.V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14: 629-645.

Power, M.E., R.J. Stout, C.E. Cushing, P.P. Harper, F.R. Hauer, W.J. Matthews, P.B. Boyle, B. Statzner, and I.R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7: 456-479.

Reid, I., and L.E. Frostick. 1989. Channel form, flows and sediments in deserts. Pages 117-135 in D.S. G. Thomas, ed. *Arid Zone Geomorphology*. Belhaven Press, London.

Renard, K.G. 1970. The hydrology of semiarid rangeland watersheds. United States Department of Agriculture, *Agricultural Research Service Publication* 41-162

Rodier, J.A. 1985. Aspects of arid zone hydrology. Pages 205-247 in J.C. Rodda, ed. *Facets of Hydrology, Volume II.* John Wiley & Sons, Ltd., New York.

Schick, A.P. 1988. Hydrologic aspects of floods in extreme arid environments. Pages 189-203 in V.R. Baker, R.C. Kochel, and P.C. Patton, eds. *Flood geomorphology.* John Wiley & Sons, Inc., New York.

Sedell, J.R., and J.L. Froggatt. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Orgeon, U.S.A., from its floodplain by snagging and streamside forest removal. *Verh. Internat. Verein. Limnol.* 22: 1828-1834.

Shalom, N.G., and Y. Gutterman. 1989. Survival of the typical vegetation in a wadi bed of a canyon after a disturbance by a violent flood at En Moor waterfall area in the Central Negev Desert Highlands, Israel. *Environmental Quality and Ecosystem Stability* IV-B: 423-431.

Sharma, K.D., J.S. Choudhari, and N.S. Vangani. 1984. Transmission losses and quality changes along a desert stream: the Luni Basin in N.W. India. *Journal of Arid Environments* 7: 255-262.

Sharma, K.D., and J.S.R. Murthy. 1994. Estimating transmission losses in an arid region. *Journal of Arid Environments* 26: 209-219.

Shelley, R.M., and C.S. Crawford. 1996. *Cnemodesmus riparius*, N. SP., a riparian milliped from the Namib Desert, Africa (Polydesmida: Paradoxosomatidae). *Myriapodologica* 4: 1-8.

Stanley, E.H., S.G. Fisher, and N.B. Grimm. In Press. Ecosystem expansion and contraction: a desert stream perspective. *BioScience*.

Stengel, H.W. 1964. The rivers of the Namib and their discharge into the Atlantic, Part I: Kuiseb and Swakop. *Scientific Papers of the Namib Desert Research Station,* No. 22, Transvaal Museum, Pretoria.

Stengel, H.W. 1966. The river of the Namib and their discharge into the Atlantic. Part II: Omaruru and Ugab. *Scientific Papers of the Namib Desert Research Station*, No. 30, Transvaal Museum, Pretoria.

Thornes, J.B. 1977. Channel changes in ephemeral streams: observations, problems, and models. Pages 317-335 in K.J. Gregory, ed. *River channel changes.* John Wiley & Sons, Chichester.

Triska, F.J. 1984. Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: a historical case study. *Verh. Internat. Verein. Limnol.* 22: 1876-1892.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Viljoen, P.J. 1989. Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. *Journal of Zoology, London* 219: 1-19.

Walker, K.F., F.Sheldon, and J.T. Puckridge. 1995. A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management* 11: 85-104.

Walters, M.O. 1989. A unique flood event in an arid zone. *Hydrological Processes* 3: 15-24.

Ward, J.D. 1987. The Cenozoic succession in the Kuiseb Valley, Central Namib Desert. *Geological Survey of Namibia, Memoir No. 9*, Windhoek. 124 pp.

Ward, J.D., and C.M. Breen. 1983. Drought stress and the demise of *Acacia albida* along the Lower Kuiseb River, Central Namib Desert: preliminary findings. *South African Journal of Science* 79: 444-447.

Ward, J.V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8: 2-8.

Ward, J.V., and J.A. Stanford. 1983. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pages 347-356 in I.T.D. Fontaine and S.M. Bartell, eds. *Dynamics of lotic ecosystems.* Ann Arbor Science Publishing, Ann Arbor.

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 (m³)	CV_{MAR}	CS_{MAR}	MAR_D (mm)	Runoff %	Area (km²)
Mean	6.83×10^6	1.55	2.21	2.92	1.00	4,652
Min	0.023×10^6	0.80	0.41	0.18	0.09	17.3
Max	29.62×10^6	3.32	3.94	14.9	3.82	21,800

Table 2. 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$_V$), and mean annual peak discharge (MAPD) for mainstem stations of the Omaruru River from 1975-1993. Total river length is 354 kilometers.

Station	MAR$_V$ (m^3)	CV$_{MAR}$	CS$_{MAR}$	MAPD (m^3 s^{-1})	MAR$_D$ (mm)	Area (km^2)
Omburo	19.62×10^6	0.99	1.32	248.8	14.9	1,320
Etemba	23.56×10^6	1.29	2.41	202.8	6.2	3,810
Henties	8.29×10^6	3.47	3.76	80.6	0.72	11,500

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), and mean annual peak discharge (MAPD) for mainstem stations of the Ugab River from 1978-1991. Total river length is 513 kilometers.

Station	MAR_V (m^3)	CV_{MAR}	CS_{MAR}	MAPD ($m^3\,s^{-1}$)	MAR_D (mm)	Area (km^2)
Petersburg	4.34×10^6	0.99	1.80	67.0	0.56	7,720
Vingerklip	16.37×10^6	1.50	2.85	118.6	1.16	14,200
Onverwag	18.86×10^6	1.24	2.64	73.8	0.87	21,800
Ugab Slab	6.38×10^6	3.08	3.15	42.4	0.22	28,900

Table 4. 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 (m^3)	CV_{MAR}	CS_{MAR}	MAR_D (mm)	Runoff %	Area (km^2)
Mean	1.88×10^6	1.31	1.50	2.25	0.76	2,796
Min	0.023×10^6	0.79	0.41	0.04	0.025	17.3
Max	6.59×10^6	2.00	2.64	7.20	2.15	14,700

Table 5. 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 1979-1993. Total river length is 560 km.

Station	MAR_V (m^3)	CV_{MAR}	CS_{MAR}	MAPD $(m^3 s^{-1})$	MAR_D (mm)	MAP $(mm)^a$	Area (km^2)
Friedenau	1.51×10^6	0.79	1.00	42.7	7.17	330	210
Us	6.22×10^6	0.88	0.69	77.7	3.27	210	1,900
Schlesien	6.59×10^6	1.16	1.41	71.9	1.01	100	6,520
Gobabeb	4.65×10^6	1.32	1.29	31.9	0.40	21	11,700
Rooibank	0.64×10^6	1.57	1.54	7.4	0.04	11	14,700

[a] - Approximate mean annual precipitation at gauging station.

Table 5 (cont). 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 1979-1993. Total river length is
560 km.

Station	Zero Years[b]	# Floods y^{-1}	# Floods[c]	Length (d)[d]	Flow (d y^{-1})[e]
Friedenau	0	7.9	118	3.7	24.4
Us	0	4.9	73	5.0	28.9
Schlesien	0	2.7	40	11.1	25.7
Gobabeb	4	1.3	21	3.9	8.7
Rooibank	9	0.9	13	2.2	3.9

[b] - Number of zero-flow years in record.
[c] - Total number of floods over record.
[d] - Mean length of floods in days.
[e] - Mean days of flow per annum.

Chapter 2:
Transport, retention, and ecological significance of woody debris
within a large ephemeral river.

Abstract - While the spatiotemporal patterns and ecological significance of CPOM (coarse particulate organic matter) and LWD (large woody debris) retention in perennial rivers and streams have been intensively studied, those within ephemeral systems are essentially unknown. I examined the influence of two characteristics unique to ephemeral systems, downstream hydrologic decay and in-channel tree growth, upon the distribution, transport, and retention of woody debris in association with floods in the ephemeral Kuiseb River in southwestern Africa. A total of 2,105 pieces of wood and 11,100 fruits (dry seed pods) of the tree *Faidherbia albida* were paint-marked at eight sites along the river channel and used to measure retention patterns. A single flood occurred during the study, with a peak discharge of 159 m^3s^{-1} at the upper end of the study area, dropping to <1 m^3s^{-1} 200 km downstream. Export of wood from the sites where they were marked totaled 59.5% (n=1,253); transport distances ranged from 1-124 km; and 34.8% (n=436) of the exported debris was recovered downstream. Pieces of wood which were not exported from the sites were significantly longer than exported material (p<0.001). Once in transport, however, there was little relationship between particle length and distance traveled (r^2=0.11, n=369). Length was a factor influencing the site of retention, however, as material retained on debris piles was significantly longer than that stranded on channel sediments (p<0.001). In-channel growth of *Faidherbia* trees was a significant factor influencing wood retention; 83.7% of marked wood not moved by the flood was associated with debris piles accumulated on *Faidherbia* trees. Similarly, 65% of the exported wood retained within downstream debris piles was associated with *Faidherbia* trees. *Faidherbia* also contributed an average of 192 kg (n=20) of fruits tree^{-1} to the channel and floodplain, representing a significant source of CPOM. All 11,100 fruits were exported from the marking site, although only 48 (0.43%) were recovered, after a mean transport distance of 20.1 km (0.4-50.2 km). Debris piles were the most important retentive obstacles, retaining 79% of the recovered fruits; the remainder stranded on channel sediments. Debris piles also play an important role in channel dynamics. By altering hydraulic resistance, they increase sediment deposition and initiate the formation of in-channel islands. Following flood recession, debris piles and their associated sediments provide moist, organic-rich microhabitats relative to the adjacent, dessicated environments of the open channel and floodplain. These sites are focal points for decomposition and secondary production, mimicking patterns reported from the channels of perennial streams and rivers. My observations suggest that the ecological significance of retentive obstacles and associated organic debris is a feature common to all fluvial ecosystems, irrespective of their hydrologic regime.

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Introduction

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

Despite the extent of this research, however, the available data are strongly skewed towards patterns in small systems. Little is known regarding the dynamics of woody debris in larger rivers, although several authors have suggested 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 today reflect extensive alterations rather than intrinsic properties (Benke 1990, Dynesius and Nilsson 1994). Such an assertion is supported by historic accounts detailing significant amounts of wood in large systems (Sedell and Froggatt 1984, Triska 1984).

Our understanding of wood dynamics in fluvial systems also reflects a focus on perennial systems in temperate climates. Virtually nothing is known regarding wood dynamics within rivers and streams of drylands. 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) have significantly reduced inputs of wood to the streams and rivers of American deserts. Least known of all fluvial systems are the ephemeral rivers of the world's drylands. To my 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 upon hydraulic characteristics within streams draining the Barrier Range in New South Wales, Australia. This lack of attention to dryland systems, and ephemeral rivers in particular, is remarkable considering they drain roughly one-third of the Earth's land surface (Jacobson, Ch.1)

Two characteristics common to ephemeral rivers are likely to have a pronounced effect upon patterns of transport and retention of wood. First, ephemeral rivers experience a downstream hydrologic decay, attributable to transmission losses associated

with infiltration and evaporation (Graf 1988). Retention of organic matter in ephemeral stream channels must obviously increase downstream, in direct response to the decrease in stream power associated with hydrologic decay. Second, ephemeral rivers and streams are often characterized by 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 in western N.S.W., Australia (Graeme and Dunkerly 1993). Similarly, large ana-trees, *Faidherbia albida*, grow within ephemeral river channels of the Namib Desert in western Namibia (Jacobson et al. 1995). In both cases, stem diameters may exceed 1.5 m at breast height, and both trees commonly exhibit a cespitose growth form, with numerous stems in close proximity. They should thus have a significant effect upon the retention of organic matter during floods. In addition, such trees also provide a direct source of organic inputs to the channel, including leaves, fruits, and wood which accumulate between floods.

I examined patterns of transport and retention of wood associated with flooding in the lower reaches of a large ephemeral river in the Namib Desert. The influence of in-channel trees (*Faidherbia albida*) and downstream hydrologic decay upon the pre- and post-flood distribution of wood was recorded, along with the relative importance of specific retention mechanisms (i.e., retention on debris piles versus stranding on channel sediments). Observations were also made regarding the geomorphologic and ecological significance of woody debris piles within this ephemeral river system.

Methods

Study area

The study area was the lower 260 km of the ~560-km-long Kuiseb River. The Kuiseb River drains a catchment of approximately 14,700 km^2 in west-central Namibia. 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. Associated with this coastal desert is a strong climatic gradient across western Namibia. Mean annual rainfall exceeds 350 mm in the Kuiseb's headwaters, which originates on the inland plateau at an elevation of ~2,000 m. At the eastern edge of the Namib Desert at the escarpment's base, mean annual rainfall drops to ~100 mm and declines westward to near zero at the coast (Namibian Weather Bureau). Evaporation is high throughout the catchment, exceeding rainfall by 7 to 200 times (Lancaster et al. 1984). As a result, surface flow occurs in direct response to strong convective storms during summer months 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). West of the 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 within this canyon, often flowing over bedrock with no alluviation due to the comparatively steep gradient (0.003-0.004 m/m) and narrow channel. This canyon broadens some 65 km from the coast, whereafter the river occupies a broad, shallow valley which finally becomes indistinct within 20 km of the coast. Within 20 km of the coast, low crescentic 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 silts. The sandy channel sediments within the lower 150 km are largely devoid of cobble or bedrock, excluding occasional bedrock dikes which cross the channel and form local knick points in the longitudinal profile (Ward, 1987).

The Namibian Department of Water Affairs (DWA) maintains five automatic gauging stations along the mainstem of the Kuiseb River, and a sixth on the Kuiseb's main tributary, the Gaub River. Distinct longitudinal trends are evident among the hydrologic records from these stations (Jacobson, Chapter 1). Mean annual runoff (MAR) (m^3) and mean peak discharge (m^3s^{-1}) exhibit a strong curvilinear relationship with distance downstream, increasing from the headwaters to the base of the escarpment and declining westward. A review of the Kuiseb's hydrology is provided by Jacobson (Ch. 1). The reach examined in the present study extends from the base of the escarpment westward to the coast; most floods dissipate well before reaching the coast (Table 1).

The most distinctive biological feature of the lower Kuiseb River is the comparatively lush riparian forest, offset by the adjacent sand and rock desert (Seely and Griffin 1986, Theron et al. 1980). *Faidherbia albida* (Del.) A. Chev. is the dominant woody species along and within the active channel of the lower river, 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). The tree occurs sporadically within the escarpment and canyon reaches, where isolated pockets of alluvium permit its growth. It achieves its most extensive growth downstream of the canyon on the extensive alluvial deposits associated with the broader channel and floodplain (Theron et al. 1980).

Discharge

Surface flow through the study reach is routinely monitored by the Namibian Department of Water Affairs. Records from two key gauges were used to monitor flow into the study area; one on the mainstem of the Kuiseb River (Schlesien Weir), approximately 160 km above Gobabeb, and another on the Gaub River (Greylingshof

Tower), the Kuiseb's main tributary, approximately 20 km upstream of the Gaub-Kuiseb confluence and ~135 km above Gobabeb. Flow within the study reach was measured 12 km downstream of Gobabeb at the Gobabeb Weir, and at its lower end at the Rooibank gauge, 57 km below the Gobabeb Weir and approximately 204 km below the confluence. These stations provided a record of peak discharge (m^3s^{-1}) and total flow volume (m^3) for each event. Flow velocity ($m \cdot s^{-1}$) was measured during floods by timing the travel of neutrally-bouyant particles. The average recurrence interval of the recorded flow was calculated using the annual peak discharge series and the Weibull plotting formula (Gordon et al. 1992).

An analysis of the annual records (n=14) from the four gauges was conducted 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 approximate mean annual flow volume at the Kuiseb-Gaub confluence. This figure was then used, in combination 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^{-1}.

Woody Debris Distribution, Transport and Retention

The relative abundance and distribution of woody debris piles within the active channel was surveyed over a 95-km reach of the lower Kuiseb River, including 70 km upstream of Gobabeb and 25 km below. I counted the number of debris piles in each km and identified each retentive structure (i.e., tree stem, rock, sediment). The approximate width of the 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 water-proof acrylic paints. Wood was marked in six 1-km long zones, located 10, 27, 33, 38, 44 and 50 km above Gobabeb. Sites were chosen for their ease of access and abundance of material for marking. All of the pieces within a zone were paint-marked with a pattern and color specific for each zone. Each piece was marked without moving it from the position in which it was found. A total of 1,687 pieces were marked among the six zones (Table 2). An additional 253 pieces were also marked over a ~10 km reach approximately 160 km upstream of Gobabeb. Finally, a total of 165 logs (>3 m long) were individually numbered with water-proof acrylic paint. Marking was restricted to wood within the active channel (~2-y flood), avoiding the adjacent floodplain and terraces. An attempt was made to mark approximately equal numbers of stranded wood (lying free within or along the active channel) and wood retained by debris piles in order to assess the retention efficiency of such piles.

Following flow, the entire channel was searched from the release zones downstream to the flood's end. The distance traveled from the release zone (km) was

recorded, along with the final position (stranded or debris pile) and the identity of the retentive structure (i.e., sediment, rock, tree stem). No search was conducted within the Kuiseb Canyon (~70-140 km upstream of Gobabeb) because of the difficulty of access. The marking zones were also searched to quantify wood retained within its original marking site. The number stranded and retained within debris piles was recorded, along with the identity of the retentive structure associated with debris piles.

Pod Production, Transport and Retention

Annual production of *Faidherbia albida* fruits from 20 trees was monitored along a 30-km reach of the lower Kuiseb River, extending from 35-65 km upstream of Gobabeb. The trees were all sexually mature and diameter-breast-height averaged 0.79 m (sd=0.20). Monitoring was restricted to this reach due to the presence of livestock further downstream. All 20 trees were within or immediately adjacent to the active channel, facilitating the quantification of yearly production because the previous year's floods had removed accumulated pods. Pods were collected from three randomly selected plots (1 m^2) beneath the canopy of each tree at the end of dry season, after pod fall was complete. The total weight (g m^{-2}) of pods was recorded for each plot and averaged among the twenty trees. Canopy area (m^2) of each tree was measured and used to estimate the mean pod production per tree. Mean tree density (stems ha^{-1}) was estimated using the T-square sampling procedure at ten sites along the 30 km reach (Krebs, 1989). The estimates of mean tree density (stems ha^{-1}), canopy area (m^2), and pod production (g m^{-2}) were used to approximate the annual input (kg ha^{-1}) of pods to the floodplain and channel.

Transport and retention of pods during riverflow was examined using 11,100 pods marked with brightly-colored, water-proof acrylic paint. Pods were marked within the lowest position of the active channel to ensure their export during subsequent floods. Following flow, the wetted channel was searched from the release point, approximately 38 km upstream of Gobabeb, downstream to the flood's end. The distance traveled from the release point (km) was recorded, along with the identity of the structure which retained the pod (i.e., sediment, rock, debris pile).

Data Analysis

The distance traveled by wood and pods fit a negative linear model (r^2=0.95-0.98) in which the slope provided an estimate of the average rate of removal of material from transport. Retention curves (sensu Speaker at al. 1984) of the material exported from the six marking zones were used to calculate mean retention rates within selected sections of the study reach. Two-sample t-tests were used to assess differences in size (m) and transport distance (km) between retained and exported material from each of the six groups. Data were examined to assess whether assumptions of normality and equal variance between samples were valid. In most cases, data departed from normality and sample groups exhibited unequal variance. Thus, comparisons between groups were made

using the Kolmogorov-Smirnov test (Sokal and Rohlf, 1995). When data were non-normal but exhibited equal variance between groups, comparisons were made 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). Regression analysis was used to examine the relationship between particle length and transport distance. All tests were considered significant at $p < 0.05$.

Results

Discharge

The transport data reported here are associated with a single ~2-day flood in January, 1994. The initial floodwave originated in the Gaub River catchment, and a peak of 159 m^3s^{-1} was recorded at the Greylingshof gauge, with a total flow volume of 2.75 Mm^3 (million cubic meters). A second floodwave originated within the Kuiseb catchment above the Schlesien gauge, but was not recorded due to an instrument failure. My observations of the flood suggest that it peaked at ~20 m^3s^{-1} 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, 140 km below the confluence, representing a transmission loss of ~52%, or 0.37% km^{-1}.

Transmission losses increased significantly from the Gobabeb gauge down to Rooibank, where the total flow volume dropped to <50,000 m^3, a ~98% reduction over 57 km, or 1.7% km^{-1}. Peak discharge exhibited a similar decay, dropping from 159 m^3s^{-1} at Greylingshof to 52 m^3s^{-1} at Gobabeb, a 67% reduction over 140 km, or 0.48% km^{-1}. A recurrence interval of ~2.6 years was calculated for this flood at the Gobabeb gauge, using the annual peak discharge series (n=17). From Gobabeb to Rooibank, peak discharge dropped from 52 m^3s^{-1} to ~1 m^3s^{-1}, a 98% reduction over 57 km, or 1.7% km^{-1}. An analysis of the annual flow record (n=14) for the three 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. Finally, flow velocity at peak discharge dropped from 2.22 $m \cdot s^{-1}$ at Greylingshof to only 1.98 $m \cdot s^{-1}$ at Homeb, ~110 km downstream. From Homeb to Rooibank, a distance of ~90 km, peak flow velocity dropped to 0.76 $m \cdot s^{-1}$.

Pre-flood Wood Distribution and Channel Morphology

The number of in-channel debris piles varied widely along the 95-km reach surveyed within the lower river, ranging from 0-30 piles km^{-1}. The distribution of debris piles was strongly influenced by the density of in-channel trees, and reaches devoid of debris piles, such as the reach from 16-22 km above Gobabeb, typically lacked in-channel

trees. Conversely, downstream peaks in debris pile abundance at 12-15 km above Gobabeb and immediately above and below Gobabeb where associated with an increase in tree density, relative to adjacent reaches. A total of 99% (n=335) of all debris piles within the survey reach were retained on trees growing within the channel; the remaining 1% were retained on rock outcrops in or along the banks. *Faidherbia albida* was the most important tree, retaining 97% of all debris piles; *Tamarix usneoides* retained the other 2%.

Channel width over the study reach ranged from less than 20 m in the canyon to more than 130 m below the Gobabeb Weir. While channel width in the upper section of the study reach is constrained within the narrow canyon (<100 m), approximately 45 km above Gobabeb the valley begins to broaden, freeing the river channel to expand onto an increasingly wide floodplain. Some 30 km below the Gobabeb Weir, the floodplain width increases to over 1,000 m. Accurate assessment of channel width below the Gobabeb Weir is complicated by the shallow and variable nature of the channel. Small floods typically flow through a comparatively narrow (<50 m) and shallow (<0.5 m) channel. During high-magnitude discharges the channel may expand to a width of hundreds of meters without a significant increase in depth. Retention may not decrease, however, as the large and durable grass, *Cladoraphis spinosa*, and the shrub, *Pechuel-loeschea leubnitziae*, become common within the channel and floodplain below the Gobabeb Weir. Although debris piles were largely absent below the weir, surficial accumulations of small pieces of wood (<0.5 m long) were common. Wood was stranded individually within the shallow channel or floodplain or racked up against grasses or shrubs, forming shallow mats of material.

The increase in channel and floodplain width below the Gobabeb Weir corresponds with a major knick point in the river's longitudinal profile. This is one of two distinct breaks evident in the longitudinal profile of the Kuiseb River, the other occurring ~80 km upstream of Gobabeb. Within the escarpment and canyon, channel slope averages 0.0034 (n=48) over 280 km of river, excluding the steep upper reaches of the headwaters (~100 km). Approximately 80 km above Gobabeb, the canyon begins to broaden, associated with a significant decrease in the mean slope to 0.0019 (n=22), which continues over the ~92-km reach downstream to the Gobabeb Weir (p<0.001). The knick point on which the Gobabeb Weir is sited occurs in response to the channel's intersection with a granitic dike. Below the weir, a significant increase in channel slope occurs over the lower 80 km of river where the slope averages 0.00466 (n=20, p<0.001).

Transport and Retention of Wood

Approximately equal numbers of retained (53.9%) and stranded wood (46.1%) were marked out of the total of 2,105 pieces. Of this number, 1,253 (59.5%) were transported out of the marking areas by the flood, of which a total of 436 (34.8%) were recovered downstream (Tables 2-3). Recovery of transported wood varied from a low of 2.65% for material marked above the Kuiseb Canyon to a high of 82.7% for marked logs.

Disregarding these two extremes, recovery averaged ~37% for the 6 zones below the canyon.

While the total percentage of wood retained within the six zones in the 50 km above Gobabeb was only 41.4%, most of this material was associated with debris piles prior to the flood. Of the total of 698 pieces retained within the six zones, 68.5% were held within debris piles, reflecting the efficiency of such piles as retentive structures (Table 2). Similarly, of 913 pieces marked within debris piles, only 435 (47.6%) were exported, in comparison to 554 (71.6%) of the stranded material. Similar patterns were observed for the zone 160 km above Gobabeb and the 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). Particle length was also a significant factor influencing the probability of export. The length of exported wood was significantly less than retained wood for the logs and all of the 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 zones, relative to the other four marking zones.

In general, transported wood from all six zones below the canyon appeared to have an equal chance of being retained by a debris pile or stranding on the sediments of the channel or floodplain. Of the 369 particles recovered, 46 % were in debris piles and 54 % were stranded (Table 3). Transported logs were retained in debris piles more frequently, however; 66 % of transported logs were recovered within debris piles in contrast to only 34 % stranded on channel and floodplain sediments. The significant increase in the mean length of exported logs (4.0 m) relative to woody debris (1.5 m) provides an explanation for the increased retention of logs within debris piles (p<0.001) (Table 4).

Among particles exported from the 50-km and 44-km zones, those retained in debris piles were longer than those stranded on channel or floodplain sediments (p<0.001) (Table 5). The mean length of material exported and then retained on debris piles was 2.17 m and 1.81 m, respectively, compared with means of 1.16 m and 1.07 m, respectively, for stranded material. The length of material transported from the four lower zones did not exhibit any significant difference between that retained in debris piles relative to that which was stranded (p>0.05). This difference 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). Longer particles are more likely to be retained in a reach with a higher density of in-channel trees. As tree density within a reach decreases, so does the influence of particle length upon retention. 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), I would expect that the increasing influence of a broader and shallower channel combined with a decreasing discharge due to the hydrologic decay would result in larger particles having a higher probability of stranding downstream.

Transport distances for wood marked within the six zones ranged from 1-75 km, with a median of 25 km (n=369). Mean values for each zone ranged from 13-32 km, with a trend of decreasing transport distance evident in the lower three 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 five upstream zones (p<0.001) (Table 3). Of the 62 logs recovered, transport averaged 18 km. The greatest movements were recorded for five pieces of wood exported from the marking zone 160 km above Gobabeb, traveling an average of 120 km before being retained downstream of the canyon. Although particle length influenced the probability of being exported from a marking zone, as discussed above, once in transport the probability of retention was largely independent of particle length. Regression analysis revealed a weak relationship between particle length and distance traveled (r^2=0.11, n=369).

Retention curves for the six marking zones below the canyon revealed that retention was not uniform over the length of transport. Proceeding downstream from the end of each marking zone, distinct variations were present in the slope of each retention curve. When plotted against a common reference point, five reaches were distinguishable in which the individual retention curves exhibited similar slopes. The mean slope of the retention curves within each reach differed among the five reaches (ANOVA, p<0.001; Table 6). Despite these reach-specific variations, the overall trend of all the curves was a negative linear relationship between the percent 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^{-1} for wood exported from the 50-km marking zone, to -3.48 % km^{-1} for the 10-km zone. While the flood waters reached >60 km downstream of the Gobabeb Weir, no marked wood was recovered beyond 12 km downstream of the weir.

Several factors likely contributed to the reach-specific variation in retention. First, based upon the estimates of the hydrologic decay, peak discharge dropped ~30% over the 62 km from the 50 km marking zone to the Gobabeb Weir, decreasing from ~99 m^3s^{-1} to 52 m^3s^{-1}. This decrease, combined with a gradual increase in channel width downstream, would tend to increase retention downstream. The density of in-channel trees and associated debris piles also varied significantly among the five reaches (p<0.001) (Table 6). The sharp drop in retention below 36 km occured in conjunction with a significant decrease in abundance of trees and debris piles, dropping from 15.7 trees km^{-1} and 9.5 piles km^{-1} above 36 km, to 4.2 km^{-1} and 1.6 km^{-1}, respectively, in the reach below. At the same time, however, the mean retention rate showed a significant increase from 16 km above to 3 km below Gobabeb and then a significant decrease from 3-10 km downstream

(p<0.001). These differences were not associated with significant differences in tree and debris pile density over the reach from 36 km above to 10 km below Gobabeb. A significant increase in the mean channel width occured 3 km below Gobabeb, in conjunction with a significant decrease in the retention rate, from -2.63 to -0.51. Finally, a significant increase in the retention rate, from -0.51 to -3.33, occured 10 km downstream of Gobabeb, in the immediate vicinity of the Gobabeb Weir, despite the lack of any significant change in debris pile or tree density or channel width (Table 6).

The proportions of transported wood being retained on debris piles and stranded on the channel and floodplain sediments varied with distance downstream. From 22-50 km above Gobabeb, 82% (n=51) of the transported wood recovered within this reach was retained on debris piles, with only 18% (n=11) stranding within the reach. From 22 km above to 10 km below Gobabeb, the relative proportions were similar, with 44% (n=94) of the recovered wood retained on debris piles, and 56% (n=120) stranding. In the vicinity of the Gobabeb Weir, however, from 10-25 km downstream of Gobabeb, only 27% (n=25) of the recovered wood was retained on debris piles, while 73% (n=68) was stranded on the channel and floodplain sediments. Stranding typically occurred on the outer edges of bends and along the gently sloping banks of broad, shallow reaches.

Faidherbia albida trees were the single most important obstacle retaining wood within the study reach. Of 594 pieces of wood retained on debris piles within the marking zones, 83.7% (n=497) were associated with piles retained by in-channel *Faidherbia albida* trees (Table 7). Of these, 62% were retained on cespitose stems, closely-spaced (<2 m) groupings of two or more trunks. Wood exported from the marking zones and retained on downstream debris piles exhibited a similar trend, with *Faidherbia* trees retaining a total of 65% of the wood, and cespitose stems retaining 55% of this total. *Tamarix usneoides* trees retained 5.1% of the wood within the marking zones, and 19% of the exported wood retained downstream. The grass, *Cladoraphis spinosa*, which forms dense thickets, retained 9.9% of the wood retained on piles within the marking zones, and 8% of the exported material retained on piles downstream. The remaining retained and exported wood held within debris piles was associated with rocks, exotic plants, other trees, or the shrub, *Pechuel-loeschea leubnitziae* (Table 7).

Pod Production, Transport and Retention

The mean density of *Faidherbia* was 15 trees ha^{-1} (n=10, sd=6) within the zone in which pod production was monitored. Mean annual pod drop beneath the canopies of the 20 monitored trees averaged 997 g m^{-2} (sd=563). With an average canopy area of 192 m^2 (sd=70), the estimated annual pod production was ~191 kg tree^{-1}. At an average of 15 trees ha^{-1}, annual pod production within the study reach may be as high as 2,865 kg ha^{-1}. This figure suggests that the fruits from *Faidherbia* trees are a significant annual input of woody debris to the river.

All 11,100 marked pods were exported from the marking site. Of this number, only 48 were recovered (0.43%). Travel distance ranged from 0.4-50.2 km, with a mean of 20.1 km (sd=13.5). Of the 48 recovered, 79% (n=38) were retained within debris piles, and the remaining 21% (n=10) were stranded on the channel sediments at the flood's edge. Stranded pods were in excellent condition, little altered from their pre-flood state. Pods recovered from debris piles, however, were extremely weathered and often consisted of little more than the acrylic paint binding together the fibrous remnants of the pod. Flood velocity within the recovery zone was ~7.1 km h^{-1}, so pods stranding after 20 km of transport may have only been subjected to the leaching and abrasion of the floodwaters for < 3 h, explaining their comparatively pristine appearance. Once retained upon a debris pile, however, pods are subjected to rapid leaching and abrasion, resulting in their disintegration. The low recovery percentage of transported pods (0.43 %), significantly less than that for marked woody debris (37.3 %), is likely a function of such physical processing. While pods were certainly overlooked, their large size (3x10 cm, 8 g, n=30), use of bright paints, and an intensive search made it unlikely that a significant number were present but overlooked.

Although the retention of pods fit a negative linear model (r^2=0.98), significant variation was evident, and associated with 4 distinct reaches. Approximately 32 km above Gobabeb, a windblown tree lying within the channel retained 6% of the transported pods. Another 15% of the transported pods were stranded in a broad (~120 m) reach of channel approximately 22 km above Gobabeb. A dense growth of the grass, *Cladoraphis spinosa*, retained another 10% of the pods when the flood flowed across a low floodplain on the outside corner of meander ~11 km above Gobabeb. Finally, a total of 28% of the transported pods were retained over a 3 km reach at Gobabeb. The high retention in this reach is associated with a narrow channel, several mid-channel islands, and a high density of debris piles within the channel (Figs. 2-3).

Discussion

A major issue regarding the organic matter dynamics of fluvial ecosystems is the extent of within-reach processing versus export. Opportunities for such processing are directly linked to a stream's ability to temporarily store organic carbon within the channel, (i.e., their retentiveness). Ephemeral systems provide an extreme case in which retentive structures, in combination with hydrologic decay, may result in no export from a reach. Continued sporadic inputs may thus serve to fuel the heterotrophic community and increase the pool of stored carbon.

Wood within the lower Kuiseb River enters the channel via fluvial transport from upstream reaches or from trees growing within the study reach. The annual litterfall from trees within the channel and floodplain provides a regular input of organic material, including fruits, which accumulate within the channel between floods. Occasional blowdowns, combined with scour and mass wasting of banks during floods, provide

additional, albeit sporadic, inputs to the channel. Once in the active channel, floods transport the material downstream to sites of retention.

Hydrologic control of transport and retention

The majority of woody debris in transport is carried in the flotation load, although several woody species contribute wood of sufficient density to move as bedload. It is possible that gradual water-logging of transported *Faidherbia* wood may result in its sinking and an increased probability of retention over time in transport, but this possibility is not supported by my observations. The buoyancy of the dry woody debris no doubt contributes to the long transport distances observed. Both 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. This contrast was attributed to drying of wood when floodplains were not inundated and subsequent floating of the dried wood when reinundated (Smock and Jones 1991).

Recoveries of transported wood revealed that the most retentive sections of the study reach corresponded with either a high density of in-channel trees or a reduced peak discharge, relative to other sections. Wood is efficiently retained within the lower Kuiseb River via 'racking up' on in-channel trees and existing debris piles or stranding upon channel and floodplain sediments. Similar observations have been made in small streams, where studies have demonstrated that retention of CPOM is related to the amount of wood in streams (Bilby and Likens 1980, Jones and Smock 1991, Webster et al. 1994). Jones and Smock (1991) reported that during low discharge, retention in low-gradient headwater streams in coastal Virginia was passive, with POM simply settling from the water column onto the sediment surface. In contrast, during high discharge, debris dams became important retainers of POM. Wherever they occur, in-channel trees and associated debris piles are the most important retentive structures within the lower Kuiseb River. In downstream reaches, however, where both the abundance of in-channel trees and the discharge have decreased markedly, stranding on the sediment surface of channel and banks becomes the predominant mode of retention.

Based upon my observations of wood distribution, transport, and retention patterns, the reach of river extending some 60 km above and 20 km below Gobabeb appears to function as a 'sink' for woody debris within the channel network. Although the annual flux of wood entering the study reach from the upstream catchment is unknown, it is clear that this material is unlikely to be transported beyond this ~80 km reach during floods of the magnitude examined in the present study (~1.6 year return interval). At present my data are insufficient to provide an understanding of how retention patterns within the study reach would vary in response to increases or decreases in flood discharge. Nonetheless, several anecdotal records combined with my own observations provide some indication of likely trends.

Within the lower Kuiseb River the decrease in abundance of in-channel trees and associated debris piles is offset by an increasingly wide and shallow channel, resulting in a downstream increase in transmission losses and an associated increase in retention. During infrequent, high-magnitude discharges (>100 m^{3}s^{-1}), however, the retentiveness of these reaches may be limited and large amounts of CPOM may be injected into the lower reaches of the 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 extensions of the deposition patterns associated with high-discharge events. Similarly, although I observed no large logs (>3 m) in transport at the Gobabeb weir in the 1994 flood, more than a hundred logs, probably associated with the 1934 and 1963 floods, are stranded on the numerous granitic outcrops in the immediate vicinity of the weir. If discharge is high enough, CPOM may be exported to the sea, as occurred on the Kuiseb in 1934, and regularly occurs on several of the more hydrologically-active rivers to the north.

Floods may also increase downstream export of CPOM by altering the retentiveness of upstream reaches. Stengel (1964) recorded the observations of Dr. Charles Koch, the founder of the Desert Ecological Research Unit, which is along the banks of the lower Kuiseb River. Koch witnessed the high-magnitude flood (>34 year return interval) of 1963, reporting that, "for almost an hour the Kuiseb appeared as a gigantic conveyor belt for the transport of wood masses ..." With regard to the function of trees as retentive structures, Koch reported that, "driftwood was dammed by their trunks and where the pressure became too great, it broke them (the trees) down." As the flood receded over the next several days, Koch observed that numerous large trees, "lay mowed down along the side of the river."

Alternatively, a temporary reduction in flood frequency and magnitude may favor recruitment of in-channel trees, increasing the retentiveness of a reach during subsequent floods. A period of extensive flooding along the lower Kuiseb River in the mid-1970's was followed by a four year absence of surface flow from 1979 to 1983 (DWA Records). This interlude allowed *Faidherbia albida* seedlings, established in the channel in response to the floods of the mid-70's, to grow to sufficient size 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 now acts as a major retention site for CPOM during floods of sufficient magnitude (~2-year RI) to fill the channels and flow onto the island. If increases or decreases in discharge were long-lasting, the average position of deposition zones would likely shift, either downstream or upstream, respectively, with concomitant alterations of the structure and functioning of the fluvial ecosystem within the lower reaches of the river.

Canyons, Fruits, and FPOM

My initial hypothesis regarding the retentiveness of the canyon reach was that its confined course and bedrock channel would serve to efficiently export any material introduced. In effect, the canyon would function as a canal, efficiently delivering any material entering it to the lower reaches of the river, thereby linking the upper catchment with the lower river. The recoveries demonstrate that a single flood of low magnitude (~1.3 yr RI) can export wood a distance of 120 km, nearly twice the maximum recorded in the lower river. Nonetheless, the low recovery (2.65%) of wood exported from the marking site does not support my original hypothesis, and the inaccessibility of the canyon restricted my searches to the lower reach of the river. I thus cannot reject the possibility that much of the exported material was retained within the canyon.

Alternatively, the extremely weathered condition of the five recoveries suggests that many marked pieces exported out of the canyon may have been unrecognizable, so worn as to be easily overlooked. The extensive weathering , including fresh abrasions on the painted surfaces as deep as 1 cm, do lend credence to the hypothesis of Sykes (1937), that the 'molar action' within narrow canyons is an important source of FPOM in desert rivers. Sykes (1937) reported that during floods on the Colorado River, wood was physically processed to fine particles via molar action in canyon-bound reaches, prior to its deposition in downstream reaches or its export to the sea. 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.

Another source of FPOM within the lower Kuiseb River is the fruits of the *Faidherbia albida* trees growing within and along the channel. Measurements of the pod production of *Faidherbia albida* suggest that it is a significant source of CPOM, which is rapidly transformed during floods to FPOM and DOM. The mean value of 191 kg y^{-1} per tree (n=20) is in close agreement with a single observation of 182.5 kg for a tree on the edge of the river course, reported by Seely et al. (1979/80 - 1980/81). *Faidherbia albida* has a broad distribution throughout southern and eastern Africa, where it is closely associated with perennial, seasonal, and ephemeral river courses (CTFT 1989). It thus may be a significant source of organic matter in other fluvial systems, particularly where it occurs in the other dryland regions of southern and eastern Africa.

Woody debris and channel morphology

The importance of in-channel trees to the retention of wood is clearly discerned from an examination of the typical structure of a debris pile. Debris dams within the lower Kuiseb River typically consist of several large elements lodged against one or more trees within the channel, upon which successive pieces of wood are retained. Wood accumulations on in-channel trunks present a significant obstacle to flowing water, and as smaller pieces of wood are retained, the pile becomes increasingly retentive to finer

material, accumulating FPOM and sediment within and downstream of the pile. Shields and Smith (1992) reported similar patterns from perennial streams, observing that channel sediments immediately adjacent to woody debris accumulations were finer and contained more organic matter relative to debris-free sites.

Because of the 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 micro-habitat following flood recession. These drapes function as 'nursery bars,' and are important sites of asexual reproduction of *Faidherbia* trees via root sprouting. My observations suggest that if these structures are not destroyed by a high-discharge flood, they may develop into elongate islands, dividing the river course into multiple channels. Such patterns are common within the reach between the canyon and Gobabeb. Similar patterns have been reported from ephemeral stream channels in the Barrier Range of western N.S.W., Australia, where large river red gum trees, *Eucalyptus camaldulensis*, grow along the banks and within the active channel (Dunkerley 1992, Graeme and Dunkerley 1993). These patterns also mimic the effects of large organic debris stranding in perennial channels, where it may alter bank stability and initiate the formation of mid-channel bars and channel braids (Keller and Swanson 1979).

Abbe and Montgomery (1996) detailed the influence of woody debris piles upon channel morphology in large alluvial (perennial) rivers, noting that woody debris jams were a principal mechanism controlling reach-level habitat diversity. Distinct jam types were found to initiate and accelerate the formation of bars, islands and side channels, affecting both in-channel and riparian habitat. The principal jam types observed paralleled patterns recorded in the present study. Abbe and Montgomery (1996) observed that 'bar top jams,' characterized by loose mats of woody material deposited upon channel bars during recession, although common, had little effect upon channel morphology, being rapidly mobilized in subsequent floods. Such accumulations are abundant along the lower Kuiseb River on low banks, channel islands and bars within the active channel, and are also highly unstable in subsequent floods. Abbe and Montgomery (1996) noted that the more stable bar apex and meander jams had the greatest effect upon 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 within the present study.

A reversed retention pattern

My observations of a general increase in the retention of wood downstream are in direct contrast to observations in smaller, perennial systems. Lienkaemper and Swanson (1987) observed that stability of large woody debris decreased in larger channels, a fact

they attributed to greater channel width and higher discharge creating a greater capacity for such channels to transport wood. Other researchers have noted similar trends in other systems (Minshall et al. 1983, Naiman et al. 1987). Webster et al. (1994) observed that retention of CPOM within small streams could be largely attributed to the probability of a particle encountering an obstruction such as a rock, log or debris pile. This probability typically decreases with an increase in discharge and depth downstream.

This simple relationship does not apply in large ephemeral channels, however, where in-channel tree growth and downstream hydrologic decay complicate such relationships and ultimately may reverse them. In ephemeral rivers, hydrologic decay results in a downstream decrease in stream power, resulting in an increase in alluviation (Bull 1979). As floods travel downstream in ephemeral rivers, an increase in channel width combined with a decrease in discharge act to decrease depth and increase the probability of retention of wood, whether on some obstacle or on the sediment itself. In addition, as a result of this alluviation, the longitudinal profile of ephemeral systems may exhibit convexity in their lower reaches. Vogel (1989) has reported such patterns from the Namib's ephemeral rivers, and the lower Kuiseb River does exhibit a convex profile (Jacobson, Ch. 1).

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 (Benke and Wallace 1990). This increase is attributed to the river lacking sufficient power to move wood from within the channel, a condition enhanced by the river's low gradient. In addition, historical accounts suggest that such patterns may have been far more common prior to the extensive alterations to which most large, low-gradient rivers have been subjected over the past century (Sedell and Froggatt 1984, Triska 1984).

In the absence of such retentive structures, the stream ecosystem functions more as a pipe or canal, with little in-stream processing due to the lack of retention. Aquatic ecologists have spent more than two decades demonstrating that perennial rivers and streams are not 'pipes' or 'canals,' emphasizing the vast array of biologically-mediated processes that occur within the water column (Hynes 1975). However, the simple view of streams as pipes or canals may be more applicable to ephemeral systems, which largely lack an aquatic community due to obvious hydrologic constraints. The stream channel, from the perspective of organic matter dynamics, serves mainly to convey materials from sites of production (terrestrial) to sites of processing (terrestrial). During episodes of transport, little biologically-mediated processing occurs, with the possible exception of microbial respiration of DOC and FPOM. Nonetheless, material transport in ephemeral systems is strongly influenced by retentive structures within the channel as it is in perennial systems. Thus, the retention of organic matter in discrete accumulations

appears to be a fundamental characteristic all fluvial ecosystems, irrespective of their hydrologic regime, and belies their portrayal as pipes or canals.

In considering the ecological significance of retention in fluvial systems, 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). When the cycling in place characteristic of terrestrial environments is combined with the longitudinal transport of fluvial systems, the result is that nutrient cycles are stretched into spirals. Research on perennial systems has shown that the turnover length, the rate at which the system utilizes carbon relative to the rate at which it transports it downstream, typically increases downstream in response to a decrease in retention efficiency (Newbold et al. 1982). Thus, headwater reaches of drainage networks are most important for the retention and oxidation of terrestrially-fixed carbon transported into the fluvial environment.

Ephemeral rivers diverge from this pattern, exhibiting retention peaks in the middle to lower reaches of the hydrologic network in response to hydrologic decay. In addition, 'spiraling' is not a continuous process in an ephemeral river such as the Kuiseb, as transport and processing are uncoupled. Transport occurs in distinct pulses associated with the highly variable hydrologic regime (Jacobson, Ch. 1), and biologically-mediated processing and uptake occur between floods within a terrestrial environment. Because of water-limitations which 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 of substrates and associated microhabitats (Jacobson et al. in review, Shelley and Crawford 1996).

Retention and biological processing

The abundance of debris piles may also influence the structure and functioning of the biotic assemblages within fluvial ecosystems. 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, and only 20% in 3rd. They attributed this pattern to the downstream increase in discharge, which decreased the retention of organic matter on the streambed. Nonetheless, they reported that where they occurred, they were very important in accumulating organic material, facilitating its biological processing. Debris dams accumulate organic matter into nearly watertight structures, as sediments and organic matter settle out in association with the hydraulic disturbance created by the structure, forming localized 'hotspots' of heterotrophic activity distributed throughout and along the channel. Hedin (1990), who examined factors controlling sediment community respiration in woodland streams, found that community respiration was three times greater in organic debris dams than in adjacent stream sediments. He concluded that organic debris dams are focal sites of metabolism and nutrient regeneration within the stream channel. Debris piles serve a similar function in ephemeral rivers, where their

water-retentive properties and increased organic matter content support biological activity long after it has ceased in the adjacent, sandy bed sediments which rapidly desiccate following floods (Shelley and Crawford 1996, Jacobson et al. in review). Although retention structures may influence decomposition and secondary production in both perennial and ephemeral systems, their importance in creating moist micro-habitats within a water-limited environment is certainly unique to ephemeral systems.

Given their importance as micro-habitats, the heterogeneous distribution of wood within the Kuiseb River 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. For example, Benke et al. (1985) reported that invertebrate assemblages on large woody debris in Southeastern U.S. streams are characterized by higher levels of species richness and diversity relative to assemblages in adjacent sandy beds. Although woody debris constituted only 4% of the available habitat, it supported the majority of the invertebrate biomass. Similarly, Smock et al. (1989) reported that an increase in abundance of woody debris dams increased organic matter storage, macroinvertebrate abundance, and retention of organic matter during storm flows in small, low-gradient headwater streams in the coastal plain of Virginia. Macro-invertebrate biomass was more than 5 times higher in debris dams relative to adjacent channel sediments.

Similar patterns occur in the Namib's ephemeral rivers with respect to the importance of woody debris piles to fungal and invertebrate communities. For example, more than 80 % of macrofungi (41 species) fruiting following floods in the lower Kuiseb River occur in association with woody debris piles (K.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 sediments (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 tended to retain 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 served a similar function in the Kuiseb River, and I frequently observed diurnal activity of small mammals in close association with debris piles, to which they rapidly fled upon approach.

Given the strong links between the hydrologic regime, and the distribution and abundance of organic matter and moist microhabitats, I believe that the frequency and

magnitude of flood pulses are a key determinant 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, I expect that further research will reveal similar patterns within this, and other, ephemeral rivers.

Acknowledgments

References

Abbe, T. B., and D. R. Montgomery. 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research & Management* 12: 201-221.

Angermeier, P.L. and J.R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. *Transactions of the American Fisheries Society*. 113: 716-726.

Benke, A. C. 1990. A perspective on America's vanishing streams. *Journal of the North American Benthoogical Society* 9: 77-88.

Benke, A.C., Henry, R.L., III, Gillespie, D.M. and R.J. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. *Fisheries* 10: 8-13.

Bilby, R. E., and G. E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61: 1107-1113.

Bull, W.B. 1979. Threshold of critical power in streams. *Geological Society of America, Bulletin* 90: 453-64.

CTFT (Centre technique forestier tropical). 1989. *Faidherbia albida (Del.) A. Chev. (Synonym Acacia albida Del.).* (English translation by P.J. Wood) Nogent-sur-Marne, France: CTFT, and Wageningen, Netherlands: Centre technique de coopération agricole et rurale. 72 pp.

Dunkerley, D. L. 1992. Channel geometry, bed material, and inferred flow conditions in ephemeral stream systems, Barrier Range, western N.S.W. Australia. *Hydrological Processes* 6: 417-433.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266: 753-762.

Gordon, N.D., McMahon, T.A. and B.L. Finlayson. 1992. *Stream hydrology: an introduction for ecologists*. John Wiley & Sons, Chichester. 526 pp.

Graeme, D., and D. L. Dunkerley. 1993. Hydraulic resistance by the river red gum, *Eucalyptus camaldulensis*, in ephemeral desert streams. *Australian Geographical Studies* 31: 141-154.

Graf, W.L. 1988. *Fluvial processes in dryland rivers*. Springer-Verlag, Berlin. 346 pp.

Harmon, M. E., J.F. Franklin, F.J. Swanson, *et al.* 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.

Hedin, L. O. 1990. Factors controlling sediment community respiration in woodland stream ecosystems. *Oikos* 57: 94-105.

Hynes, H. B. N. 1975. The stream and its valley. *Verh. Internat. Verein. Limnol.* 19: 1-15.

Jacobson, K.M., Jacobson, P.J. and O.K. Miller, Jr. in review. The autecology of *Battarrea stevenii* (Liboshitz) Fr. in ephemeral rivers of southwestern Africa. *Mycological Research.*

Jacobson, P.J., K.M. Jacobson, and M.K. Seely. 1995. *Ephemeral rivers and their catchments: sustaining people and development in western Namibia.* Desert Research Foundation of Namibia, Windhoek. 160 pp.

Keller, E. A., and F. J. Swanson. 1979. Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes* 4: 361-380.

Krebs, C.J. 1989. *Ecological methodology.* Harper & Row, New York. 654 pp.

Lancaster, J., Lancaster, N. and M.K. Seely. 1984. Climate of the Central Namib. *Madoqua* 14(1): 5-61.

Lienkaemper, G. W., and F. J. Swanson. 1987. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. *Canadian Journal of Forestry Research* 17: 150-156.

Maser, C., and J. R. Sedell. 1994. *From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans.* St. Lucie Press, Delray Beach.

Mason, D. T. 1989. Small mammal microhabitats influenced by riparian woody debris. Pages 697-709 in R. R. Sharitz and J. W. Gibbons, eds. *Freshwater wetlands and wildlife.* USDOE Office of Scientific and Technical Information, Oakridge, TN.

Minckley, W. L., and J. N. Rinne. 1985. Large woody debris in hot-desert streams: an historical review. *Desert Plants* 7: 142-152.

Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* 53: 1-25.

Naiman, R. J., J. M. Melillo, M. A. Lock, and T. E. Ford. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology* 68: 1139-1156.

Newbold, J. D., P. J. Mulholland, J. W. Elwood, and R. V. O'Neill. 1982. Organic carbon spiraling in stream ecosystems. *Oikos* 38: 266-272.

Prochzaka, K., Stewart, B.A. and B.R. Davies. 1991. Leaf litter retention and its implications for shredder distribution in two headwater streams. *Archiv für Hydrobiologie* 120: 315-325.

Sedell, J. R., and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. *Verh. Internat. Verein. Limnol.* 22: 1828-1834.

Seely, M. K., and M. Griffin. 1986. Animals of the Namib Desert: interactions with their physical environment. *Revue Zool. afr.* 100: 47-61.

Seely, M. K., W.H. Buskirk, W.J. Hamilton, J.E.W. Dixon. 1979/80 - 1980/81. Lower Kuiseb River perennial vegetation survey. *Southwest African Scientific Society* 34/35: 57-86.

Shelley, R. M., and C. S. Crawford. 1996. *Cnemodesmus riparius*, N. SP., a riparian millipede from the Namib Desert, Africa (Polydesmida: Paradoxosomatidae). *Myriapodologica* 4: 1-8.

Shields, F. D., Jr., and R. H. Smith. 1992. Effects of large woody debris removal on physical characteristics of a sand-bed river. *Aquatic Conservation: Marine and Freshwater Ecosystems* 2: 145-163.

Smock, L. A., G. L. Metzler, and J. E. Gladden. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* 70: 764-775.

Sokal, R.R. and F.J. Rohlf. 1995. *Biometry.* 3rd ed. W.H. Freeman and Company, New York. 887 pp.

Speaker, R., K. Moore, and S. Gregory. 1984. Analysis of the process of retention of organic matter in stream ecosystems. *Verh. Internat. Verein. Limnol*. 22: 1835-1841.

Stengel, H. W. 1964. *The rivers of the Namib and their discharge into the Atlantic, Part I: Kuiseb and Swakop.* Scientific Papers of the Namib Desert Research Station, No. 22, Transvaal Museum, Pretoria.

Sykes, G. 1937. *The Colorado Delta.* American Geographic Society, New York.

Theron, G. K., N. v. Rooyen, and M. W. v. Rooyen. 1980. Vegetation of the lower Kuiseb River. *Madoqua* 11: 327-345.

Triska, F. J. 1984. Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: a historical case study. *Verh. Internat. Verein. Limnol.* 22: 1876-1892.

Vannote, R. L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Vogel, J. C. 1989. Evidence of past climatic change in the Namib Desert. *Palaeogeography, Palaeoclimatology, Palaeoecology* 70: 355-366.

Ward, G. M., and N. G. Aumen. 1986. Woody debris as a source of fine particulate organic matter in coniferous forest stream ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1635-1642.

Ward, J. D. 1987. *The Cenozoic succession in the Kuiseb Valley, Central Namib Desert.* Geological Survey of Namibia, Windhoek. 124 pp.

Webster, J.R. and B.C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. *Ecological Monographs* 49: 51-72.

Webster, J. R., A. P. Covich, J. L. Tank, and T. V. Crockett. 1994. Retention of coarse organic particles in streams in the southern Appalachian Mountains. *Journal of the North American Benthological Society* 13: 140-150.

Table 1. Hydrologic gauging stations within the study area and their mean annual runoff volume (MAR_V) (m^3) and mean annual peak discharge (MAPD) (m^3s^{-1}).

Station	Catchment (km^2)	Elevation (m)	Gradient (m/m)	MAR_V (m^3)	MAPD (m^3s^{-1})
Schlesien	6,520	760	0.0040	6.59×10^6	71.9
Greylingshof	2,490	720	0.0055	2.77×10^6	68.0
Confluence[1]	~9,500	620	0.0035	9.51×10^6	-
Gobabeb	11,700	360	0.0030	4.65×10^6	31.9
Rooibank	14,7000	120	0.0039	0.64×10^6	7.4

[1] - Mean of annual sums of Schlesien and Greylingshof.

Table 2. Total numbers and positions of wood marked within each zone, and the number retained or exported within each zone in response to the flood. Numbers in parentheses represent percentages of the total number marked.

Zone	Marked		Retained		Exported	
	Debris Pile	Stranded	Debris Pile	Stranded	Debris Pile	Stranded
160 km	152	101	60	4	92	97
	(60.1)	(39.9)	(39.5)	(4.0)	(60.5)	(96.0)
50-10 km	913	774	478	220	435	554
	(54.1)	(45.9)	(52.4)	(28.4)	(47.6)	(71.6)
Logs	70	95	56	34	14	61
	(42.4)	(57.6)	(80.0)	(35.8)	(20.0)	(64.2)
Totals	1,135	970	594	258	541	712
	(53.9)	(46.1)	(52.3)	(26.6)	(47.7)	(73.4)

Table 3. Mean transport distances for wood from each marking zone and number and final position after transport for recovered wood.

Zone	Distance (km)	Total Recoveries[1]	Debris Pile[2]	Stranded[2]
160 km	120	5 (2.65)	5 (100)	0 (0)
50 km	32	42 (50.0)	23 (54.8)	19 (45.2)
44 km	27	63 (35.4)	33 (52.4)	30 (47.6)
38 km	32	49 (35.8)	22 (55.1)	27 (44.9)
33 km	29	83 (33.5)	38 (45.8)	45 (54.2)
27 km	23	77 (39.9)	27 (35.1)	50 (64.9)
10 km	13	55 (36.9)	27 (49.1)	28 (50.9)
Logs	18	62 (82.7)	41 (66.1)	21 (33.9)
Totals		436 (34.8)	216 (49.5)	220 (50.5)

[1] - Percent of total number exported in parentheses.

[2] - Percent of total number recovered in parentheses.

Table 4. Mean length (m) of retained and exported wood for each marking zone.

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

Values in a row followed by different letters are statistically different at $p<0.05$ level.

Table 5. Mean length (m) of wood exported from each zone retained in a debris pile relative to that stranded on channel or floodplain sediments.

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

Values in a row followed by different letters are statistically different at p<0.05 level.

Table 6. Mean retention curve slope and channel characteristics for five sections within the lower Kuiseb River study area.

Zone	Slope	Debris Piles (km^{-1})	Channel Trees (km^{-1})	Channel Width (m)
50 - 36 km	-3.25	9.5	15.7	45
36 - 16 km	-1.14	1.6	4.2	59
16 - -3 km	-2.63	2.7	3.2	64
-3 - -10 km	-0.51	1.0	1.7	84
-10 - -16 km	-3.33	0	0	78

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

	Faidherbia	*Faidherbia*[1]	*Tamarix*	*Cladoraphis*	Other[2]
Marking Zone Recoveries[3]					
	191 (32.2%)	306 (51.5%)	30 (5.1%)	59 (9.9%)	8 (1.3%)
Downstream Recoveries[4]					
	63 (29.0%)	78 (36.0%)	41 (19.0%)	18 (8.0%)	18 (8.0%)

[1] - Cespitose (2 stems)

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

[3] - (n=594)

[4] - (n=216)

Chapter 3:
Variation in material transport and water chemistry along a large ephemeral river in the Namib Desert.

Abstract: The chemical characteristics of floodwaters in ephemeral rivers are little known, particularly with regard to their organic loads. These rivers typically exhibit a pronounced downstream hydrologic decay but few studies have documented its effect upon chemical characteristics and material transport. To develop a better understanding of the dynamics of floods and associated material transport in large ephemeral rivers, floods of the ephemeral Kuiseb River in southwestern Africa were tracked and repeatedly sampled at multiple points along the river's lower 220 km. Total suspended sediments averaged 35.3 g/l during peak flows and increased at downstream stations. Fine particulate organic matter (FPOM) made up 11.8 % of the suspended sediments, averaging 4.17 g/l, and also increased at downstream stations. Levels of dissolved organic matter (DOM) were significantly lower, averaging 0.082 g/l, and exhibited a slight increase at downstream stations. On average, dissolved organic matter represented only 2.4 % of the total organic load transported during floods. A 2-day flash flood transported 24,000 metric tons of suspended sediments out of the river's headwaters and into its lower 200 km; 12.9 % of the load was organic matter. Hydrologic decay resulted in the complete deposition of all transported material within the lower reaches of the Kuiseb River. None of the material was exported to the Atlantic Ocean. Cation and anion concentrations increased downstream. This was particularly so for sodium and chloride which exhibited a five-fold increase over the river's lower 200 km. The spatial variation in surface flow, and associated patterns of material transport, renders the lower river a sink for materials transported from upstream sources. This pattern has important implications for the structure and functioning of this ephemeral river ecosystem. In particular, the transport and deposition of large amounts of organic matter, much of which may be highly-labile, is an important supplement to heterotrophic communities within the river's lower reaches. Finally, the sediment deposition and downstream increases in ion concentration are likely key factors influencing soil characteristics of ephemeral river floodplains.

Introduction

Unlike most perennial systems, ephemeral rivers exhibit a pronounced downstream hydrologic decay, attributable to transmission losses associated with infiltration and evaporation (Graf 1988). This downstream attenuation in both flow volume and discharge is perhaps the best known characteristic of ephemeral rivers and has been documented for a number of systems of varying sizes (Jacobson, Ch. 1). Associated with this attenuation is a downstream decrease in stream power and a corresponding increase in alluviation (Bull 1979), and the resulting alluvial deposits are the most extensively studied aspect of ephemeral systems (Picard and High 1973, Baker et al. 1988, Graf 1988, Warner 1988).

While the episodic floods characteristic of dryland rivers and streams have long fascinated the desert traveler (Van Dyke 1901), their chemical composition and transport dynamics have only recently been examined. Fisher and Minckley (1978) were the first to document temporal variation in the chemical characteristics of a 'flash flood' 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.

Sharma et al. (1984a & 1984b) provided details on the spatial variation in transmission losses, water chemistry, and patterns of sediment transport during a flood in the ephemeral Luni River in arid northwestern India. This study was the first to examine changes in chemical characteristics as a desert flood traveled downstream, in this case over a distance of several hundred kilometers. The concentrations of sediment and selected ions increased in association with a decrease in discharge and total flow volume. In both studies, however, chemical analyses were largely restricted to inorganic constituents. With the exception of Fisher and Minckley's (1978) report that 11 % of the total suspended sediments was organic matter, no information was provided on the organic loads transported by these floods.

While recent studies have more closely examined organic matter dynamics in intermittent Sycamore Creek (Fisher and Grimm 1985, Jones et al. 1996), patterns in ephemeral systems remain unknown. Further study is warranted because the hydrologic decay exhibited by ephemeral systems is likely to result in patterns of material transport and deposition that diverge from those of their more mesic counterparts. In addition, ephemeral rivers occur throughout the arid and semi-arid regions that cover roughly a third of the world's surface (Thornes 1977), making them one of the most common, yet least known, types of fluvial ecosystems.

To assess the influence of hydrologic decay on the spatial patterns of water chemistry and material transport, I sampled floods traveling down the ephemeral Kuiseb River in western Namibia from 1993 to 1995. In particular, I quantified the composition

and transport of the organic load in relation to longitudinal hydrologic patterns associated with the downstream hydrologic decay. Source and sink areas for transported materials were identified, and the composition and transport dynamics of the organic matter load were compared to those described from more mesic systems.

Methods

Study Area

The Kuiseb River drains a catchment of approximately 14,700 km^2 in west-central Namibia and flows for 560 km from its headwaters to the Atlantic Ocean. The driest country in southern Africa, Namibia is named for the coastal Namib Desert, running the length of the country and extending inland ~150 km to the base of the Great Western Escarpment. Associated with the desert is a strong east-west climatic gradient. Mean annual rainfall exceeds 350 mm in the headwaters, which begin on the inland plateau at an elevation of ~2,000 m. Moving westward, mean annual rainfall drops to ~100 mm at the eastern edge of the Namib Desert at the escarpment's base, then to near zero at the coast (Namibian Weather Bureau). Evaporation is high throughout the catchment, exceeding rainfall by 7 to 200 times (Lancaster et al. 1984). As a result, surface flow occurs in direct response to strong convective storms, primarily during the summer months, and rapidly ends after the cessation of localized rains.

From the headwaters westward the river has eroded a shallow, sinuous valley into schists and quartzites, the source of much of the sandy bedload transported within the lower river (Ward 1987). West of the 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 within this canyon, often flowing over bedrock with no alluviation due to the comparatively steep gradient (0.003-0.004 m/m) and narrow channel. This canyon broadens some 65 km from the coast, whereafter the river occupies a broad, shallow valley which finally becomes indistinct within 20 km of the coast. There, low crescentic dunes cross the river, producing several poorly defined channels that terminate near Walvis Bay. Gradients below the canyon average 0.001-0.002 m/m; they increase 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 suspension load high in silts. The sandy channel sediments within the lower 150 km are largely devoid of cobble or bedrock, excluding occasional bedrock dikes that cross the channel and form local knick points in the longitudinal profile (Ward 1987).

The Namibian Department of Water Affairs (DWA) maintains a series of automatic gauging stations along the mainstem of the Kuiseb River and on its various tributaries. Distinct longitudinal trends are evident among the hydrologic records from these stations, particularly among the mainstem stations (Jacobson, Chapter 1). Mean annual runoff (MAR) and mean annual peak discharge (MAPD) exhibit a strong decay

from the base of the escarpment westwards to the coast (Table 1). A more detailed review of the hydrology of the Kuiseb River is provided by Jacobson (Ch. 1).

Discharge

Surface flow in the Kuiseb River is routinely monitored by the Namibian Department of Water Affairs. Records from two gauges were used to monitor flow out of the upper catchment where most floods originate: one on the mainstem of the Kuiseb River (Schlesien), approximately 172 km above the Gobabeb gauge, and another on the Gaub River (Greylingshof), the Kuiseb's main tributary, approximately 20 km upstream of the Gaub-Kuiseb confluence and ~147 km above the Gobabeb gauge. Flow within the study reach was measured at the Gobabeb gauge and at Rooibank, 57 km downstream. These stations, equipped with automatic chart recorders, provided a record of the flood hydrograph from which the peak discharge (m^3s^{-1}) and total flow volume (m^3) for each flood were calculated. The Namibian Department of Water Affairs provided access to hydrographic records and previously established rating curves, which were used to calculate discharge. Total flow volumes were estimated by integrating discharge over the course of the hydrograph, using the trapezoidal rule for unequally spaced x-values (Sigma Plot, Jandel Corporation). Gauge floats frequently jammed during recession flows due to the high particulate loads carried by floods. Recession curves were then estimated, based upon floods of similar magnitudes previously recorded at the individual stations. Occasionally, gauges malfunctioned completely, preventing any approximation of flood volume.

Floodwater analysis

Water samples were collected in acid-washed, 500-ml polyethylene bottles. Whenever possible samples were collected mid-channel, although this was not possible during high-magnitude discharges. When safety considerations precluded such sampling, samples were collected within 2 m of the bank. In all cases, the uncapped bottle was lowered into the flow to the channel bottom or to a maximum depth of ~0.5 m and retracted at an even rate to obtain a depth-integrated sample. Samples were taken from bores (leading edges), at peak discharge, and during recession flows. One flood was intercepted as it exited the escarpment providing an opportunity to examine the longitudinal variation in water chemistry and organic matter transport.

Water samples were stored unpreserved at 4 °C and filtered upon return to the laboratory. Samples were pre-filtered through a 1-mm sieve and filtered through pre-weighed Whatman GF/F glass fiber filters. Total suspended solids (TSS) were determined gravimetrically after drying filters to a constant weight at 90 °C. Fine particulate organic matter (FPOM) was determined as loss on ignition (550 °C, 2 h) of filtered materials and expressed as ash-free dry mass. Dissolved organic matter (DOM) was measured by dichromate oxidation (Maciolek 1962), using a 20-ml aliquot of filtrate evaporated to

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dryness at 90 °C. Conductivity and pH were determined with a YSI Model 33 S-C-T and a Fisher Model 640 meter, respectively. Sodium, potassium, calcium, and magnesium were measured using a Phillips PU 9200/9390 atomic absorption spectrophotometer. Alkalinity was determined titrimetrically, using sulfuric acid, sulfate turbidimetrically, with $BaCl_2$, and chloride titrimetrically, with $AgNO_3$.

The concentration of coarse particulate organic matter (CPOM) transported in the leading edge of a flood was measured by sampling the bore and the subsequent flow using a 9-l bucket with a 30-cm opening. After sampling, contents were poured through a 1-mm sieve and the contents dried and weighed. Following flood recession, lateral deposits of FPOM and CPOM were sampled from replicated (n=4) 1-m^2 plots randomly selected from along the flood's lateral strand line. Samples were collected at three sites separated by 25-40 km to examine longitudinal changes in POM transport in association with the hydrologic decay. One-way analysis of variance (ANOVA) was used to compare means among sites (Zar 1984).

Material transport rates ($kg \cdot s^{-1}$) were calculated for organic matter and suspended solids as the product of discharge ($m^3 s^{-1}$) and concentration ($kg \cdot m^{-3}$). The total mass of material transported past sampling points during a flood was estimated by integrating the material transport rates over the course of the hydrograph, using the trapezoidal rule for unequally spaced x-values (Sigma Plot, Jandel Corporation). No attempt was made to express transport rates or total mass values in terms of export per unit area of drainage basin. The large size of the catchment combined with the low density of rainfall recording stations prevented an accurate estimation of the location and spatial extent of source areas for individual floods.

Results

Discharge

A total of 12 floods occurred during the study period, although discharge data are only available for the 1993 and 1994 floods. The duration of individual floods ranged from 1-8 days at Gobabeb, with a mean of 3 days (sd=2). Floods were preceded by a bore ranging from <5 cm to ~50 cm in height. Bore height increases in response to increasing discharge and channel gradient and decreases with increasing channel width. Flood bores traveled at an average speed of 2.1 $m \cdot s^{-1}$ (sd=0.1, n=4) above Gobabeb and decreased to 0.8 $m \cdot s^{-1}$ (sd=0.1, n=3) downstream, from Swartbank to Rooibank. The interval between bore arrival and peak discharge was short, ranging from 3 to 15 minutes. Flood rise and recession were both rapid, reflecting the importance of Hortonian overland flow (over the surface after initial ponding) in generating streamflow in dryland environments (Reid and Frostick 1989). Multiple peaks often occurred, reflecting the influence of tributary inflows and multiple storm events. The peak discharge recorded during the period was 322 $m^3 s^{-1}$, associated with a flood in the Gaub River, the Kuiseb's main tributary, in

January 1993. The discharge of all recorded floods decayed to zero from 440 to 550 km downstream from the headwaters. The furthest reach of the floodwaters varied over a distance of 40 km during the three years. The maximum occurred in 1993 when the floods reached 550 km downstream from the headwaters; the minimum of 510 km occurred in 1995.

In January 1994 a 2-day flood was intercepted as it flowed out of the escarpment; this flood typifies the hydrologic decay of all observed floods. The initial floodwave originated in the Gaub River catchment, and a peak of 159 m^3s^{-1} was recorded at the Greylingshof gauge, with a total flow volume of ~2.75 Mm^3 (million cubic meters). A second floodwave originated within the Kuiseb catchment above the Schlesien gauge, but was not recorded due to an instrument failure. My observations of the flood suggest that it peaked at ~20 m^3s^{-1} at the Schlesien gauge, with an estimated flow volume of ~2 Mm^3. The combined flow volume estimated for the Kuiseb-Gaub confluence was thus ~4.75 Mm^3. A total of 2.3 Mm^3 was measured at the Gobabeb gauge, 140 km below the confluence, representing a transmission loss of ~52%, or 0.37% km^{-1}.

Transmission losses increased significantly from the Gobabeb gauge down to Rooibank, where the total flow volume had dropped to ~50,000 m^3, a 98% reduction over 57 km, or 1.7% km^{-1}. The peak discharge exhibited a similar decay, dropping from 159 m^3s^{-1} at Greylingshof, to 52 m^3s^{-1} at Gobabeb, a 67% reduction over 140 km, or 0.48% km^{-1}. A recurrence interval of ~2.6 years was calculated for this flood at the Gobabeb gauge, using the annual peak discharge series (n=17). From Gobabeb to Rooibank, peak discharge dropped from 52 m^3s^{-1} to ~1 m^3s^{-1}, a 98% reduction over 57 km, or 1.7% km^{-1}. These estimates are similar to values calculated from an analysis of the annual flow record (n=14) for the three stations, which also indicate that transmission losses from the Kuiseb-Gaub confluence average ~52% (sd=21%) and losses between the Gobabeb and Rooibank gauges average ~86% (sd=12%) (Jacobson Ch.2). Flow velocity at peak discharge dropped from 2.2 $m·s^{-1}$ at Greylingshof to 2.0 $m·s^{-1}$ at Homeb, ~110 km downstream. From Homeb to Rooibank, a distance of ~90 km, peak flow velocity dropped to 0.8 $m·s^{-1}$.

Floodwater analysis

Floodwaters transported high concentrations of total suspended sediments (TSS) at peak discharge, with a mean value of 35.3 g/l (sd=20.6, n=20). The highest value measured was 139.7 g/l from a bore sample collected at Swartbank, while the lowest was 0.016 g/l from a recession flow (<1 m^3s^{-1}) sample collected at Greylingshof. Peak TSS values were associated with flood bores traveling between Gobabeb and Swartbank, and a downstream increase in concentration was observed among the sampling sites. A downstream increase, from Greylingshof to Gobabeb, was also observed in TSS values measured in the January 1994 flood, although a significant decrease occurred from Gobabeb downstream to Rooibank (Table 2). Fine particulate organic matter (FPOM)

contributed an average of 11.8 % (sd=2.7, n=20) of the total suspended sediments collected during discharge peaks, increasing to 39.8 % (sd=3.1, n=12) during recession flows less than 1 $m^3 \cdot s^{-1}$. Samples collected from bores were similar to those at peak discharge, averaging 13.9 % (sd=4.1, n=17).

FPOM ranged from 0.014 g/l in a recession flow sample (<1 $m^3 s^{-1}$), to 22.1 g/l in a bore sample collected at Swartbank during the first flood of 1993. FPOM averaged 4.17 g/l (sd=2.50, n=17) in samples collected during peak discharge. The concentration tended to increase downstream, as reflected in samples collected during the January 1994 flood (Table 2). Levels of dissolved organic matter were significantly lower, averaging 0.082 g/l (sd=43.5, n=17) during peak discharge. DOM concentrations ranged from 0.0056 g/l in a recession flow (<1 $m^3 s^{-1}$) sample collected at Greylingshof, to 0.228 g/l in a bore sample collected at Swartbank during the first flood of 1993. DOM concentration did not exhibit any distinct downstream trend, excluding a small increase observed from Gobabeb to Rooibank in the January 1994 flood. The ratio of DOM to POM averaged 0.024 (sd=0.025, n=17) in samples collected during peak discharge. This ratio did not differ from that of bore samples, which averaged 0.023 (sd=0.021, n=17). However, the ratio increased significantly in samples collected during the final stages of flood recession (<1 $m^3 s^{-1}$) averaging 0.450 (sd=0.332, n=12). The proportion of POM in the organic load transported by the January 1994 flood increased markedly between Greylingshof and Gobabeb and then decreased downstream to Rooibank (Table 2).

Integration of the discharge and concentration data for the January 1994 flood revealed a marked downstream decrease in the total transport of organic matter in association with the reduction in flow volume (Table 3). While ~3,100 metric tons were exported out of the escarpment into the lower river, only ~100 tons were transported past Rooibank (Table 3). However, while flow volume and DOM mass exhibited a ~50 % reduction between Greylingshof and Gobabeb, the mass of POM increased to 4,600 tons. The greatest change occurred between Gobabeb and Rooibank; a 98 % reduction in flow volume, DOM, and POM mass occurred over this 58 km reach. TSS transport increased from 24,000 to 46,000 tons between the escarpment and Gobabeb, followed by a ~98 % reduction between Gobabeb and Rooibank. The organic proportion of the TSS ranged from 10.0 % to 12.9 % from the escarpment to Rooibank (Table 3).

The concentration of CPOM (>1 mm) in a flood bore varied as it traveled downstream, increasing from 137.0 g/l to 181.4 g/l between Homeb and Swartbank, followed by a sharp decline to 12.6 g/l at Rooibank. The lateral deposition of particulate organic matter exhibited a similar pattern among these sites (Table 4). Strandline deposits at Homeb averaged 1,344 $g \cdot m^{-2}$ (sd=768), increasing to 11,296 (5,408) $g \cdot m^{-2}$ at Swartbank, 65 km downstream (p=0.003). At Rooibank, another 30 km downstream, no measurable deposits were produced during flood recession. The composition of the deposits also differed; 76 % of the material deposited at Homeb was larger than 1 mm, the proportion

decreasing to 32 % at Swartbank. The spatial extent of the deposits also varied, increasing from an average width of 30 cm (sd=11) at Homeb to 110 cm (sd=33) at Swartbank.

Floodwater pH averaged 7.29 (sd=0.05, n=20) for samples collected at peak discharge, ranging from a low of 6.70 in a bore sample at Schlesien to 8.00 for a recession flow (<1 m^3s^{-1}) sample at Gobabeb. The pH of bore samples was slightly lower, averaging 7.13 (sd=0.06, n=17), while pH tended to increase during recession, averaging 7.68 (sd=0.19, n=12). Low bore pH was associated with high POM levels, and organic acids may have contributed to the decrease in pH.

Conductivity also varied among bore, peak, and recession samples, as well as exhibiting a downstream increase (Table 2). Conductivity averaged 620 µS·cm^{-1} (sd=185, n=20) in peak discharge samples, increasing to 815 µS·cm^{-1} (sd=251, n=17) in bore samples. In contrast, recession flow (<1 m^3s^{-1}) samples averaged 294 µS·cm^{-1} (sd=107, n=12). The highest values were consistently recorded at Rooibank, where a bore sample measured 1,415 µS·cm^{-1}.

Sodium, potassium, calcium, magnesium, and chloride all exhibited a downstream increase from Greylingshof to Rooibank during the January 1994 flood (Table 2). The exception to this trend was sulphate with no distinct change among the sites. Sodium and chloride exhibited the most dramatic change with five-fold increase from Greylingshof to Rooibank. Alkalinity also increased downstream, more than doubling between Greylingshof and Rooibank (Table 2).

Discussion

Hydrologic controls of transport and deposition

The composition, transport, and deposition patterns of materials carried in Kuiseb River floodwaters clearly diverge from those characteristic of more mesic systems, and much of this variation is attributable to the downstream hydrologic decay. Most significantly, the termination of floods within the river's lower 100 km renders the reach a sink for materials exported from upstream source areas. The existence of localized deposition areas within the lower reaches of the rivers was also noted by Vogel (1989), who observed that large ephemeral rivers in the Namib Desert tended to drop their inorganic sediment loads along a specific stretch of riverbed that corresponded to the average reach of the floods. He observed that this deposition often resulted in a convex deviation in the river's longitudinal profile near the coast. My observations of sediment transport revealed that deposition patterns do correspond with the convexity observed in the lower reaches of the Kuiseb's longitudinal profile (Jacobson Ch. 2).

Ephemeral rivers and streams are well known for the vast quantities of sediment moved during floods (Graf 1989). Records from the Rio Puerco, an ephemeral river in central New Mexico, indicate that suspended sediment concentrations may reach 68 % solids (by weight) (Bondurant 1951). This is much higher than the peak of 14 % measured in a flood bore in the lower Kuiseb River. Sharma et al. (1984b) observed a downstream increase in sediment concentrations associated with a flood in the ephemeral Luni River in northwest India. Mean sediment concentration increased from 6.1 g/l near the headwaters to 16.8 g/l roughly 300 km downstream, associated with a decrease in total runoff from 22.31×10^6 to 6.82×10^6 between the two sites. This pattern parallels that observed in the Kuiseb, where TSS increased downstream in association with hydrologic decay.

While TSS levels varied, the organic proportion of TSS remained comparatively constant with an average of 11.8 % organic matter. POM in rivers is often expressed as a percentage of the TSS, and values from the world's rivers range from 1.3 to 8.4 %, with POM and TSS concentrations ranging from 0.6 to 14.2 mg/l and 5 to 1500 mg/l, respectively (Ittekkot and Laane 1991). The relative proportions of organic matter within suspended sediment samples from dryland rivers are at or beyond the upper end of this range. Suspended solids peaked at 55.2 g/l in a flash food in Sycamore Creek, and the organic fraction of the sediment load ranged from 9-13 % (mean=11 %) (Fisher and Minckley 1978). Similarly, Sykes (1937) reported that sediments deposited in the Colorado River delta were ~8 % organic matter (by weight). Minckley and Rinne (1985) provided an historical review of large woody debris in desert streams of the southwestern USA, and noted that such debris provided a significant source of FPOM delivered to the downstream reaches of desert systems. Woody debris may also be an important source of FPOM within the Kuiseb River (Jacobson Ch. 2).

Organic matter transport and deposition exhibited patterns similar to those observed for inorganic sediments. Jacobson (Ch.2) recorded a downstream increase in the retention of woody debris in the Kuiseb River, largely attributable to hydrologic decay. The deposition of fine particulate organic matter (FPOM) within the lower river is similarly affected, and the bulk of transported FPOM is deposited within the lower river in response to the hydrologic decay.

The hydrologic decay and associated increase in retention also results in downstream sorting of the organic load. The concept of stream power or ability of water to do work, although traditionally applied in the context of inorganic particles (Leopold et al. 1964), has also been applied to the transport and sorting of particulate organic matter in rivers and streams. However, Sedell et al. (1978) found only a weak correlation between stream power and POM transport, noting that the low specific gravity and high surface to volume ratio of organic particulates results in differing behaviors, relative to inorganic sediments. Nonetheless, physical sorting of the organic load does occur within ephemeral rivers. The decline in stream power associated with the hydrologic decay (Ch.

2 Jacobson) causes the percentage of large organic particles in transport to decrease downstream.

The principal deposition zone for woody debris is in an 80 km reach immediately upstream of the Gobabeb gauge, while that for FPOM occurs in the 50 km downstream to the Rooibank gauge. The transport and deposition patterns of woody debris within the lower Kuiseb River were examined by Jacobson (Ch. 2), who found that the 80 km reach above the Gobabeb gauge functioned as a 'sink' for woody debris within the channel network. Although the mass of woody debris imported into the lower river from upstream sources was unknown, the study suggested that significant amounts of woody debris were unlikely to be transported beyond this ~80 km reach by floods of the magnitude observed in the present study (~2 year return interval).

The concentration and composition of the dissolved load also varied along the channel network, with a significant downstream increase in the concentration of many ions. Interannual hydrologic variation will shift the position of deposition zones for dissolved and particulate material, both organic and inorganic. The positions within the channel network will vary with flood magnitude, shifting upstream or downstream with decreases or increases, respectively (Jacobson Ch. 2). When this inter-annual variability is averaged over many years, a mean deposition zone for transported materials can be defined in relation to the 'average reach of the floods,' as noted by Vogel (1989). In the case of the Kuiseb River, the lack of any export from the lower reach of the river renders it a sink for material exported from upstream source areas. This deposition zone can thus accumulate large standing crops of organic matter. Such a pattern has been noted in observations of the transport and retention of large woody debris in the lower Kuiseb River (Jacobson Ch. 2). Ultimately, the spatial and temporal extent of such accumulations within ephemeral systems is directly dependent upon the dynamics of the hydrologic regime.

In addition, the downstream increase in inorganic solute concentration may, over the long-term, increase the salinity of alluvial soils within the lower reaches of ephemeral systems. It is unknown whether accumulations sufficient to affect plant productivity could develop in association with such deposition and evaporative concentration. Sharma et al. (1984a) observed a similar downstream increase in conductivity and the concentrations of selected ions during floods along the ephemeral Luni River and commented on the negative implications for downstream water quality. Fisher and Grimm (1985) reported a slight rise in conductivity prior to the cessation of flow in headwater washes of a desert stream in the Sonoran Desert, USA. This terminal rise was attributed to the longer contact time between this final runoff fraction and the soil compartment. Similar terminal rises in both conductivity and dissolved organic matter were often observed in the Kuiseb River when recession flows dropped below 1 m^3s^{-1} and may reflect both increased contact time with alluvial sediments as well as evaporative

concentration, particularly in the reach between Swartbank and Rooibank where the highest levels where observed.

Organic load dynamics

Lotic ecologists have reported that the largest component of organic loading in streams is in the dissolved state (Moeller et al. 1979, Thurman 1985, Allan 1995), although the ratio of DOM to POM has been found to vary from 0.09 to 70 (Moeller et al. 1979). This tenet does not apply in the Kuiseb River, however, as particulate organic carbon constituted the largest component of the organic load, with DOM constituting only 2.4 % of the total organic load during peak discharges, when the overwhelming bulk of carbon transport occurs. Jones et al. (1996) reported an even higher figure for a flash flood in Sycamore Creek within the Sonoran Desert, estimating that DOM was only 0.3 % of the total carbon exports.

Despite the predominance of particulate matter, the Kuiseb River transports high concentrations of both dissolved and particulate organic matter during floods, and both often exhibit a downstream increase. Although not directly comparable, Mulholland and Watts (1982) reported that total organic matter (TOM) concentrations for streams throughout North America ranged from 3.2 to 43.4 mg/l. In contrast, average levels during flow in the Kuiseb River were in excess of 4,000 mg/l. The downstream increase in FPOM may be associated with the decrease in flow volume. In addition, the extensive riparian forest within the lower river is a significant source of organic matter which accumulates in the channel between floods.

The *Faidherbia albida* trees in and along the channel are an important source of organic matter in the river downstream of the escarpment, dropping large amounts of dry fruits onto the channel and floodplain prior to floods (Jacobson Ch. 2). These fruits are exported downstream during floods, rapidly degrading during transit. This contribution is only significant in the first flood of the season, however, as fruits are flushed from the channel. Nonetheless, FPOM levels do not drop significantly in subsequent floods. While antecedent storms may greatly deplete transportable materials in dryland watersheds (Fisher and Grimm 1985), the high temporal and spatial variability of precipitation, combined with the large size of the Kuiseb catchment, may have limited the extent to which such depletion was observed, as source areas for floods varied across the catchment.

The in-channel and floodplain accumulations in the Kuiseb River, as well as the downstream increase in riparian inputs, strongly resemble patterns reported from prairie streams in the USA. In prairie streams, organic matter accumulates in the channel during the dry season and is flushed downstream by subsequent floods (Gurtz et al. 1988). Much of this material is redeposited on banks downstream. Headwaters streams in these grassland biomes receive comparatively low levels of organic inputs and store little

organic matter, relative to downstream reaches which are influenced by gallery forest. On average, streams flow for only four months of year (Gurtz et al. 1988).

It is generally accepted that the combination of primary production and decomposition rates of plant matter control the amount of DOM in water, and thus arid environments have been thought to have inherently low DOM concentrations (Thurman 1985). However, as noted above, the riparian vegetation associated with large ephemeral rivers may deliver a significant amount of organic matter to the typically dry channel. As a result of low decomposition rates during interflood periods, large accumulations may accrue, resulting in high DOM levels when surface flow resumes. *Faidherbia* fruits may be an important source of DOM within the lower reaches of the river. The highest DOM levels observed during the study (up to 228 mg/l) were measured in the lower reaches of the river (Swartbank) during the first flood of the season, which flushed accumulated *Faidherbia* fruits downstream. Leaching experiments with fresh plant litter have shown that up to 40 % of the organic matter of the plant may be dissolved in 24 hours (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 (CTFT 1989).

The general increase in DOM concentration observed between Gobabeb and Rooibank may also be partly attributable to evaporative concentration. Flood speeds drop significantly in this reach and evaporative losses are extremely high (Lancaster et al. 1984). While the spatial variability of DOM concentration among catchments reveals no general trend (Sedell and Dahm 1990), I believe the downstream increase in the Kuiseb River may be an inherent feature of ephemeral rivers. In addition to the downstream increase in allocthonous loading, the amount of material leached from organic matter increases with time in solution (Suberkropp et al. 1976). Thus, as floods travel downstream transporting their load of organic particulates, DOM would gradually increase.

The DOM concentrations in floodwaters of the lower Kuiseb River are among the highest reported from any aquatic system. DOM concentrations measured in the lower Kuiseb River ranged from 5.6 to 228 mg/l, with an average of 82 mg/l at peak discharge, greatly exceeding the estimated global average for streams and rivers of 10 mg/l (Meybeck 1982). While the high levels may be partly attributable to inter-flood accumulations of fresh, carbohydrate-rich organic matter within the stream channels, the physical processing associated with fluvial transport in a warm (30-32 °C), abrasive, and turbulent environment must contribute to the observed levels by facilitating rapid leaching of soluble organic material. The highest DOM levels recorded in the Kuiseb River were measured in flood bores within the lower reaches of the river. These bores also carried the highest levels of particulate organic matter. This high DOM levels may thus be a function of the "tea bag effect," which Sedell and Dahm (1990) used in reference to the leaching of DOM from floodplain vegetation. In the case of a flood in an ephemeral river, the 'tea

bag' is carried along with the advancing flood wave for 1-3 days over distances up to several hundred kilometers, steeping in the 30-32 °C water with continual additions of unleached organic matter.

Similar or higher DOM concentrations were reported from aquatic environments in the vicinity of the Mt St Helens volcanic blast zone in southwestern Washington, USA (Baross et al. 1982). Cold, oligotrophic aquatic environments were temporarily transformed into warm, organic-rich aquatic environments after receiving massive inputs of wood debris and pyrolized soluble organics from adjacent destroyed forests, resulting in greatly elevated DOM levels. The temperature of Spirit Lake rose from ~10 °C to 34 °C within 24 h of the eruption, and DOM levels climbed to 102.2 mg/l within 3 months of the blast, triggering a significant increase in microbial activity (Baross et al. 1982).

Blackwater rivers and streams have provided the highest levels of DOM measured within unaltered perennial systems. Meyer (1986) recorded an average DOM concentration of 25.4 mg/l for the Ogeechee River, in Georgia, USA, and 30.8 mg/l for Black Creek, a tributary of the Ogeechee. Although much of this material consisted of refractory high-molecular weight fractions, a significant proportion (from 10-20 %) was low-molecular weight and presumably highly labile. Such labile organic matter provides an important energy source for the microbial component of the food web within blackwater rivers and streams (Meyer 1990). Given the limited decomposition that occurs during interflood periods in drylands, an even larger percentage of the DOM in ephemeral rivers may be labile, although fueling heterotrophic respiration by terrestrial bacterial and fungal communities, rather than their aquatic counterparts.

In Sycamore Creek, an intermittent stream in the Sonoran Desert, DOM concentration was significantly higher during floods (mean 13.2 mg/l) than during base flow discharge (9.6 mg/l) (Jones et al. 1996). Mulholland (1997) noted that these comparatively high levels may be attributable to watershed characteristics, including lower mineralization rates, limited sorption of DOM in sandy soils, and rapid delivery of water from the catchment to the channel. As a result, dryland watersheds may export a significantly larger proportion of their annual primary production as DOM and POM relative to more mesic watersheds (Mulholland 1997).

A major issue in examining the organic matter dynamics of streams concerns the extent of in-stream processing occurring relative to this 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). Ephemeral rivers such as the Kuiseb are an extreme example, where retentive structures in combination with hydrologic decay often result in no export from a reach or the system as a whole. In the Kuiseb River, the deposition zone within the river's lower reaches functions as a storage site or sink for fluvially-transported organic matter. The large amount of particulate organic matter deposited in the lower reaches of the river is an important energy source for flood-

activated heterotrophs, particularly fungi and invertebrates (Jacobson et al. In Review, Shelley and Crawford 1996, Jacobson Ch. 2). I suggest that the influence of hydrologic variability on the distribution and composition of fluvially-transported organic matter, and hence, on the structure of downstream heterotrophic communities, may be a feature common to all fluvial ecosystems, irrespective of their hydrologic regime.

Acknowledgments

References

Allan, J.D. 1995. *Stream ecology: structure and function of running waters*. Chapman & Hall, London. 388 pp.

Baker, V.R., R.C. Kochel, and P.C. Patton, eds. 1988. *Flood geomorphology.* John Wiley & Sons, New York. 503 pp.

Baross, J.A., C.N. Dahm, A.K. Ward, M.D. Lilley, J.R. Sedell. 1982. Initial micro-biological response in lakes to the Mt St Helens eruption. *Nature* 296: 49-52.

Bondurant, D.C. 1951. Sedimentation studies at Conchas Reservoir in New Mexico. *Transactions, American Society Civil Engineers* 116: 1292-1295.

CTFT (Centre technique forestier tropical). 1989. *Faidherbia albida (Del.) A. Chev. (Synonym Acacia albida Del.*). (English translation by P.J. Wood) Nogent-sur-Marne, France: CTFT, and Wageningen, Netherlands: Centre technique de coopération agricole et rurale. 72 pp.

Fisher, S. G., and N. B. Grimm. 1985. Hydrologic and material budgets for a small Sonoran Desert watershed during three consecutive cloudburst floods. *Journal of Arid Environments* 9: 105-118.

Fisher, S. G., and W. L. Minckley. 1978. Chemical characteristics of a desert stream in flash flood. *Journal of Arid Environments* 1: 25-33.

Graf, W.L. 1988. *Fluvial processes in dryland rivers*. Springer-Verlag, Berlin. 346 pp.

Gurtz, M.E., G.R. Marzolf, K.T. Killingbeck, D.L. Smith, and J.V. McArthur. 1988. Hydrologic and riparian influences on the import and storage of coarse particulate organic matter in a prairie stream. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 655-665.

Ittekkot, V., and R. W. P. M. Laane. 1991. Fate of riverine particulate organic matter. Pages 233-243 in E. T. Degens, S. Kempe, and J. E. Richey, eds. *Biogeochemistry of major world rivers.* John Wiley & Sons, Ltd., New York.

Jacobson, K.M., Jacobson, P.J. and O.K. Miller, Jr. In Review. The autecology of *Battarrea stevenii* (Liboshitz) Fr. in ephemeral rivers of southwestern Africa. *Mycological Research*.

Jones, J. B., Jr., S. G. Fisher, and N. B. Grimm. 1996. A long-term perspective of dissolved organic carbon transport in Sycamore Creek, Arizona, USA. *Hydrobiologia* 317: 183-188.

Lancaster, J., N. Lancaster, and M.K. Seely. 1984. Climate of the Central Namib. *Madoqua* 14(1): 5-61.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. *Fluvial processes in geomorphology*. W.H. Freeman, San Francisco. 522 pp.

Maciolek, J.A. 1962. *Limnological organic analyses by quantitative dichromate oxidation*. Research Report No. 60, United States Fish and Wildlife Service, 61 pp.

Meybeck, M. 1982. Carbon, nitrogen, and phosphorus transport by world rivers. *American Journal of Science* 282: 401-450.

Meyer, J.L. 1986. Dissolved organic carbon dynamics in two subtropical blackwater rivers. *Archiv für Hydrobiologie* 108: 119-134.

Meyer, J. L. 1990. A blackwater perspective on riverine ecosystems. *BioScience* 40: 643-651.

Minckley, W. L., and J. N. Rinne. 1985. Large woody debris in hot-desert streams: an historical review. *Desert Plants* 7: 142-152.

Moeller, J. R., G.W. Minshall, K.W. Cummins, *et al.* 1979. Transport of dissolved organic carbon in streams of differing physiographic characteristics. *Organic Geochemistry* 1: 139-150.

Mulholland, P. J., and J. A. Watts. 1982. Transport of organic carbon to the oceans by rivers of North America: a synthesis of existing data. *Tellus* 34: 176-186.

Mulholland, P.J. 1997. Dissolved organic matter concentration and flux in streams. Pages 131-141 in J.R. Webster and J.L. Meyer (eds.). Stream organic matter budgets. *Journal of the North American Benthological Society* 16: 3-141.

Picard, M.D. and L.R. High, Jr. 1973. *Sedimentary structures of ephemeral streams.* Elsevier Scientific Publishing Company, Amsterdam. 223 pp.

Reid, I., and L. E. Frostick. 1989. Channel form, flows and sediments in deserts. Pages 117-135 in D. S. G. Thomas, ed. *Arid Zone Geomorphology*. Belhaven Press, London.

Sedell, J. R., and C. N. Dahm. 1990. Spatial and temporal scales of dissolved organic carbon in streams and rivers. Pages 261-279 in E. M. Perdue and E. T. Gjessing, eds. *Organic acids in aquatic ecosystems.* John Wiley & Sons, Ltd.

Sedell, J. R., R. J. Naiman, K. W. Cummins, G. W. Minshall, and R. L. Vannote. 1978. Transport of particulate organic material in streams as a function of physical processes. *Verh. Internat. Verein. Limnol.* 20: 1366-1375.

Sharma, K. D., J. S. Choudhari, and N. S. Vangani. 1984a. Transmission losses and quality changes along a desert stream: the Luni Basin in N.W. India. *Journal of Arid Environments* 7: 255-262.

Sharma, K. D., N. S. Vangani, and J. S. Choudhari. 1984b. Sediment transport characteristics of the desert streams in India. *Journal of Hydrology* 67: 261-272.

Shelley, R. M., and C. S. Crawford. 1996. *Cnemodesmus riparius*, N. SP., a riparian millipede from the Namib Desert, Africa (Polydesmida: Paradoxosomatidae). *Myriapodologica* 4: 1-8.

Suberkropp, K., Godshalk, G.L. and Klug, M.J. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. *Ecology* 57: 720-727.

Sykes, G. 1937. *The Colorado Delta.* American Geographical Society. New York.

Thornes, J.B. 1977. Channel changes in ephemeral streams: observations, problems, and models. Pages 317-335 in K.J. Gregory, ed. *River channel changes*. John Wiley & Sons, Chichester.

Thurman, E. M. 1985. *Organic geochemistry of natural waters.* Martinus Nijhoff / Dr. W. Junk Publishers, Dordrecht.

Van Dyke, J.C. 1901. *The Desert*. Scribners, New York. 233 pp.

Vogel, J.C. 1989. Evidence of past climatic change in the Namib Desert. *Palaeogeography, Palaeoclimatology, Palaeoecology* 70: 355-366.

Ward, J. D. 1987. *The Cenozoic succession in the Kuiseb Valley, Central Namib Desert*. Geological Survey of Namibia, Windhoek. 124 pp.

Warner, R.F., ed. 1988. *Fluvial geomorphology of Australia.* Academic Press, Sydney. 373 pp.

Webster, J.R. and J.L. Meyer. 1997. Stream organic matter budgets—introduction. *Journal of the North American Benthological Society* 16: 5-13.

Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 pp.

Table 1. Catchment area, elevation, channel gradient, mean annual runoff (MAR), and mean annual peak discharge (MAPD) for hydrologic gauging stations within the lower Kuiseb River. Runoff and discharge values are based upon the annual flow series from 1979-1993.

Station	Catchment (km^2)	Elevation (m)	Gradient (m/m)	MAR (m^3)	MAPD (m^3·s^{-1})
Schlesien	6,520	760	0.0040	6.59×10^6	71.9
Greylingshof	2,490	720	0.0055	2.77×10^6	68.0
Confluence[1]	~9,500	620	0.0035	9.51×10^6	-
Gobabeb	11,700	360	0.0030	4.65×10^6	31.9
Rooibank	14,7000	120	0.0039	0.64×10^6	7.4

[1] - Mean of annual sums of Schlesien and Greylingshof.

Table 2. Variation in water chemistry characteristics among sites along the lower Kuiseb River. Samples were collected during the peak discharge at each site during a ~2-day flood in January 1994. Standard deviation is indicated in parentheses (n=3). (DOM - dissolved organic matter, POM - particulate organic matter, TSS - total suspended solids).

Site	km[1]	Discharge $(m^3 \cdot s^{-1})$	DOM $(g \cdot l^{-1})$	POM $(g \cdot l^{-1})$	DOM/POM	TSS $(g \cdot l^{-1})$
Greylingshof	0	159	0.0390 (0.005)	0.78 (0.06)	0.050	11.8 (0.9)
Homeb	105	—	0.0557 (0.014)	1.90 (0.06)	0.029	30.3 (5.7)
Gobabeb	140	51	0.0492 (0.014)	3.24 (0.90)	0.015	48.0 (12.3)
Rooibank	197	<1	0.0831 (0.013)	2.36 (0.32)	0.035	19.7 (1.7)

[1] - Distance downstream from Greylingshof

Table 2 (cont.). Variation in water chemistry characteristics among sites along the lower Kuiseb River. Samples were collected during the peak discharge at each site during a ~2-day flood in January 1994. Standard deviation is indicated in parentheses (n=3). Ion concentrations are in parts per million.

Site	Conductivity ($\mu S \cdot cm^{-1}$)	pH	Alkalinity ($mg \cdot l^{-1}$)	Na	K	Ca	Mg	Cl
Greylingshof	302	7.33	166	11	9	156	34	17
	(69)	(0.06)	(2)	(3)	(1)	(22)	(2)	(6)
Homeb	627	7.13	290	26	20	229	55	38
	(38)	(0.06)	(30)	(3)	(6)	(14)	(7)	(4)
Gobabeb	703	7.43	354	29	24	280	70	41
	(72)	(0.21)	(117)	(8)	(7)	(93)	(21)	(10)
Rooibank	1,035	7.30	373	60	21	282	70	79
	(252)	(0.10)	(90)	(3)	(3)	(98)	(14)	(14)

Table 3. Total water (H$_2$O), dissolved (DOM) and particulate organic matter (POM) and suspended solids (TSS) transported during a ~2-day flood of the Kuiseb River in January 1994. (Flow volume in million cubic meters and organic matter in metric tons; % is proportion of TSS).

Site	H$_2$O	DOM	POM	DOM/POM	TSS	% Organic
Escarpment	4.75	238	3,100	0.050	24,110	12.9
Gobabeb	2.30	131	4,610	0.028	46,300	10.0
Rooibank	0.05	4	102	0.039	810	12.6

Table 4. Variation in lateral deposits (strand lines) of particulate organic matter ($g \cdot m^{-2}$) following a flood in the Kuiseb River. Standard deviation is indicated in parentheses (n=4).

Site	km[1]	Dry Weight ($g \cdot m^{-2}$)	>1 mm (%)
Homeb	0	1,344	76
		(768)	(4)
Gobabeb[2]	25	3,200	39
		(1,696)	(7)
Swartbank	65	11,296	32
		(5,408)	(11)
Rooibank	95	Trace	—

[1] - Distance downstream from Homeb
[2] - Research station (12 km above Gobabeb gauge)

Chapter 4:

**Hydrologic influences on soil properties along ephemeral rivers
in the Namib Desert.**

Abstract: While alluvial soils within perennial river floodplains have been intensively studied, the soils of ephemeral river floodplains have received comparatively little attention, particularly regarding soil properties which may influence the distribution and abundance of plants and animals. I examined floodplain soils along three ephemeral rivers in the Namib Desert to study the influence of hydrologic regime upon longitudinal trends in soil properties. Soils consisted of layers of fluvially deposited, organic-rich silts, interstratified with sands of both fluvial and aeolian origin. Levels of organic carbon, nitrogen and phosphorous covaried with silt content. Silt deposits also influenced patterns of moisture availability and plant rooting, and created and maintained micro-habitats for various organisms. Extractable micro- and macronutrients varied among rivers, and were attributable to variations in catchment geology. Localized salinization occurred in association with wetland sites in two of the rivers, and the soluble salt content increased downstream. This increase reflected the influence of the hydrologic decay and an associated downstream increase in solute concentration within floodwaters. The most significant influence of the ephemeral hydrologic regime upon soil properties was related to the downstream alluviation associated with the decline in stream power. This alluviation increased the proportion of silt within floodplain soils in the lower reaches of the rivers. Given the strong association between silt and macronutrients, and the influence of silt upon moisture availability and habitat suitability for many organisms, such alluviation has important implications for the structure and function of ephemeral river ecosystems.

Introduction

While there is a large body of research examining the role of fluvial processes in shaping sedimentological features in dryland rivers (Picard and High 1973, Baker et al. 1988, Graf 1988, Warner 1988), less attention has been given to the influence of these processes upon soil properties of significance to riparian communities. Studies to date have shown moisture and nutrient availability, as well as soil salinity, are key factors influencing primary production in dryland riparian ecosystems (Jolly et al. 1993, Busch and Smith 1995). Their research was conducted on perennial systems, however, and ephemeral rivers, characterized by their highly variable hydrologic regimes, have received little ecological study despite their abundance in the world's drylands (Jacobson, Ch. 1).

The rivers crossing the Namib Desert in southwestern Africa are among the most studied ephemeral systems in the world, although the two decades of research has focused largely on their fluvial geomorphology (Seely 1990). In particular, numerous sedimentological analyses have examined the Late Pleistocene silt deposits characterizing many of the larger rivers (Ward 1987, Vogel 1989, Smith et al. 1993). The principal goal of this research was to develop a better understanding of palaeoclimatic regimes and their influences on geomorphic processes within the Namib Desert.

While these relict alluvial deposits have been intensively studied, little attention has been given to recent alluvial deposits in active floodplains of these rivers. Scholz (1972) provided a brief morphological description of alluvial soils within the Kuiseb River floodplain, but the influence of hydrologic processes upon pedogenesis, and the soil's role in shaping the structure and productivity of associated riparian woodlands remains largely unknown. A single study has addressed the influence of fluvial processes upon ecologically-relevant soil properties within the Namib's rivers (Abrams et al. 1997). This survey of soil chemical properties across the central Namib Desert examined the importance of landscape position and plant community association to soil nutrient status. Flood inputs were identified as the key factor regulating organic matter and nutrient accumulation within the floodplain of the ephemeral Kuiseb River. These irregular inputs into the riparian ecosystem were concluded to be more important than the effect of the plant community upon nutrient accumulation (Abrams et al. 1997).

Although Abrams et al. (1997) did not examine inter-site variability along the channel network, the pronounced downstream attenuation in both mean flood frequency and magnitude should influence soil characteristics (Jacobson, Ch. 1). If flooding is the key factor regulating soil characteristics within ephemeral river floodplains, I would expect distinct longitudinal gradients of soil properties to be associated with the hydrologic gradients that characterize these systems. In turn, such gradients would likely influence the structure and productivity of the biotic communities within these riparian ecosystems.

Vogel (1989) noted that the large ephemeral rivers draining the Namib Desert tend to have an "unusual" convex profile near the coast, attributing this fact to the hydrologic decay associated with floods moving through these systems. He went on to note that, "a further consequence of this flow pattern is that the rivers tend to drop their loads along a specific stretch of riverbed which corresponds to the average reach of the floods." Although the 'load' Vogel was referring to was inorganic fluvial sediments, the transport, retention, and deposition of woody debris and fine particulate organic matter (FPOM) exhibit similar patterns. The position of organic matter retention and deposition zones varies with flood magnitude, shifting upstream or downstream with decreases or increases, respectively (Jacobson, Ch. 2 & 3). When this inter-annual variability is averaged over many years, a mean deposition zone for organic matter can be defined in relation to the 'average reach of the floods,' as noted by Vogel (1989). The concentration and composition of the dissolved load also varies along the channel network, with a significant downstream increase in the total dissolved solids (TDS) (Jacobson, Ch. 3). Thus, floods within ephemeral rivers should 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.

The principal objectives of this study were to examine the longitudinal variation in soil characteristics within the Namib's ephemeral rivers; assess their relationship to the hydrologic regime and associated patterns of material transport and deposition; and consider their potential influence upon the structure and productivity of the rivers' riparian ecosystems.

Methods

Study Area

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 series of ephemeral rivers drain this escarpment, flowing westward across the Namib Desert. I studied the soils within the lower reaches of three of these rivers; the Kuiseb, Huab, and Hoanib. The Kuiseb River drains a catchment of approximately 14,700 km^2 in west-central Namibia, while the Huab and Hoanib Rivers drain catchments of 14,800 km^2 and 17,200 km^2, respectively, in northwestern Namibia. A strong climatic gradient occurs across all three catchments, in association with the Namib Desert. Mean annual rainfall exceeds 300 mm in the headwaters of the three rivers, which originate on the inland plateau at an elevation of ~1,500 - 2,000 m. At the eastern edge of the Namib Desert at the escarpment's base, mean annual rainfall drops to ~100 mm and declines westward to near zero at the coast (Namibian Weather Bureau). Evaporation is high throughout the catchments, exceeding rainfall by 7 to 200 times (Lancaster et al. 1984). As a result, channel flow occurs in direct response to strong convective storms during summer months, and rapidly ends after the cessation of

localized rains. Isolated wetlands, formed where localized groundwater discharge produces short reaches of perennial surface flow, provide the only exception. When in flood, the rivers' lower reaches transport a sandy bedload and a suspended load high in silts. The sandy channel sediments within the lower reaches of the rivers are largely devoid of cobble or bedrock, excluding occasional bedrock dikes that cross the channel, forming knick points in the longitudinal profile (Ward 1987).

The hydrology of the Kuiseb River is best known, relative to the Huab and Hoanib Rivers (Jacobson, Ch. 1). While the main stem of the Kuiseb River is monitored by 5 automatic gauges, reliable records are only available from a single station each on the Hoanib and Huab Rivers. As a result, longitudinal hydrologic patterns can only be characterized for the Kuiseb River. Along the Kuiseb, distinct longitudinal trends are evident among the five mainstem stations (Table 1). Mean annual runoff (MAR) (m^3) and mean peak discharge ($m^3 \cdot s^{-1}$) exhibit a strong curvilinear relationship with distance downstream, increasing from the headwaters to the base of the escarpment, and declining westward (Table 1). Most floods dissipate well before reaching the coast. While similar patterns characterize the Hoanib and Huab Rivers, their magnitude, as well as the temporal and spatial variability of transmission losses, is largely unknown.

The most distinctive biological feature of all three rivers is the comparatively lush riparian forest, relative to the adjacent sand and rock desert (Seely and Griffin 1986, Theron et al. 1980, Viljoen 1990). *Faidherbia albida* (Del.) A. Chev. is the dominant woody species along and within the river channels, 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). While the tree occurs sporadically within the escarpment and canyon reaches of the rivers where isolated pockets of alluvium permit its growth, it grows most extensively in the rivers' lower reaches. Within these reaches it occurs on the extensive alluvial deposits associated with the broader channel and floodplain, often growing within the active channel (Theron et al. 1980).

Sampling sites were dispersed along the channel, including both escarpment reaches with steep gradients and little alluviation, as well as in downstream reaches with extensive alluvial deposits and well-developed riparian forests. Sites were distributed along the river to encompass the average reach of annual floods and the associated alluviation zones within the lower half of the rivers. A total of nine sites were chosen within the Kuiseb River and four within both the Huab and Hoanib Rivers, including a wetland site within the Hoanib and Huab, where groundwater discharge maintained perennial surface flow.

Sampling and Analysis

Four replicate soil samples where collected from the floodplain at each site, within 5 m of the active channel. Each site consisted of a ~1 km-long reach divided into 0.1-km segments, and a single sample was taken from four randomly-selected segments. A 2-cm diameter soil probe, inserted to a depth of 30 cm, was used to collect samples. Air-dried samples were passed through a 2 mm mesh screen and stored for later analysis. Particle size analysis was conducted for each sample using wet sieving and pipette analysis (Gee and Bauder 1986). Sands (0.05-2.0 mm) were determined by wet sieving through a 0.05 mm screen, and the fraction smaller than 0.05 mm was analyzed by pipetting to determine the concentrations of silt and clay.

Each sample was extracted with ammonium bicarbonate-DTPA (diethylene triamine pentaacetic acid) at a ratio of 1:2 (12.5 g soil: 25 ml extractant) (Soltanpour and Schwab 1977). Samples were shaken for 15 min with an Eberbach shaker (~180 cycles/min) in unstoppered 125-ml Erlenmeyer flasks and then vacuum filtered through a Whatman 42 filter. Extractants were analyzed by inductively coupled plasma spectrometry (ICP) for P, Ca, Mg, K, Na, Fe, Mn and Zn using a Jarrell Ash ICAP 61 simultaneous spectrometer. Effective cation exchange capacity (ECEC) was calculated for each sample as the sum of the Ca, Mg, K, and Na. Exchangeable sodium percentage (ESP) was calculated as the ratio of Na to the sum of exchangeable Na, Ca, and Mg (Singer and Munns 1987). A 1:2 volume extract of soil to distilled, deionized water was used to measure the pH and electrical conductivity (EC) (Sonneveld and Ende 1971). After shaking for 1 hr in stoppered 125-ml Erlenmeyer flasks, pH was measured and samples were vacuum filtered through a Whatman 42 filter. The conductivity of this filtrate was measured with a conductivity bridge following calibration of the meter against a known standard. A subsample of each soil was treated with 10% hydrochloric acid overnight to remove inorganic carbonates, and then analyzed for organic carbon (OC) and total N by dry combustion with a LECO CNS 2000 analyzer (Bremner and Mulvaney 1982, Nelson and Sommers 1982).

Bivariate plots were examined to determine whether physical and chemical soil characteristics were related to longitudinal position within the channel network. Analysis of variance (ANOVA), followed by Scheffe's multiple comparison procedure, was used to compare mean values of soil characteristics among sites within each river. Comparisons were also made among mean values calculated for each river. Wetland sites were excluded from means calculated for the Hoanib and Huab Rivers. When data were nonnormal, the Kruskal-Wallis test was employed to compare medians (Zar 1984). Pearson correlation analysis was used to examine the relationships among the measured variables and identify variables that covaried significantly (Zar 1984). All tests were considered significant at $p < 0.05$.

Results

Classification and Texture

Soils within the rivers are in the Fluvent suborder, characterized by alternating layers of fluvially-deposited silts and sands of both fluvial and aeolian origin. These interstratified sediments also exhibit an irregular carbon distribution with depth. Carbon-rich layers originate from buried O- or A-horizons or fluvially-deposited organic matter. O- and A-horizons are absent on recently-flooded surfaces but do occur on the infrequently-flooded, alluvial terraces which border the lower reaches of the rivers. Soils are typically well-drained, although silt and clay horizons may act as hydraulic barriers, limiting infiltration. The highly variable soil moisture regime associated with irregular flood pulses complicates further classification. Terrace and floodplain soils may be dry to depths below one meter for several years or more in the absence of flooding. Alternatively, these same soils may remain moist at depths >30 cm from several weeks to a year following flooding. The soils sampled in the current study exhibited a torric soil moisture regime and are best classified as Typic Torrifluvents (Soil Survey Staff 1992).

Based upon particle size analysis, the majority of soils sampled within the three rivers were sands or loamy sands, with silt contents ranging from ~10-20 % (Tables 2-4). Sandy loams were present at only two sites within the study; the wetland site on the Huab River, and the Clado site in the lower Kuiseb River (Table 3 & 4). No significant differences were detected in particle size composition among the rivers, excepting a slight increase in clay within the Hoanib River (Table 5). However, significant differences were detected among sites within the rivers. Soils within all three rivers exhibited a downstream increase in silt percentage, followed by a decrease at the most downstream sites (Tables 2-4). This trend was most pronounced on the Kuiseb River, where the mean silt percentage gradually increased from 10.9 % to 30.0 % over a distance of 277 km, followed by a downstream decline to ~20 % (Table 4).

Chemical Properties

Results of soil elemental analyses indicated that most exchangeable cation levels were indistinguishable among study sites within each river system but different among river systems (Tables 2-5). Exceptions within rivers occurred at wetland sites and the lowermost site in the Kuiseb River, where cation levels exceeded those at other sites. This increase was reflected in significantly higher EC values at these sites. The exchangeable sodium percentages (ESP) and EC values of soils at the wetland sites within the Huab and Hoanib Rivers, as well as the lowermost site on the Kuiseb River (Rooibank), are high enough to classify them as sodic or, in the case of the Opdraend wetland on the Huab River, saline (Tables 2-4) (Singer and Munns 1987).

Soil chemistry differed among the three rivers. Soil pH was significantly higher in the Huab and Hoanib Rivers, relative to the Kuiseb (Table 5). Except for Mg, levels of macronutrients did not differ among the rivers. Soils from the Hoanib River contained higher Mg levels, relative to the Kuiseb River. Huab River soils also contained higher levels of Mg, relative to the Kuiseb, although the difference was not statistically significant (Table 5). Conversely, soils from the Kuiseb River contained significantly higher levels of micronutrients, relative to the Huab and Hoanib Rivers. Finally, OC, N, and P were all significantly higher in Kuiseb River soils, relative to those from either the Huab or Hoanib Rivers.

Soil OC, N, and P tended to increase downstream. Pearson correlation analysis revealed that OC, N, and P covaried with the percentage of silt at all sites. The amount of silt was positively correlated with the amounts of OC (r=0.74), N (r=0.78), and P (r=0.70) within the Kuiseb River. A similar pattern occurred among samples from the Hoanib and Huab Rivers.

Discussion

While the principal objective of this study was to examine soil characteristics along the individual rivers, variations in soil properties were also observed among the three rivers (Table 5). Differences in levels of micro- and macronutrients among the three rivers reflect catchment geology. While the Kuiseb catchment is largely underlain by micaceous schists, the Hoanib catchment contains a significant amount of dolomite, a source for the greater amount of Mg within its alluvium. In addition, levels of OC, N, and P were two to three times higher in Kuiseb River soils, relative to those in the Huab and Hoanib rivers (Table 5). These differences may in part be due to catchment geology, particularly with respect to P levels, although their exact cause and their influence on patterns of primary production are unknown. Despite these differences, however, hydrologic patterns inherent to the systems gave rise to soil characteristics common to all three rivers. Chief among these were site-specific variations in soil salinity and, in particular, the longitudinal pattern of silt deposition.

Soil Salinity

Soil salinity is a significant factor controlling the distribution, morphology, and productivity of riparian tree species along dryland rivers (Busch and Smith 1995, Jolly et al. 1993) and may be an important factor in selected reaches of ephemeral rivers. Soil enrichment of soluble salts may occur where floods transport high solute loads into the lower reaches of ephemeral rivers. The downstream increase in the solute load of floodwaters, attributable to the combined effects of infiltration and evaporative concentration, may be responsible for the increase in soluble salts observed at the lowermost sampling sites on the Huab and Kuiseb Rivers (Tables 3 & 4) (Jacobson, Ch. 3). Nonetheless, while solute-rich floodwaters may increase soluble salt concentrations,

the levels observed in this study are below those likely to influence the distribution and production patterns of plants (Singer and Munns 1987).

Soil salinization may occur at wetland sites, however, where capillary movement of water from shallow groundwater to the surface and its loss via evaporation concentrates salts within the upper sections of the soil profile. Wetland soils in the Hoanib and Huab Rivers are saline (Tables 2 & 3) and often exhibited a salt accumulation on their surface. This salinity may explain the absence of *Faidherbia albida* trees at wetland sites, and their replacement by halophytic species. Elevated soil salinity, associated with either naturally-high groundwater tables or induced via hydrologic alterations, is known to negatively affect tree health, triggering dieback of many woody species. Jolly et al. (1993) observed a dieback of *Eucalyptus largiflorens* along the Lower Murray River in southern Australia, attributable to salt accumulation in alluvial soils. Similarly, Busch and Smith (1995) observed that hydrologic alterations along the Colorado River triggered the decline of formerly dominant *Populus*, due to increases in soil salinity and changes in moisture availability.

The extent of soil salinization is influenced by depth to groundwater, concentration and composition of solutes, frequency of rainfall or flooding, soil physical properties, and local climate (Gary 1965, Peck 1978, Yarie et al. 1993). In ephemeral rivers, infrequent high-magnitude floods may flush soils, temporarily reducing soluble salt concentrations. Nonetheless, biologically-significant soil salinization appears to be limited to isolated sites with shallow (<1 m) water tables. Of far greater significance to soil properties within ephemeral rivers is the effect of flooding and the downstream discharge decay upon patterns of material transport and deposition.

Hydrologic decay and alluviation

Graf (1988) reviewed the literature on dryland rivers and reported that downstream trends in sorting have been varied, with some authors reporting decreases in mean and maximum grain sizes and others reporting increases. Changes in stream power associated with local variations in channel conditions, along with tributary contributions of materials, introduced great variation in the downstream distribution of particle sizes. Despite such factors, the present study suggests that the hydrologic decay that characterizes ephemeral rivers has an overriding influence on soil properties.

Transmission losses in the lower Kuiseb River are high, ranging from ~0.4-1.7 % km^{-1}, resulting in a rapid downstream decrease in stream power and capacity (Jacobson, Ch. 2). As stream power and capacity decrease, alluviation must increase (Bull 1979). The downstream increase in silt percentage observed in the Kuiseb River, which parallels the downstream reduction in mean discharge, supports this assertion. The longitudinal profile of the Kuiseb River does exhibit convexity in its lower reaches, delimiting the alluviation zone as suggested by Vogel (1989). Sampling sites within this alluviation zone

exhibited elevated silt levels, relative to upstream sites (Table 4). Although the hydrologic patterns along the Hoanib and Huab Rivers are unquantified, the available data suggest that similar trends occur in these rivers. Given the significant positive covariance between silt and OC, N, and P, any factor influencing alluviation patterns will also directly influence the nutrient status of the alluvial soils.

Abrams et al. (1997) observed a lack of nutrient enrichment under *Faidherbia albida* in the floodplain of the lower Kuiseb River, in direct contrast to reports from upland sites in western Africa (CTFT 1989). They suggested that fluvial inputs and exports, both organic and inorganic, tended to homogenize the nutrient levels within the floodplain, and the present study suggests that this generalization could be extended to much of the alluviation zone within the lower reaches of ephemeral systems. Despite this fluvially-mediated homogenization, ecologically-significant heterogeneity does exist within individual sampling sites, both vertically and horizontally within the soil profile. In particular, the localized heterogeneity in the distribution of silt and organic matter has an important influence on the structure and functioning of ephemeral river ecosystems.

The ecology of silt

Without question, one of the most important characteristics associated with silt alluviation in ephemeral rivers is its influence upon moisture dynamics within floodplain soils and in turn its influence on decomposition, production, and habitat suitability. Silt layers within the soil profile act as hydraulic barriers, slowing the downward movement of moisture. Following overbank floods, moisture stored in floodplain soils is discharged at channel banks from silty layers within the soil profile. These moist silt exposures lining the active channel become key microhabitats for a diverse community of blue-green algae; fungi - including both basidio- and ascomycetes; lower plants - including mosses and liverworts; and invertebrates (Shelley and Crawford 1996, Jacobson et al. 1995).

During flood recession, silt layers are deposited on the floodplain surface and act to retard the desiccation of underlying sediments. While exposed sands can dry to depths of more than 30 cm within weeks of a flood, several cm of silt can maintain soil moisture levels of 4-6 % by weight to depths within 30 cm of the soil surface. The maintenance of this subsurface moisture has important implications for nutrient cycling within these otherwise arid environments, as it supports the decomposition of silt-associated fine particulate organic matter (FPOM) by an unusual assemblage of Basidiomycetes, including the fungus *Battarrea stevenii* (Liboshitz) Fr.. This large fungus fruits from the moist silts, breaking through the surface silt crusts, from several months to a year after a flood has inundated the floodplain (Jacobson et al. In Review).

An important source of silt-associated FPOM is the physical processing of woody debris and *Faidherbia albida* fruits during floods, which yields a significant amount of highly-labile, sediment-associated organic matter (Jacobson, Ch. 2). Minckley

and Rinne (1985) reviewed the dynamics of large woody debris in desert streams, detailing the many references to fine particulate organic matter in desert floodwaters. For example, Sykes (1937) observed that the molar action of streams passing through canyons quickly reduced large woody debris to finer particles, and observed that the sediments deposited within the Colorado River Delta were approximately 8% organic matter. Forbes (1902) noted that Arizona floodwaters are rich in organic matter, and noted the "fertilizing value" of these materials.

Fluvial deposition of inorganic sediments buries surficial organic accumulations, including litterfall and fluvial deposits. Once buried, these organic accumulations are exposed to more constant regimes of temperature and moisture than surface organic matter, favoring a higher and sustained level of decomposition than that experienced by organic matter on the floodplain surface. Flood pulses, in addition to depositing nutrient-rich sediment, also trigger the activity of soil microorganisms, which directly influence decomposition and mineralization rates (Jacobson et al. In Review). The pulse of C- and N-mineralization associated with drying and rewetting cycles has been described from soils across a range of climates (Cabrera 1993, Van Gestel et al. 1993), although the effect may be particularly pronounced in the water-limited ecosystems associated with ephemeral rivers.

Variations in channel morphology, such as meanders or mid-channel islands, influence deposition patterns, often resulting in large accumulations of fine and coarse particulate organic matter, and organic-rich silts. Such deposits often accumulate on the outside of channel bends or point bars in the form of expansive mats, several centimeters in depth. These deposits may be mobilized in subsequent floods or incorporated into the soil profile. Spot sampling within the lower Kuiseb River has shown that these accumulations typically may contain as much as 20-40 % organic matter by weight, and 20-50 % silt. Fine roots of *Faidherbia 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 adventageous rooting in response to higher moisture availability. Van Cleve et al. (1993) observed similar patterns of organic matter stratification and variation in root density with depth in the floodplain of the Tanana River in central Alaska, noting the probable influence of organic matter burial upon decomposition rates and associated element supply to plants.

While the deposition and burial of organic material increases the vertical heterogeneity of floodplain soils, the horizontal distribution of organic matter on channel and floodplain surfaces is equally heterogeneous. During flooding, variations in perennial vegetation abundance (both woody and herbaceous), floodplain microtopography, and channel morphology influence deposition patterns and create localized accumulations of organic material (Jacobson, Ch. 2 & 3). Soil enrichment occurs in association with woody debris piles retained on in-channel trees (Jacobson, Ch. 2). Increased hydraulic resistance at such sites induces the deposition of additional organic matter and nutrient-rich silts.

These sites act as both nurseries for young trees, as well as organic- and moisture-rich microhabitats for many organisms (Jacobson, Ch. 2). Thus, the heterogeneous distribution of organic matter, both within and across floodplain soils, is a key feature of these ephemeral river ecosystems.

Finally, as surficial silt deposits dry, they shrink and crack into large, polygonal plates up to 0.5 m across. These plates can be more than 10 cm thick, separated by cracks of a similar depth and widths of several centimeters. The silt plates also curl slightly at the edges, separating from underlying sands. This highly dissected surface and subsurface creates a unique microhabitat for animals living within the riparian zones. The moist microclimates within deeper cracks and under silt plates provide refugia for frogs (*Tomopterna delalandei*) and various invertebrates, including millipedes and isopods. In addition, the cracks are also favorite foraging sites for insectivores, including scorpions (*Parabuthus villosus*) and shrews (*Crocidura cyanea*). These silt layers are often mobilized in subsequent floods, and are the source of 'mud pebbles' commonly seen in fluvial deposits within the lower river. These features are well known from ephemeral rivers flowing over interstratified alluvial sands and silts (Picard and High 1973).

Given that primary and secondary production in dryland ecosystems is typically limited by low soil water content and nutrient-poor soils (West 1991), floods, providing both water and nutrient-rich sediments, are keystone events within ephemeral river systems. Alluviation zones, with their organic- and nutrient-rich silts, and associated increases in moisture availability, should thus be the most biologically productive reaches of ephemeral river ecosystems. Preliminary data on the density of *F. albida* along the Kuiseb River appear to support this hypothesis, as the peak in tree density corresponds with the peak in soil silt and nutrient content within the mid-reaches of the Kuiseb's alluviation zone (Jacobson, unpublished data). I suggest that the hydrologic regime, through its control of soil characteristics, particularly nutrient and moisture availability, is the principal factor controlling the structural and functional characteristics of ephemeral river ecosystems. In turn, any alterations in the hydrologic regime, whether induced via natural (i.e., climatic variation) or anthropogenic (i.e., impoundments) means, will produce a concomitant shift in the structure and productivity of these systems.

Acknowledgments

References

Abrams, M.M., P.J. Jacobson, K.M. Jacobson, and M.K. Seely. 1997. Survey of soil chemical properties across a landscape in the Namib Desert. *Journal of Arid Environments* 35: 29-38.

Baker, V.R., R.C. Kochel, and P.C. Patton, eds. 1988. *Flood geomorphology.* John Wiley & Sons, New York. 503 pp.

Bremner, J.M. and C.S. Mulvaney. 1982. Nitrogen-total. In: Page, A.L. (Ed.), *Methods of soil analysis*, Part 2, pp. 539-580. American Society of Agronomy, Madison, WI. 1188 pp.

Bull, W.B. 1979. Threshold of critical power in streams. *Geological Society of America, Bulletin* 90: 453-64.

Busch, D.E. and S.D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecological Monographs* 65: 347-370.

Cabrera, M.L. 1993. Modeling the flush of nitrogen mineralization caused by drying and rewetting soils. *Soil Science Society of America Journal* 57: 63-66.

CTFT (Centre technique forestier tropical). 1989. *Faidherbia albida* (Del.) A. Chev. (Synonym *Acacia albida* Del.). (English translation by P.J. Wood) Nogent-sur-Marne, France: CTFT, and Wageningen, Netherlands: Centre technique de coopération agricole et rurale. 72 pp.

Forbes, R.H. 1902. The river-irrigating waters of Arizona-their character and effects. *Univ. Ariz. Agric. Exp. Sta. Bull*. 44: 143-214.

Gary, H.L. 1965. Some site relations in three flood-plain communities in Central Arizona. *Journal of the Arizona Academy of Science* 3: 209-212.

Gee, G.W. and J.W. Bauder. 1986. Particle-size analysis. In *Methods of soil analysis*. Part 1. Physical and mineralogical methods. 2nd ed. Edited by A. Klute. *Agronomy* 9(1): 383-411.

Graf, W.L. 1988. *Fluvial processes in dryland rivers*. Springer-Verlag, Berlin. 346 pp.

Jacobson, K.M., P.J. Jacobson, and O.K. Miller, Jr. In Review. The autecology of *Battarrea stevenii* (Liboshitz) Fr. in ephemeral rivers of southwestern Africa. *Mycological Research*.

Jacobson, P.J., K.M. Jacobson, and M.K. Seely. 1995. *Ephemeral rivers and their catchments: sustaining people and development in western Namibia*. Desert Research Foundation of Namibia, Windhoek. 160 pp.

Jolly, I.D., G.R. Walker, and P.J. Thorburn. 1993. Salt accumulation in semi-arid floodplain soils with implications for forest health. *Journal of Hydrology* 150: 589-614.

Lancaster, J., N. Lancaster, and M.K. Seely. 1984. Climate of the Central Namib. *Madoqua* 14: 5-61.

Minckley, W.L. and J.N. Rinne. 1985. Large woody debris in hot-desert streams: an historical review. *Desert Plants* 7: 142-152.

Nelson, D.W. and L.E. Sommers. 1982. Total carbon, organic carbon, and organic matter. In: Page, A.L. (Ed.), *Methods of soil analysis*, Part 2, pp. 539-580. American Society of Agronomy, Madison, WI. 1188 pp.

Peck, A.J. 1978. Note on the role of a shallow aquifer in dryland salinity. *Aust. J. Soil Res.* 16: 237-40.

Picard, M.D. and L.R. High, Jr. 1973. *Sedimentary structures of ephemeral streams.* Elsevier Scientific Publishing Company, Amsterdam. 223 pp.

Scholz, H. 1972. The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua* 1: 33-51.

Seely, M.K., ed. 1990. *Namib ecology: 25 years of Namib Research*. Transvaal Museum Monograph No. 7, Transvaal Museum, Pretoria. 230 pp.

Shelley, R.M. and C.S. Crawford. 1996. Cnemodesmus riparius, N. SP., a riparian millipede from the Namib Desert, Africa (Polydesmida: Paradoxosomatidae). *Myriapodologica* 4: 1-8.

Singer, M.J. and D.N. Munns. 1987. *Soils: an introduction*. MacMillan Publishing Company, New York. 492 pp.

Smith, R.M.H., T.R. Mason, and J.D. Ward. 1993. Flash-flood sediments and ichnofacies of the Late Pleistocene Homeb Silts, Kuiseb River, Namibia. *Sedimentary Geology* 85: 579-599.

Soil Survey Staff. 1992. *Keys to soil taxonomy*. SMSS Technical Monograph No. 19. 5th ed. Pocahontas Press, Inc. Blacksburg, VA. 541 pp.

Soltanpour, P.N., and A.P. Schwab. 1977. A new soil test for simultaneous extraction of macro- and micro-nutrients in alkaline soils. *Commun. in Soil Science and Plant Analysis* 8: 195-207.

Sonneveld, C. and J.v.d. Ende. 1971. Soil analysis by means of a 1:2 volume extract. *Plant and Soil* 35: 505-516.

Sykes, G. 1937. *The Colorado Delta.* Amer. Geogr. Soc., New York. 193 pp.

Van Cleve, K., C.T. Dyrness, G.M. Marion, and R. Erickson. 1993. Control of soil development on the Tanana River floodplain, interior Alaska. *Can. J. For. Res.* 23: 941-955.

Van Gestel, M., R. Merckx, and K. Vlassak. 1993. Microbial biomass responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soils from different climates. *Soil Biol. Biochem.* 25: 109-123.

Vogel, J.C. 1989. Evidence of past climatic change in the Namib Desert. *Palaeogeography, Palaeoclimatology, Palaeoecology* 70: 355-366.

Ward, J.D. 1987. *The Cenozoic succession in the Kuiseb Valley, Central Namib Desert*. Geological Survey of Namibia, Windhoek. 124 pp.

Warner, R.F., ed. 1988. *Fluvial geomorphology of Australia.* Academic Press, Sydney. 373 pp.

West, N.E. 1991. Nutrient cycling in soils of semiarid and arid regions. In: J. Skujins (ed.) *Semiarid lands and deserts: soil resource and reclamation*. Marcel Dekker, New York.

Yarie, J., K. Van Cleve, C.T. Dyrness, L. Oliver, J. Levison, and R. Erickson. 1993. Soil-solution chemistry in relation to forest succession on the Tanana River floodplain, interior Alaska. *Can. J. For. Res.* 23: 928-940.

Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs. NJ. 718 pp.

Table 1. Mean annual runoff (MAR) and mean annual peak discharge (MAPD) for mainstem gauging stations along the ~560-km Kuiseb River.

Station	km[1]	MAR (m^3)	MAPD (m^{3}s^{-1})
Friedenau	58	1.505e6	42.7
Us	176	6.218e6	77.7
Schlesien	304	6.588e6	71.9
Gobabeb	479	4.654e6	31.9
Rooibank	535	0.638e6	7.4

[1] - Distance from headwaters.

Table 2. Variability in soil characteristics among four sites along the Hoanib River. Means (n=4) in a row followed by different letters are statistically different at p<0.05 level.

	Units	Khowarib	Dubis[1]	Ganamub	Floodplain
Location[2]	km	138	198	213	260
pH		7.34 b	8.18 a	7.52 ab	7.68 a
EC	$\mu S \cdot cm^{-1}$	262 b	1,815 a	329 b	226 b
Sand	%	84 a	88 a	76 a	86 a
Silt	%	15 ab	10 b	23 a	12 b
Clay	%	1 a	2 a	1 a	2 a
OC	%	0.21 a	0.30 a	0.37 a	0.10 a
N	%	0.02 a	0.03 a	0.05 a	0.01 a
P	$mg \cdot kg^{-1}$	6.69 a	4.83 a	9.69 a	5.73 a
Ca	$cmol \cdot kg^{-1}$	2.27 a	1.98 b	2.12 ab	1.96 b
Mg	$cmol \cdot kg^{-1}$	1.18 a	1.47 a	1.29 a	1.36 a
Na	$cmol \cdot kg^{-1}$	0.06 b	2.65 a	0.24 ab	0.21 ab
K	$cmol \cdot kg^{-1}$	0.52 a	0.84 a	0.47 a	0.31 a
ECEC	$cmol \cdot kg^{-1}$	4.02 a	6.94 a	4.11 a	3.84 a
ESP	%	1.71 c	38.07 a	6.42 b	5.78 b
Mn	$mg \cdot kg^{-1}$	5.42 a	5.34 a	8.07 a	2.38 a
Zn	$mg \cdot kg^{-1}$	0.37 a	0.31 a	0.43 a	0.23 a
Fe	$mg \cdot kg^{-1}$	4.93 a	4.13 a	12.13 a	7.85 a

[1] - Wetland site.
[2] - Distance from headwaters.

Table 3. Variability in soil characteristics among four sites along the Huab River. Means (n=4) in a row followed by different letters are statistically different at p<0.05 level.

	Units	Annabis	Noute	Opdraend[1]	Vrede
Location[2]	km	110	158	192	219
pH		7.42 b	7.46 b	7.90 a	7.56 b
EC	$\mu S \cdot cm^{-1}$	149 b	215 bc	3,709 a	538 ac
Sand	%	90 a	78 a	70 a	80 a
Silt	%	10 a	21 a	27 a	20 a
Clay	%	0 b	1 ab	3 a	0 ab
OC	%	0.29 a	0.31 a	0.80 a	0.27 a
N	%	0.01 b	0.03 ab	0.08 a	0.03 ab
P	$mg \cdot kg^{-1}$	6.27 a	8.72 a	11.37 a	9.01 a
Ca	$cmol \cdot kg^{-1}$	1.90 b	2.36 a	1.90 b	2.14 ab
Mg	$cmol \cdot kg^{-1}$	0.52 b	0.73 b	2.42 a	1.34 ab
Na	$cmol \cdot kg^{-1}$	0.07 b	0.05 b	8.01 a	0.42 ab
K	$cmol \cdot kg^{-1}$	1.24 a	0.27 b	0.69 ab	0.58 ab
ECEC	$cmol \cdot kg^{-1}$	3.73 b	3.42 b	13.02 a	4.51 ab
ESP	%	2.71 b	1.69 b	44.70 a	10.42 ab
Mn	$mg \cdot kg^{-1}$	3.65 a	6.24 a	9.48 a	6.28 a
Zn	$mg \cdot kg^{-1}$	0.78 a	0.57 a	1.60 a	0.95 a
Fe	$mg \cdot kg^{-1}$	7.61 a	12.13 a	22.85 a	9.68 a

[1] - Wetland site.
[2] - Distance from headwaters.

Table 4. Variability in soil characteristics among nine sites along the Kuiseb River. Means (n=4) in a row followed by different letters are statistically different at p<0.05 level.

	Units	Us	Poort	Alley	Nara	Rooibank
Location[1]	km	180	400	433	480	530
pH		6.48 b	7.31 a	7.07 a	7.06 a	7.03 a
EC	$\mu S \cdot cm^{-1}$	501 b	254 b	311 a	336 b	1,033 a
Sand	%	89 ab	85 abc	73 cdef	79 bcde	77 cde
Silt	%	11 de	15 cde	27 abc	20 bcd	21 bcd
Clay	%	0 b	0 ab	0 b	1 ab	2 a
OC	%	0.43 a	0.47 a	0.56 a	0.70 a	1.02 a
N	%	0.05 ab	0.05 ab	0.07 ab	0.08 ab	0.10 a
P	$mg \cdot kg^{-1}$	11.60 ab	11.82 ab	16.56 ab	18.49 ab	25.47 a
Ca	$cmol \cdot kg^{-1}$	2.32 a	2.26 a	2.26 a	2.18 ab	2.04 b
Mg	$cmol \cdot kg^{-1}$	0.59 b	0.48 bc	0.61 b	0.63 b	0.80 a
Na	$cmol \cdot kg^{-1}$	0.05 a	0.08 a	0.04 a	0.09 a	0.89 a
K	$cmol \cdot kg^{-1}$	0.54 ab	0.18 b	0.29 ab	0.50 ab	0.59 a
ECEC	$cmol \cdot kg^{-1}$	3.50 a	3.00 a	3.19 a	3.40 a	4.32 a
ESP	%	1.60 a	2.78 a	1.45 a	3.10 a	18.35 a
Mn	$mg \cdot kg^{-1}$	11.11 ab	6.41 b	10.49 ab	12.47 ab	31.97 a
Zn	$mg \cdot kg^{-1}$	0.58 a	0.56 a	0.87 a	0.66 a	1.04 a
Fe	$mg \cdot kg^{-1}$	20.20 b	28.17 ab	39.99 ab	44.36 ab	43.72 ab

[1] - Distance from headwaters.

Table 5. Mean soil characteristics among the Hoanib, Huab and Kuiseb rivers.

	Units	Hoanib[1,2]	Huab[1,2]	Kuiseb[3]
pH		7.52 a	7.48 a	7.06 b
EC	$\mu S \cdot cm^{-1}$	272 a	301 a	434 a
Sand	%	82 a	83 a	81 a
Silt	%	17 a	17 a	19 a
Clay	%	1 a	0 b	0 b
OC	%	0.22 b	0.23 b	0.61 a
N	%	0.03 b	0.02 b	0.07 a
P	$mg \cdot kg^{-1}$	7.37 b	8.00 b	16.49 a
Ca	$cmol \cdot kg^{-1}$	2.11 a	2.13 a	2.20 a
Mg	$cmol \cdot kg^{-1}$	1.28 a	0.88 ab	0.59 b
Na	$cmol \cdot kg^{-1}$	0.17 a	0.18 a	0.19 a
K	$cmol \cdot kg^{-1}$	0.43 a	0.70 a	0.38 a
ECEC	$cmol \cdot kg^{-1}$	3.99 a	3.89 a	3.37 b
ESP	%	4.64 a	4.94 a	5.15 a
Mn	$mg \cdot kg^{-1}$	5.29 b	5.39 b	12.97 a
Zn	$mg \cdot kg^{-1}$	0.34 b	0.77 a	0.73 a
Fe	$mg \cdot kg^{-1}$	8.31 b	9.81 b	33.93 a

[1] - Excluding wetland sites (Hoanib-Dubis; Huab-Opdraend)
[2] - (n=12)
[3] - (n=36)

Chapter 5:
The influence of elephants on *Faidherbia albida* trees in the northern Namib Desert: a reappraisal.

Abstract: Elephants (*Loxodonta africana*) are well known for the tremendous effect they can exert on their habitat. The Namibian media expressed concern in the early 1980's regarding the influence of desert-dwelling elephants on vegetation within the lower Hoanib River in the northern Namib Desert. A subsequent survey reported no detrimental effects, although my observations in 1994 suggested significant tree damage had occurred since. I resurveyed the area in 1995 to quantify the changes that had occurred in the past 12 years, and considered several hypotheses to explain them. I found that a significant change had occurred in the size structure of the *Faidherbia albida* forest. Of the 638 trees I examined within the lower Hoanib River, 196 (30 %) were dead and exhibited evidence suggesting they had been killed by elephants. Of the 196 dead trees, 142 (73 %) were <20 cm in diameter. As a result of this selective feeding and associated lack of recruitment, the current size distribution of trees is strongly skewed towards older trees, likely to be more susceptible to die-off should environmental conditions change significantly. The cause of this change in foraging is unclear. Elephant density has not increased nor has their been any significant hydroclimatic variation since the early 1980's. Subtle shifts in resource use patterns, possibly triggered by prior human-associated disturbance (primarily poaching), may be responsible for the observed decline in tree survival and recruitment. In combination with proposed hydrologic alterations of the Hoanib River associated with agricultural developments, this skewed age structure could result in a massive die-off of *Faidherbia* trees along the lower river.

Introduction

The African elephant, *Loxodonta africana* Blumenbach, has long been recognized as a major force affecting vegetation communities throughout its range (Laws 1970). In particular, when combined with human-induced shifts in population density and available foraging area, such effects can be severe and result in the decimation of affected vegetation (Anderson and Walker 1974, Barnes 1983a & b). Because of their comparatively low productivity, dryland vegetation communities may be particularly susceptible to damage by foraging elephants, although there are many conflicting views (see Behnke et al. 1993 for a recent review). Thus, the desert-dwelling elephants of the northern Namib Desert, the only remaining desert elephant population in the world, presumably have great potential to degrade their habitat.

The Namib elephants, particularly those in the most arid regions, subsist in a series of ephemeral river courses and associated floodplains that provide food and water resources within an otherwise hostile landscape (Viljoen 1989a, Viljoen 1989b). In the early 1980's, concern was expressed by the Namibian media regarding the potential effect of the elephants on the riparian vegetation within these rivers, particularly the large *Faidherbia albida* (Del.) A. Chev. trees that grow in and along the channel of the Hoanib River in northwestern Namibia (Schoeman 1982). *Faidherbia albida*, formerly *Acacia albida* Del., is a large tree, reaching a height of over 15 m and a diameter in excess of 2 m within the Hoanib River. These stately trees produce large amounts of fruits, and a single tree can produce more than 200 kg of the dry indehiscent pods in a single year (Jacobson Ch. 2, CTFT 1989). Aside from their aesthetic appeal, the trees have great ecological importance as a source of forage, providing pods, foliage, and bark for the region's elephants. Despite the concern that the desert-dwelling elephants may have been having an adverse effect on the trees, a study completed in 1983 concluded that there was no evidence of such an effect (Viljoen and Bothma 1990a). Although trees were occasionally ring-barked, having the bark removed from the entire circumference of their trunks, the frequency was estimated to be less than the recruitment rate and not significant to the long-term viability of the population.

I first visited the river in 1994, and my observations made me question whether this conclusion was still valid. Although Viljoen and Bothma (1990a) reported no negative effect on the river's vegetation other than the occasional debarking of *Faidherbia* trees, I observed evidence that elephants were actively breaking down *Faidherbia* trees up to ~40 cm in diameter. I thus initiated a study to reexamine the influence of elephants upon the recruitment and size structure of *Faidherbia albida* trees within the lower Hoanib River. My objectives were to resurvey the reach of the river surveyed by Viljoen and Bothma (1990a), quantifying the changes in stand structure occurring in the past 12 years; to examine several hypothesis to explain the observed differences, with particular attention to the influence of poaching on the spatial patterns of foraging; and to discuss the findings

with respect to current land use patterns in the region and the conservation of the elephants and their habitat.

Methods

Study Area

The Hoanib River drains a catchment of ~17,000 km^2 in northwestern Namibia, flowing a distance of ~300 km from its headwaters near the Etosha National Park, westward to the Atlantic Ocean. *Faidherbia albida* trees occur most of the river's length, but reach their greatest size and abundance within the lower 100 km of the river laying within the Namib Desert. The trees' survival depends upon the occasional floods that originate within the upper reaches of the catchment, bringing water and nutrient-rich sediments to the lower river (Jacobson, Ch. 1 & 4). While floods have flowed occurred in the lower Hoanib every year since record keeping began in 1977, their duration and magnitude are highly variable. Floods are an essential source of water, as the median annual rainfall along the lower river decreases from ~75 mm at Sesfontein, some 100 km inland, to <20 mm at the coast. Germination and recruitment of woody species, as well as annual grasses and forbs, is therefore almost entirely dependent upon floods.

The river traverses a mountainous landscape interspersed with large valleys and sandy or stony plains. A series of small tributaries enter the river along its lower 100 km, and although they contribute little to the annual runoff, they serve as important corridors for wildlife moving across the region's rugged landscape. This is particularly true for the mainstem of the Hoanib River, which is the region's principal east-west wildlife corridor. Approximately 20 km from the sea, the river's course is blocked by the coastal dunefield of the northern Namib Desert. Only in years of exceptional flooding does the river reach the sea, an event that has occurred only four times in the past 33 years (1963, 1982, 1984, and 1995). In most years floodwaters are impounded by the dunes and spread across a broad plain, commonly referred to as the 'Hoanib floodplain' (Viljoen 1989a). This terminal floodplain is an important resource for the region's wildlife during periods when floods have stimulated the growth of grasses and forbs and serves as a key wet-season resource patch for the region's elephants (Viljoen 1989a, Viljoen 1989b).

Viljoen (1989b) studied the seasonal distribution of elephants within the lower Hoanib River and noted distinct shifts corresponding to changes in food and water availability. In particular, the wet season core areas for two family groups centered on the lower Hoanib River floodplain, while their dry season core areas shifted to wetlands in the Hoarusib River, ~60 km to the north, and the Dubis wetland, ~65 km upstream in the Hoanib River. These wetlands occur where variations in bedrock geology result in groundwater discharge, producing isolated reaches of surface flow up to several hundred meters or more in length.

The Dubis wetland is an important focal point for elephants within the Hoanib River, providing a key dry-season water source. The concerns expressed over the potential effect of elephants upon the river's vegetation (Schoeman 1982) focused largely on the 65-km reach from the Dubis wetland downstream to the floodplain. The subsequent study by Viljoen and Bothma (1990a) examined the effect of elephants upon the *Faidherbia* trees within this reach.

Vegetation Surveys

Viljoen and Bothma (1990a) used several methods to examine the effect of elephants upon the vegetation within the lower Hoanib River, including an examination of multiple sets of aerial photos for changes in the number of large trees, measures of selected trees to assess age structure and mortality patterns, and transect surveys to assess the extent of bark removed. As the precise locations of Viljoen's surveys were unclear, I distributed my survey effort evenly over the 65-km reach between the Dubis wetland and the floodplain, which was divided into eight ~8-km sections. I initially planned a complete survey of the *Faidherbia* trees within the first kilometer of each section, but a preliminary survey revealed that the density of trees downstream of the wetland was less than 2 trees km^{-1} for the first 12 km. Thus, I divided this 12 km reach into two 6-km sections, and conducted a complete survey of each section. The remaining 53 km was divided into six equal sections, and the first kilometer of each section was surveyed.

Within each survey section the total number of living and dead *Faidherbia* trees was counted. Dead trees included standing dead, as well as the stumps of broken-off trees. The stem diameter at ~1.5 m height was measured on both living and standing dead trees, and in cases where cespitose clumps occurred, the diameter of each stem was measured separately. For stumps, the diameter was also measured at 1.5 m, or at its highest point if less than 1.5 m tall. Standing dead trees were examined to determine if ring-barking was the probable cause of death. The percentage of bark removed relative to the tree's circumference was estimated for all live and dead standing trees. Trees exhibiting any debarking were also examined for signs of wood boring beetle infestations. All stumps were examined for the presence of root or stem sprouts. Finally, following the 1995 floods, sections were resurveyed to record the number and size of trees removed by the floods.

Results

The current size distribution of *Faidherbia* trees in the lower Hoanib River differs markedly from that observed in 1983 by Viljoen and Bothma (1990a) (χ^2=145.3, p<<0.001, df=5) (Table 1). In particular, the number of 2-20-cm trees (0.2 %) measured in 1995 is more than two orders of magnitude below the 30.1 % reported from the 1983 survey. Of the 638 trees examined within the lower Hoanib River, 196 (30.7 %) were

dead and exhibited evidence suggesting they had been killed by elephants. In contrast, in 1983 a sample of 238 *Faidherbia* trees contained 14 (5.9 %) trees killed by elephants (Viljoen and Bothma 1990a). The average diameter of the dead trees in the 1995 survey was 21 cm (±12.5), ranging from 2-64 cm. The diameter of the 442 live trees averaged 78.4 cm (±33.1), ranging from 18-226 cm.

Viljoen and Bothma (1990a) reported that the size distribution of *Faidherbia* trees in 1983 conformed to a "reverse J-shaped curve ... indicative of a climax population," concluding that, "the *Acacia albida* population in the Hoanib River is a healthy climax and stable population." In contrast, the current distribution exhibits a pronounced absence of trees in the 2-20-cm size class and a decrease in the 20-40 cm class as well. Of the 638 trees measured, 196 (30.7 %) were dead, and 142 (72.5 %) of these were within the 2-20-cm size class. The percentage of dead trees within each reach ranged from 12.5 to 26.3 %, and the mean of the three reaches within 20 km of the Dubis wetland (20.8 %) did not differ from that of the lower three reaches (21.3 %), 28-44 km downstream .

The incidence of ring-barking was low; only 5 (0.9 %) *Faidherbia* trees from a sample of 535 mature trees were ring-barked, comparable with that recorded in 1983 (Viljoen and Bothma 1990a), when 5 of 213 (2.3 %) individuals had been killed through ring-barking. The five ring-barked trees in the 1995 survey averaged 46 cm (±4.6) in diameter, compared to an average of 20.7 cm (±12.1) for the 191 tree stumps. Viljoen and Bothma (1990a) reported that 31.6% (45 of 142) of a sample of mature *Faidherbia* trees had >20 % of their bark removed by elephants. In contrast, I observed that elephants had removed >20 % of the bark from 74 % (124 of 168) of mature trees. Although Viljoen and Bothma (1990a) reported that wood borers were absent from bark-damaged trees in the Hoanib River, they had colonized 4 of 168 (2.4 %) living trees at sites of bark damage.

Debarking stimulated a dramatic alteration of the vascular cambium in 33 % of a sample of 402 mature *Faidherbia* trees, resulting in the development of numerous deep convolutions, which ran parallel to the longitudinal axis of the trunk. These folds in the surface of the trunk appeared to offer some protection from ring-barking, as bark could only be removed from the outermost surface of the folds. The frequency of their occurrence decreased with distance from water. Within 12 km of the Dubis wetland, 76 % of the mature *Faidherbia* trees exhibited these convolutions, dropping to 9 % at a distance of 44 km. Viljoen and Bothma (1990a) did not report these features, which may be a recent development in response to the increased incidence of debarking.

I found no evidence that elephants were uprooting trees in the Hoanib River. Viljoen and Bothma (1990a) reported a similar absence, in contrast to reports from savanna habitats (Laws 1970). As suggested by Viljoen, the absence of uprooted trees, despite the heavy browsing pressure, may be a function of *Faidherbia albida's* strong tap root (CTFT 1989). The stability that this rooting structure confers may actually

contribute to stem breakage, rather than uprooting, when an elephant applies pressure to the tree while feeding. However, Viljoen and Bothma (1990a) did not observe elephants breaking down trees and saplings.

The largest tree that appeared to have been broken off by elephants had a 64-cm-diameter stump standing ~1 m. The broken trunk was heavily colonized by shot-borer beetles (Bostrychoidea) and a white-rot fungus, both of which would have weakened the trunk, increasing its susceptibility to breakage. Although high-winds occasionally topple mature *Faidherbia* trees, such events are rare. Only 4 cases were observed during a three-year period in the ephemeral Kuiseb River, all involving large trees (>80 cm) which toppled without breaking. The presence of wood boring beetles and white-rot fungi, in combination with the advanced age of the trees, may have contributed to their collapse (Jacobson, personal observations). No blow-downs or wind-induced breakage of small trees (<40 cm) were observed.

Faidherbia trees broken off at or near ground level by elephants, or with roots damaged by floods, tended to sprout new shoots. These shoots were heavily browsed by elephants and various ungulates. The frequency of root and stump sprouts increased downstream from the Hoanib wetland, reflecting the increased browsing pressure closer to water. No root or stump sprouts were observed within 20 km of the wetland, despite the presence of stumps and damaged trees. Sprouts were present on 22 of 28 (79 %) *Faidherbia* stumps, 28-36 km downstream, but the sprouts were browsed to within 1-2 cm of their origin. A dramatic increase in both the frequency and the size of root and stump sprouts was observed within the 44-km survey reach (44 km downstream of Dubis), where 79 of 100 damaged *Faidherbia* exhibited sprouts. Although they were heavily browsed, sprouts ranged from <10 cm to >3 m in height.

The 1995 flood eroded 18 of the 638 (2.8 %) *Faidherbia* trees measured. Trees were washed out via lateral channel erosion and associated mass wasting of banks, as well as the scour of bed sediments within the active channel. The eroded trees had an average diameter of 80 cm (±37), ranging from 30-190 cm. While many of the trees were washed away, some fell but were held in place by intact roots. These trees, while not killed outright by the floods, were eaten by elephants within three months; branches up to 8 cm in diameter were consumed.

Discussion

While Viljoen and Bothma (1990a) concluded that elephants had no effect on large trees in the Hoanib River from 1963 to 1983, in the twelve years since elephants have radically altered the age structure of the *Faidherbia albida* forest between the Dubis wetland and the terminal floodplain of the Hoanib River. Although the intensity of debarking appears to have increased, the frequency of trees killed via ring-barking has not changed. The low mortality rate associated with ring-barking, observed by Viljoen and

Bothma (1990a) in 1983, and again in the 1995 survey, has also been reported from the Zambezi Valley, where Dunham (1991) recorded only two deaths attributable to ring-barking during an eight-year study of 53 mature trees. In addition, no uprooting of *Faidherbia* trees was observed in the 1983 (Viljoen and Bothma 1990a) or 1995 surveys in the Hoanib River. Dunham (1989) noted that elephants could not push over healthy *Faidherbia albida* along the Zambezi River because of their deep roots, although they did occasionally kill trees by ring-barking. Although bark damage does allow the introduction of borer beetles, which may weaken the tree and lead to its collapse (Laws 1970, Anderson and Walker 1974, Barnes 1983a), the low incidence of such infestations (<3 %) in the Hoanib River suggests that this was not a significant factor affecting the size distribution. Thus, it appears that the change in the size distribution within the lower Hoanib River is largely attributable to the selective destruction of small trees (2-20 cm) by elephants.

The effects of such preferential feeding by elephants have been previously noted by Laws (1970), who summarized several studies in Uganda that revealed a marked preference by elephants for small trees, resulting in strongly skewed size distributions. Barnes (1983a) observed a similar pattern in the Ruaha National Park, Tanzania. Severe damage to *Faidherbia* woodlands has also been reported from Tanzania (Barnes 1983b). Feely (1965) observed that recruitment of *Faidherbia albida* was severely limited in the Luangwa Valley in Zambia, where the foraging by elephants and various ungulates kept saplings pruned. Finally, Anderson and Walker (1974) observed that old stumps of *Acacia tortilis* were common along the Sengwa and Lutope Rivers in northern Zimbabwe. The tree was reported to be very susceptible to attack by wood-boring insects; once elephants had stripped some of the bark, it invariably died. Continued pressure from elephants resulted in an uneven age structure along the rivers, as dry season concentrations of browsing animals prevented any significant recruitment of trees. While similar patterns of selective feeding are clearly responsible for the development of a comparatively even-aged stand in the lower Hoanib River, it is unclear what change in conditions occurred between 1983 and 1995 to induce this difference.

The destruction of vegetation by elephants has often been associated with an increase in the local elephant density (Laws 1970, Barnes 1983b). Nonetheless, elephant numbers in the lower Hoanib River have remained relatively stable; surveys from 1982-1995 consistently report approximately 25 animals (Viljoen 1982, Viljoen 1987, Lindeque and Lindeque 1991, personal observations). In addition, no dramatic changes have occurred in the hydrologic or climatic regimes during this period. Rather, it appears that some unknown factor triggered a shift in foraging patterns, resulting in increased foraging pressure on the *Faidherbia* trees within the lower Hoanib River.

Foraging and movement patterns

The seasonal movements and foraging patterns of elephants within the northern Namib Desert were intensively studied by Viljoen in the early 1980's (1989a, 1989b, Viljoen and Bothma 1990b). He recognized the importance of isolated resource patches (i.e., springs and vegetation) to the survival of region's elephants. The riparian vegetation associated with the Hoanib and Hoarusib Rivers was particularly important, both during the dry and wet seasons. Viljoen (1989a) noted that ephemeral river courses and their floodplains, while representing only 3.2 % of the 14,750 km^2 study area in the northern Namib Desert, provided the only habitat upon which elephants could rely for long-term survival. Similarly, Kerr and Fraser (1975) observed that alluvial plains in the Zambezi Valley, while comprising less than 5 % of their study area, supported roughly 50% of the elephant population during the dry season. They also viewed the maintenance of these areas as essential to the long-term viability of the region's elephant population.

In order to use isolated resource patches, however, elephants must be capable of moving among them. The harsh landscape of the northern Namib Desert provides only isolated respites for any elephant moving across it. Viljoen (1989b) observed that desert-dwelling elephants were well-adapted to the desert and able to go up to four days without drinking water. This ability allowed them to use food resources up to 70 km from water. Not surprisingly, elephants in western Namibia are known to have the largest home ranges of any population studied to date, with estimates of mean home ranges ranging from 2,172 km^2 (Viljoen 1989b) to ~5,800 km^2 (Lindeque and Lindeque 1991).

Elephants, both lone bulls and family units, regularly move the ~60 km from the Hoanib floodplain north to the lower Hoarusib River (Viljoen 1989, Lindeque and Lindeque 1991). Lindeque and Lindeque (1991) observed three such movements during eight months study. Viljoen (1989b) observed that elephants rarely traveled more than 20-40 km from water during the dry season, with a mean distance of 25.7 km (sd=13.2) and a maximum of 70 km. This range corresponds with the length of the reach of the lower Hoanib River between the Dubis wetland and the Mudorib confluence, where *Faidherbia* trees were most severely damaged and the greatest dry season concentration of elephants occurs (Viljoen 1989b).

Following floods, elephants exhibited a strong preference for the Hoanib River floodplain (vlei), where floods trigger an abundance of grasses and forbs. Elephants shifted from a dry season distribution centered around the Dubis wetland area, to a wet season distribution centered on the terminal floodplain, remaining as long as fresh forage was available (Viljoen 1989a). The river course served as a key corridor during these seasonal movements from the Dubis wetland to the floodplain, a distance of ~70 km (Viljoen 1989b). Seasonal movements between a dry season distribution, related to surface water availability, and wet season distribution taking advantage of better food resources, have also been reported from the Tsavo Park (Laws 1970), although these

movements occurred over distances of only 25-40 km. Similar seasonal movement patterns have been reported from the Zambezi Valley in Zimbabwe (Kerr and Fraser 1975).

While isolated habitat patches are of obvious importance to the survival of desert-dwelling elephants, so too are the linking corridors. As Viljoen (1989) observed, critical resource patches are often separated by distances of up to 60 km. In the hyper-arid Namib Desert, any error in navigation between such sites could prove fatal. Thus, the disruption of corridors between key resource patches could have obvious detrimental effects. If access to isolated foraging areas is hindered, pressure on the remaining resource patches within the home range would logically increase, potentially resulting in the over-utilization of accessible patches.

Poaching: the precursor of vegetation change?

Uncontrolled poaching has undoubtedly been the greatest impact on elephants in the northern Namib Desert and has significantly changed their distribution in northwestern Namibia over the past several decades (Viljoen 1987). I hypothesize that poaching induced changes in the movement and foraging patterns of elephants within northwestern Namibia, as has been observed elsewhere in Africa (Caughley 1976, Lewis 1986). However, Viljoen (1989b) recorded no cases of elephants moving into new ranges as a result of hunting or other pressures. While elephants moved extensively within large home ranges, fidelity to these ranges was high, even when animals suffered heavy hunting pressures (Viljoen 1987). Viljoen (1989b) noted that this conflicted with the 'compression hypothesis' (Caughley 1976), which has been used to explain mass shifts of elephant populations due to human pressure. The 'compression hypothesis' suggests that elephants are driven into sanctuary areas by increasing levels of disturbance, resulting in localized concentrations that may seriously damage vegetative communities (Caughley 1976). It is also possible, however, that elephants losing only part of their home range to human activity may be 'compressed' into the remainder, as was noted by Viljoen (1989).

'Compression' need not imply only a shift in distribution and an associated change in density, but could also be applied to situations where disturbances force animals to avoid localized portions of their normal range, and spend more time foraging in disturbance-free areas. Such shifts might be too subtle to be perceived as an alteration in elephant distribution or density across a landscape. Yet, such shifts could affect resource utilization patterns within the northern Namib Desert. If, for example, a key habitat patch is lost, animals would be forced to restrict their activity to the remaining patches. The density of animals within any given patch would not necessarily increase, but use of some patches could become excessive. Viljoen (1989) noted the reluctance of elephants to move into new areas within western Namibia, which might act to increase the probability of the 'home range compression' previously described. While admittedly speculative, such a

scenario may explain the significant habitat alterations that have occurred within the lower Hoanib River.

Similar effects have been observed in the Luangwa Valley in Zambia, where poaching induced changes in food preferences and range patterns of elephants (Lewis 1986). These changes restricted food availability, resulting in a decline in the region's woodland. Lewis noted that the increased browsing pressure was the result of altered feeding behaviors (i.e., time spent within particular habitat patches) rather than increased elephant density (Caughley 1976). Elephants in the Luangwa Valley rapidly returned (within 1-2 years) to former foraging areas once anthropogenic disturbances were controlled (Lewis 1986).

It is unclear, however, whether the human disturbances, particularly poaching, induced such shifts in the patterns of resource utilization within elephant home ranges in the Namib. Intensive studies of the distribution and movements of individual elephants and family units only began in October 1980 (Viljoen 1989b). By this time, significant disturbances had already occurred throughout the study area, including hunting (Viljoen 1987). In fact, Viljoen's study period, from October 1980 to January 1983 coincided with intensive poaching and other disturbances. From July 1979-July 1982, a total of 121 elephants were killed within northwestern Namibia, some 35% of the total population (Viljoen 1982).

An aerial census in 1982 revealed the extent of the poaching which was occurring in the immediate vicinity of the Hoanib River and its tributaries (Viljoen 1982). While 25 elephants were observed within the Hoanib River west of Sesfontein, 11 carcasses were also seen. To the north, zero live and 11 dead were observed in the Hoarusib River; to the south, zero live and 6 dead on the Kharokhaob Plain; to the east, 11 live and 18 dead on the Khowarib Plain; and upstream of the Khowarib Canyon, 38 live and 41 dead. Ground surveys confirmed that 90 % had been shot within the past three years (Viljoen 1982). No observations of movement patterns were made before the poaching, however, obstructing any attempt to assess whether poaching triggered shifts in foraging patterns.

An uncertain future

The future of the forest, the elephants, and the river itself, is uncertain. A wide range of development plans have been proposed for the Hoanib River, with particular emphasis upon expanded agricultural activities that rely upon the water resources of the Hoanib River (MAWRD 1994). Ground-water pumping of the alluvial aquifer of the Hoanib River, between Khowarib and Anabeb, and construction of a dam in the Khowarib Canyon, are two options for agricultural development. Either option will likely have serious impacts upon the lower Hoanib River ecosystem. A reduction in flood frequency or extensive groundwater pumping would lower the water table within the lower Hoanib River, having multiple effects upon the region's biota.

Hydrologic alterations could lead to the desiccation of the Dubis wetland, a critical dry-season resource for the region's elephants, and trigger the senescence of the even-aged *Faidherbia* forest along the lower river. Young and Lindsay (1988) noted that environmental stressors may act to trigger synchronous die-offs within even-aged stands. Such a die-off occurred in the lower Kuiseb River during the early 1980's when 4 years without floods triggered the collapse of large *Faidherbia albida* trees (Ward and Breen 1983). A similar die-off occurred within the lower Swakop River, along with the desiccation of wetlands, in response to hydrologic alterations induced by an upstream impoundment (Jacobson et al. 1995).

Avoiding such dramatic changes is contingent upon the maintenance of key ecological processes, particularly flooding, critical to the maintenance of the elephant's principal resource patches (i.e., springs and vegetation). Floods in ephemeral rivers act to decouple elephants from fluctuations in the harsh local climate. Although local rainfall may differ by more than 100 % among years, mean daily movements of elephants may remain unchanged, as floods originating in the upper catchment provide water and stimulate vegetation growth along the rivers and their floodplains (Viljoen 1989b).

If the *Faidherbia* forest within the lower Hoanib River is to recover, the browsing pressure and associated destruction of young trees must decrease. Eastward extensions of the elephants' range could provide an outlet to reduce pressure on the river's vegetation, although they could also lead to increased conflicts with humans. Prior to the heavy poaching of the 1970's and early 1980's, Owen-Smith (1971) observed that elephants ranged from the Hoanib River west of Sesfontein across the Khowarib Plains, and drank at Anabeb and from small springs in the mountains south of Warmquelle and Sesfontein. An aerial census in 1975 counted only five elephants in the Hoanib River west of Sesfontein but 33 on the plains to the south (Viljoen 1987). An elephant traveling upstream from the Dubis wetland could reach Sesfontein in ~30 km, Anabeb in ~45 km, and the Khowarib canyon in ~70 km. Moving southeast through the mountains, elephants could reach the canyon in ~50 km. Such movements would significantly increase access to vegetation resources, relative to those currently utilized in the vicinity of the lower Hoanib River. While it remains to be seen if such movements will occur, their probability will increase in response to further declines in resource availability in the lower reaches of the river. This would be particularly true in the event of any significant alterations of the river's surface or subsurface hydrologic regimes. At present, uncoordinated land use within the region leaves the future of the lower Hoanib River and its natural resources uncertain.

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References

Anderson, G.D. and B.H. Walker. 1974. Vegetation composition and elephant damage in the Sengwe Wildlife Research Area, Rhodesia. *Journal of the Southern African Wildlife Management Association* 4: 1-14.

Barnes, R.F.W. 1983a. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology* 20: 521-540.

Barnes, R.F.W. 1983b. The elephant problem in Ruaha National Park, Tanzania. *Biological Conservation* 26: 127-148.

Behnke, R.H. Jr., I. Scoones and C. Kerven (eds.). 1993. *Range ecology at disequilibrium: new models of natural variability and pastoral adaptation in African savannas*. Overseas Development Institute, Regent's College, London. 248 pp.

Caughley, G. 1976. The elephant problem - an alternative hypothesis. *East African Wildlife Journal* 14: 265-283.

CTFT (Centre technique forestier tropical). 1989. *Faidherbia albida (Del.) A. Chev. (Synonym Acacia albida Del.).* (English translation by P.J. Wood) Nogent-sur-Marne, France: CTFT, and Wageningen, Netherlands: Centre technique de coopération agricole et rurale. 72 pp.

Dunham, K.M. 1989. Long-term changes in Zambezi riparian woodlands, as revealed by photopanoramas. *African Journal of Ecology* 27: 263-275.

Feely, J.M. 1965. Observations on *Acacia albida* in the Luangwa Valley. *The Puku*, Occ. Papers Dept. Game and Fisheries 3: 67-70.

Jacobson, P.J., K.M. Jacobson and M.K. Seely. 1995. *Ephemeral rivers and their catchments: sustaining people and development in western Namibia*. Desert Research Foundation of Namibia, Windhoek. 160 pp.

Kerr, M.A. and J.A. Fraser. 1975. Distribution of elephant in a part of the Zambezi Valley, Rhodesia. *Arnoldia* 7: 1-14.

Laws, R.M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21: 1-15.

Lewis, D.M. 1986. Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. *African Journal of Ecology* 24: 227-241.

Lindeque, M. and P.M. Lindeque. 1991. Satellite tracking of elephants in northwestern Namibia. *African Journal of Ecology* 29: 196-206.

MAWRD. 1994. *Sustainable development in the Sesfontein/Khowarib basin*. Namibian Ministry of Agriculture, Water and Rural Development, Windhoek. Final Draft. 188 pp.

Owen-Smith, G.L. 1971. *The Kaokoveld: an ecological base for future development planning*. Pinetown, South Africa. 67 pp.

Schoeman, A. 1982. The 'big and hairy' syndrome re: Damaraland and Kaokoland: a diagnosis. Pages 4, no. 9969. *The Windhoek Advertiser*, Windhoek, Namibia.

Viljoen, P.J. 1982. *Western Kaokoland, Damaraland and the Skeleton Coast Park aerial game census*. Namibia Wildlife Trust, Windhoek. Unpublished Report. 31 pp.

Viljoen, P.J. 1987. Status and past and present distribution of elephants in the Kaokoveld, South West Africa/Namibia. *South African Journal of Zoology* 22: 247-257.

Viljoen, P.J. 1989a. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib Desert, South West Africa/Namibia. *African Journal of Ecology* 27: 227-240.

Viljoen, P.J. 1989b. Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. *Journal of Zoology, Lond.* 219: 1-19.

Viljoen, P.J. and J. du P. Bothma. 1990a. The influence of desert-dwelling elephants on vegetation in the northern Namib Desert, South West Africa/Namibia. *Journal of Arid Environments* 18: 85-96.

Viljoen, P.J. and J. du P. Bothma. 1990b. Daily movements of desert-dwelling elephants in the northern Namib Desert. *South African Journal of Wildlife Research* 20: 69-72.

Ward, J.D. and C.M. Breen. 1983. Drought stress and the demise of *Acacia albida* along the Lower Kuiseb River, Central Namib Desert: preliminary findings. *South African Journal of Science* 79: 444-447.

Young, T.P. and W.K. Lindsay. 1988. Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. *African Journal of Ecology* 26: 69-72.

Table 1. The distribution of stem diameters (cm) in samples of living *Faidherbia albida* trees along the lower Hoanib River in the northern Namib Desert, Namibia. The values assigned to each size class are percentages of the total sample.

River	n	2-20	21-40	41-60	61-80	81-100	100-120	>120
Hoanib[1]	442	0.2	11.8	30.4	22.9	12.9	9.1	12.7
Hoanib[2]	206	30.1	25.2	20.9	11.7	4.9	5.3	1.9

[1] - Current study.
[2] - Viljoen (1990).

General Conclusions

Poff and Ward (1989, 1990) proposed that hydrology was the key organizer of the physical habitat template in fluvial ecosystems. As has been discussed in the previous pages, the overwhelming majority of research in lotic ecology has focused on more mesic systems. I believe there are sound reasons to expand our current perspective of fluvial ecosystems.

The adjective fluvial refers to anything, "pertaining to, or inhabiting a river or stream, or any feature produced by the action of flowing water." (Anonymous 1982). While this definition has broad scope, lotic ecologists have purloined the term, commonly using it in strict reference to flowing-water habitats that support an aquatic biota. While admittedly not all lotic ecologists take such a narrow view, and many would and do include floodplain environments in their definition of fluvial ecosystems, I argue that a broader view of fluvial ecosystems is needed. Fluvial geomorphologists have not been as "hydrologically constrained" in their studies of fluvial systems, having examined the influence of fluvial processes on physical features within rivers spanning the entire hydrologic continuum. From desert palaeochannels that last flowed during the Pleistocene to large perennial floodplain rivers such as the Amazon or Mississippi, and everything in between, these geologists have sought to develop a better understanding of how fluvial processes shape the features of these systems.

I suggest that a similarly broad approach is needed to study the biotic characteristics associated with fluvial systems. The influence of hydrologic variability on the structure and function of fluvial ecosystems should be examined across the full spectrum of fluvial systems, from wet to dry. While the biotic assemblages will undoubtedly differ across such a range of systems, shifting from largely aquatic to primarily terrestrial along the transition from wet to dry, commonalties may emerge along with important differences. The development of such a hydrologic continuum would likely have important heuristic value for the study of fluvial ecosystems, and in particular, their response to hydrologic alteration. Identifying the hydrologic thresholds at which transitions in the structural and functional characteristics of fluvial communities occur would have an obvious predictive utility.

One commonality that emerged from my study was the great ecological significance of organic matter retention to the structural and functional attributes of fluvial ecosystems, despite the obvious divergence among their hydrologic regimes. For example, although the spatial patterns of transport and retention of woody debris may vary between perennial headwater streams and large ephemeral rivers, woody debris plays a similar role in regulating habitat availability, energy flow and nutrient cycling, and channel morphology among the systems.

Another motif that spans a broad portion of the hydrologic continuum is the importance of flood pulses in regulating various ecological processes. Junk et al. (1989) proposed the flood pulse concept to describe the importance of regular flood pulses to the biota of large floodplain rivers and to the regulation of organic matter dynamics. Floods and their associated stimulation of organic matter processing within floodplain environments were viewed as 'batch processes,' in contrast to the more continuous patterns observed in smaller mesic systems (Vannote et al. 1980). Such batch processing also occurs in ephemeral systems, where organic matter transport and processing are uncoupled and discontinuous.

The recent application of patch dynamics to mesic fluvial ecosystems (Pringle et al. 1988) also has broad application to more xeric systems. Fluvial processes in ephemeral rivers create and maintain discrete habitat patches critical to the persistence of associated biota. At the same time, the ephemeral rivers themselves are important habitat patches within the context of the arid landscapes they drain.

In addition to these commonalties, distinct differences occur along the hydrologic continuum. The predominance of batch processing of organic matter in ephemeral systems, in contrast to the comparatively continuous processes in mesic rivers and streams is highly significant. These batch events are triggered by flood pulses in ephemeral rivers, as they are in large floodplain rivers as previously mentioned. As a result, the definition of a hydrologic disturbance may vary substantially in relation to a system's hydrologic regime. While floods may be viewed as disturbances to the comparatively stable biotic communities of temperate perennial streams (Reice et al. 1990), the lack of floods would constitute a severe hydrologic disturbance in both floodplain rivers such as the Amazon (Junk et al. 1989) and ephemeral rivers such as the Kuiseb.

In addition, the underlying physical processes inherent to all fluvial systems may vary in accordance with the hydroclimatic conditions of the catchment. In particular, the rainfall-runoff response of dryland catchments is known to be markedly different from that of more mesic systems, becoming increasingly non-linear with decreasing mean annual precipitation (Rodier 1985, Dahm and Molles 1992). As a result, the significance of regional climatic shifts to fluvial systems may be much more pronounced for rivers and streams at the xeric end of the hydrologic continuum. Reductions in annual flow are likely to be far more significant to the water-limited ecosystems of ephemeral rivers than to those of their more mesic counterparts.

Hydrologic alterations, induced both via regional climate changes and the construction of impoundments and water diversions, will continually threaten the world's fluvial ecosystems in the years ahead (Postel et al. 1996). Ironically, dryland systems are among the least known ecologically yet the most threatened by the human enterprise. A broader understanding of the dynamics of fluvial ecosystems across the hydrologic

spectrum could have a tremendous heuristic value in formulating hypotheses regarding the response of individual systems to hydrologic alteration. I believe that the development of this more inclusive perspective of fluvial ecosystems, emphasizing those on the xeric end of the hydrologic continuum, will be an important contribution to the management of the world's imperiled fluvial ecosystems.

References

Anonymous. 1982. *The American Heritage Dictionary*. Houghton Mifflin Company, Boston. 1568 pp.

Dahm, C.N. and M.C. Molles. 1992. Streams in semi-arid regions as sensitive indicators of global climate change. Pages 250-260 in P. Firth and S.G. Fisher (eds.). *Global climate change and freshwater ecosystems*. Springer-Verlag, New York.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The Flood Pulse Concept in river-floodplain systems. Pages 110-127 in D. P. Dodge, ed. *Proceedings of the International Large River Symposium*. Can. Spec. Publ. Fish. Aquat. Sci.

Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Science* 46: 1805-1818.

Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environ. Management* 14: 629-645.

Postel, S.C., G.C. Daily, and P.R. Ehrlich. 1996. Human appropriation of renewable freshwater. *Science* 271: 785-788.

Pringle, C.M., R.J. Naiman, G. Bretschko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme, and M.J. Winterbourn. 1988. Patch dynamics in lotic ecosystems: the stream as a mosaic. *Journal of the North American Benthological Society* 7: 503-524.

Reice, S.R., R.C. Wissmar, and R.J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitat in lotic ecosystems. *Environmental Management* 14: 647-659.

Rodier, J.A. 1985. Aspects of arid zone hydrology. Pages 205-247 in J.C. Rodda (ed.). *Facets of hydrology, Vol II*. John Wiley and Sons, New York.

Vannote, R. L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Vita

Peter James Jacobson

Peter James Jacobson was born in Belleville, Illinois on August 27, 1964 to James and Anita Jacobson. The family lived in Collinsville, Illinois, where Peter completed his secondary education in 1982. He then attended Washington University in St. Louis, Missouri, where he completed a Bachelor of Arts degree in Chemistry in 1987. While completing his BA, he met Kathryn Margaret Banghart, and the couple married in 1988 after traveling to Virginia Tech to begin their graduate studies in Biology. Peter completed a Master of Science degree in 1990 under the direction of Dr. Donald S. Cherry and Dr. Richard J. Neves, having investigated the sensitivity of glochidial stages of freshwater mussels (Bivalvia: Unionidae) to copper. He then traveled to the Namib Desert and spent a year assisting his wife, Kathy, who was conducting her doctoral research in the central Namib dunefield. While based at the Desert Ecological Research Unit of Namibia, which sits on the northern bank of the ephemeral Kuiseb River, Peter had an opportunity to observe a flash flood and develop a keen interest in the dynamics of these unusual fluvial ecosystems. In 1991 he returned to Virginia Tech to commence his Ph.D. studies on the ephemeral rivers of the Namib Desert. From December 1992 to December 1995 he conducted his field research in western Namibia as a research associate of the Desert Research Foundation of Namibia. He returned to Virginia Tech in January 1996 to complete his studies for a Doctorate of Philosophy in Biology.