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

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Soils were examined along three ephemeral rivers in the Namib Desert to assess the influence of their hydrologic characteristics on soil properties. Soils consisted of layers of fluvially deposited, organic-rich silts, interstratified with fluvial and aeolian sands. The most significant influence of the ephemeral hydrologic regime upon soils was related to the downstream alluviation associated with hydrologic decay. This alluviation increased the silt proportion of soils in the lower reaches of the rivers. Organic carbon, nitrogen and phosphorous were correlated with silt content, and silt deposition patterns influenced patterns of moisture availability and plant rooting, creating and maintaining micro-habitats for various organisms. Localized salinization occurred in association with wetland sites and soluble salt content tended to increase downstream. Because of the covariance between silt and macronutrients, and the influence of silt upon moisture availability and habitat suitability, alluviation patterns associated with the hydrologic regime strongly influence the structure, productivity, and spatial distribution of biotic communities in ephemeral river ecosystems.

**Keywords:** alluvial soils; hydrology; silt; soil nutrients; organic matter; soil moisture; salinity; Africa

## Introduction

While a large body of research has examined the role of fluvial processes in shaping sedimentological features along dryland rivers (Picard & 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 the riparian biota. Studies to date have shown that moisture and nutrient availability, as well as soil salinity, are key factors

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influencing primary production in dryland riparian ecosystems (Jolly *et al.*, 1993; Busch & Smith, 1995). The majority of this research has focused on perennial rivers, however, and ephemeral rivers, characterized by their highly variable hydrologic regimes, have received little ecological study despite their occurrence throughout the world's drylands.

The rivers crossing the Namib Desert in south-western 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). A principal objective of this research has been to develop a better understanding of palaeoclimatic regimes and their influences on geomorphic processes within the Namib Desert.

In contrast, little attention has been given to recent alluvial deposits along these rivers. Scholz (1972) provided a brief morphological description of alluvial soils within the Kuiseb River floodplain. More recently, Abrams *et al.* (1997) considered the influence of fluvial processes upon ecologically-relevant soil properties at a site within the floodplain of the Kuiseb River. Their 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. We expected distinct longitudinal gradients of soil properties to be associated with the hydrologic decay that characterizes these systems. Such gradients, in turn, could have a strong influence on 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 sediments, the transport, retention, and deposition of woody debris and fine particulate organic matter (FPOM) exhibit similar patterns (Jacobson *et al.*, 1999*a*, in press). The position of organic matter retention and deposition varies, shifting upstream or downstream in response to decreases or increases in flood magnitude, respectively. 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 *et al.*, in press). 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 objectives of this brief survey were to examine selected soil properties 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.

## Materials and methods

### *Study sites*

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 (Fig. 1). A series of ephemeral rivers drain this escarpment, flowing westward across the Namib Desert. We 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

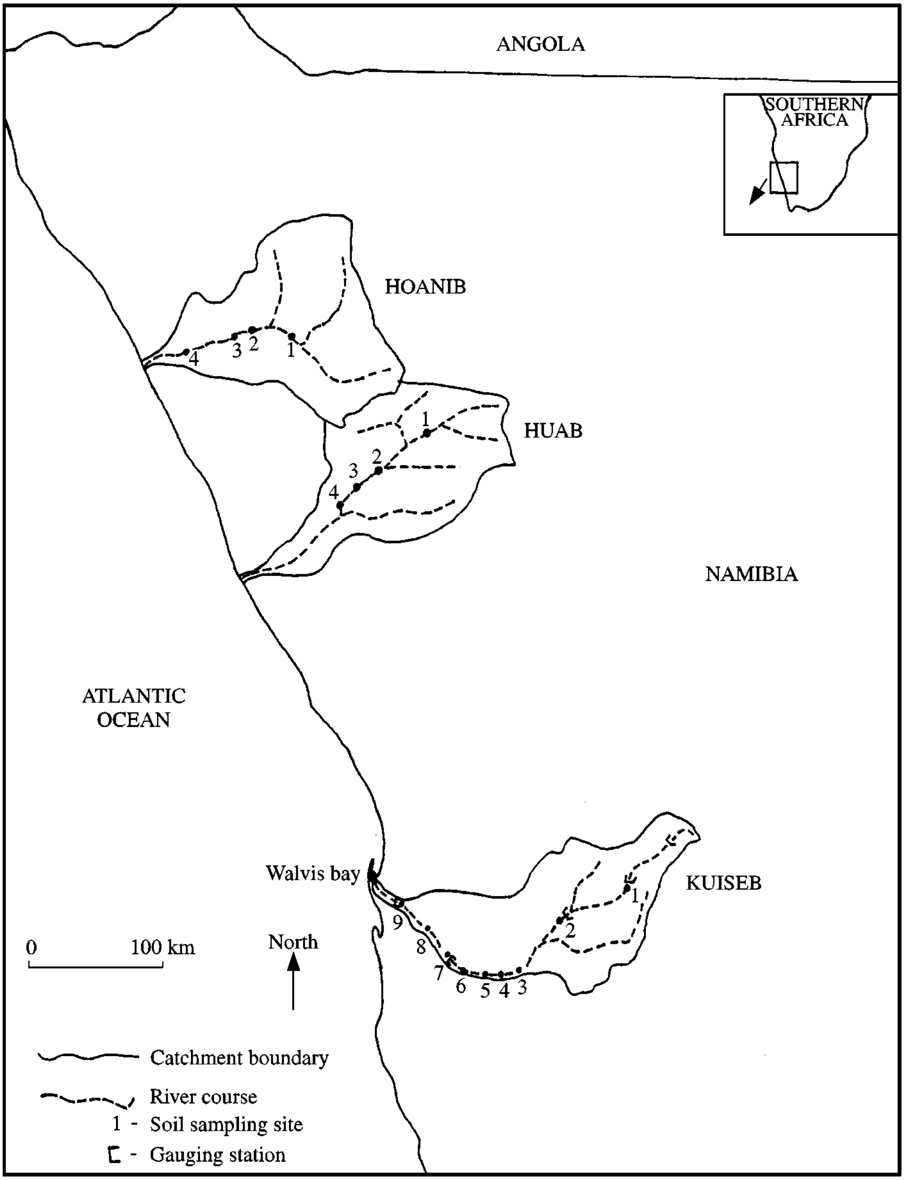

**Figure 1.** Soil sampling sites along the Huab, Hoanib, and Kuiseb Rivers in western Namibia.

Hoanib rivers drain catchments of 14,800 $km^2$ and 17,200 $km^2$, respectively, in north-western Namibia (Fig. 1). 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 elevations from 1500 to 2000 m. At the eastern edge of the Namib Desert at the escarpment's base, mean annual rainfall averages $\sim$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 hydrology of the Kuiseb River is well-known relative to the Huab and Hoanib rivers (Jacobson, 1997). While the main stem of the Kuiseb River is monitored by five automatic gauges, reliable records are 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 ($m^3 s^{-1}$) 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 biotic feature of the rivers is their comparatively lush riparian forest, a stark contrast to the adjacent sand and rock desert and a critical resource for the region's wildlife (Seely & Griffin, 1986). *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). The tree occurs sporadically within the escarpment and canyon reaches of the rivers on isolated pockets of alluvium. The most expansive stands are in the rivers' lower reaches where it grows on the extensive alluvial deposits associated with the broader channels and floodplains. Jacobson *et al.* (1999*b*) and Jurgens *et al.* (1997) provide a more detailed analysis of the rivers' riparian vegetation.

Sampling sites were dispersed along the rivers, including both escarpment reaches with steep gradients and little alluviation, and downstream reaches with extensive alluvial deposits and well-developed riparian forests. Sites were distributed along the rivers to

**Table 1.** *Mean annual runoff (total volume and peak discharge) for main-stem gauging stations along the $\sim$560-km Kuiseb River*

| Station | km* | MAR ($m^3$) | MAR ($m^3 s^{-1}$) |
|---|---|---|---|
| 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 |

*Distance from headwaters.

encompass the average reach of annual floods and the associated alluviation zones within the lower sections of the rivers. Nine sites were chosen within the Kuiseb, and four within both the Huab & Hoanib (Fig. 1). The Hoanib & Huab samples each included a wetland site, where a shallow water-table maintained perennial surface flow.

### *Sample collection and analysis*

Four replicate 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 & Bauder, 1986). Sands (0·05–2·0 mm diameter) were determined by wet sieving through a 0·05-mm-mesh screen, and the fraction smaller than 0·05 mm was analysed 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 & Schwab, 1977). Samples were shaken for 15 min with an Eberbach shaker ( ~180 cycles per min) in unstoppered 125-ml Erlenmeyer flasks, and then vacuum filtered through a Whatman 42 filter. Extractants were analysed by inductively coupled plasma spectrometry (ICP), using a Jarrell Ash ICAP 61 simultaneous spectrometer, for P, Ca, Mg, K, Na, Fe, Mn and Zn. 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 & Munns, 1987). A 1:2 volume extract of soil to distilled, deionized water was used to measure the pH and electrical conductivity (EC) (Sonneveld & Ende, 1971). After shaking for 1 h 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 conductance 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 analysed for organic C (OC) and total N by dry combustion with a LECO CNS 2000 analyser (Bremner & Mulvaney, 1982; Nelson & 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 and among rivers. Wetland sites were excluded from means calculated for the Hoanib and Huab rivers. When data were non-normal, 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 $p < 0{\cdot}05$.

## Results

### *Classification and texture*

Soils sampled within the rivers were in the Fluvent suborder, characterized by alternating layers of fluvially-deposited silts and sands of both fluvial and aeolian origin. These interstratified sediments also exhibited an irregular carbon distribution with depth. Carbon-rich layers originated from buried O- or A-horizons, or fluvially-deposited

**Table 2.** *Variability in soil characteristics among four sites along the Hoanib River. Site numbers (in parentheses) correspond to site locations in Figure 1. Means (n = 4) in a row followed by different letters are statistically different at p < 0·05 level*

| | Units | Khowarib (1) | Dubis* (2) | Ganamub (3) | Floodplain (4) |
|---|---|---|---|---|---|
| Location† | km | 138 | 198 | 213 | 260 |
| pH | | 7·34 b | 8·18 a | 7·52 ab | 7·68 a |
| EC | $\mu$S 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 kg$^{-1}$ | 6·69 a | 4·83 a | 9·69 a | 5·73 a |
| Ca | cmol kg$^{-1}$ | 2·27a | 1·98 b | 2·12 ab | 1·96 b |
| Mg | cmol kg$^{-1}$ | 1·18 a | 1·47 a | 1·29 a | 1·36 a |
| Na | cmol kg$^{-1}$ | 0·06 b | 2·65 a | 0·24 ab | 0·21 ab |
| K | cmol kg$^{-1}$ | 0·52 a | 0·84 a | 0·47 a | 0·31 a |
| ECEC | cmol 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 kg$^{-1}$ | 5·42 a | 5·34 a | 8·07 a | 2·38 a |
| Zn | mg kg$^{-1}$ | 0·37 a | 0·31 a | 0·43 a | 0·23 a |
| Fe | mg kg$^{-1}$ | 4·93 a | 4·13 a | 12·13 a | 7·85 a |

* Wetland site.
† Distance from headwaters.

organic matter. O- and A-horizons were absent on recently-flooded surfaces, but did occur on the infrequently-flooded, alluvial terraces that border the lower reaches of the rivers. Soils were typically well-drained, although silt and clay horizons acted as hydraulic barriers, limiting infiltration as well as desiccation of underlying sediments. The highly variable soil moisture regime associated with irregular flood pulses complicated further classification. Terrace and floodplain soils may be dry to depths below one metre for several years 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 moisture regime, and were best classified as Typic Torrifluvents (Soil Survey Staff, 1992), or Fluvisols under the FAO-UNESCO soil classification system.

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 and 4). No significant differences were detected in particle size composition among the rivers, except a slight increase in clay within the Hoanib River (Table 5). 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).

**Table 3.** *Variability in soil characteristics among four sites along the Huab River. Site numbers (in parentheses) correspond to site locations in Figure 1. Means (n = 4) in a row followed by different letters are statistically different at* $p < 0.05$ *level*

| | Units | Annabis (1) | Noute (2) | Opdraend* (3) | Vrede (4) |
|---|---|---|---|---|---|
| Location† | km | 110 | 158 | 192 | 219 |
| pH | | 7·42 b | 7·46 b | 7·90 a | 7·56 b |
| EC | $\mu$S cm$^{-1}$ | 149 b | 215 bc | 3709 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 kg$^{-1}$ | 6·27 a | 8·72 a | 11·37 a | 9·01 a |
| Ca | cmol kg$^{-1}$ | 1·90 b | 2·36 a | 1·90 b | 2·14 ab |
| Mg | cmol kg$^{-1}$ | 0·52 b | 0·73 b | 2·42 a | 1·34 ab |
| Na | cmol kg$^{-1}$ | 0·07 b | 0·05 b | 8·01 a | 0·42 ab |
| K | cmol kg$^{-1}$ | 1·24 a | 0·27 b | 0·69 ab | 0·58 ab |
| ECEC | cmol 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 kg$^{-1}$ | 3·65 a | 6·24 a | 9·48 a | 6·28 a |
| Zn | mg kg$^{-1}$ | 0·78 a | 0·57 a | 1·60 a | 0·95 a |
| Fe | mg kg$^{-1}$ | 7·61 a | 12·13 a | 22·85 a | 9·68 a |

* Wetland site.
† Distance from headwaters.

### *Chemical properties*

Results of soil elemental analyses indicated that most exchangeable cation levels were indistinguishable among study sites within each river system, but did differ among river systems (Tables 2–5). Exceptions within rivers occurred at wetland sites and the lower-most 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 lower-most 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 & Munns, 1987).

Soil chemistry differed among the three rivers. Soil pH was significantly higher in the Huab and Hoanib than in the Kuiseb (Table 5). Except for magnesium, levels of macronutrients did not differ among the rivers. Soils from the Hoanib River contained higher Mg levels, relative to the Kuiseb River. 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 (Table 5).

Soil phosphorus, nitrogen, and organic carbon tended to increase downstream. The amount of silt was positively correlated with the amounts of organic carbon ($r = 0{\cdot}74$), nitrogen ($r = 0{\cdot}78$), and phosphorous ($r = 0{\cdot}70$) within the Kuiseb River. A similar pattern was observed in samples from the Hoanib and Huab rivers.

**Table 4.** *Variability in soil characteristics among nine sites along the Kuiseb River. Site numbers (in parentheses) correspond to site locations on Figure 1. Means ($n = 4$) in a row followed by different letters are statistically different at $p < 0·05$ level*

| | Units | Us (1) | Bridge (2) | Poort (3) | Sarib (4) | Alley (5) | Clado (6) | Nara (7) | Swartbank (8) | Rooibank (9) |
|---|---|---|---|---|---|---|---|---|---|---|
| Location* | km | 180 | 308 | 400 | 418 | 433 | 457 | 480 | 505 | 530 |
| pH | | 6·48 b | 7·32 a | 7·31 a | 7·11 a | 7·07 a | 6·97 a | 7·06 a | 7·10 a | 7·03 a |
| EC | $\mu$S cm$^{-1}$ | 501 b | 320 b | 254 b | 332 b | 311 a | 367 b | 336 b | 448 b | 1033 a |
| Sand | % | 89 ab | 90 ab | 85 abc | 78 bcde | 73 cdef | 69 ef | 79 bcde | 90 ab | 77 cde |
| Silt | % | 11 de | 10 de | 15 cde | 22 bcd | 27 abc | 30·0 ab | 20 bcd | 10 de | 21 bcd |
| Clay | % | 0 b | 0 ab | 0 ab | 0 ab | 0 b | 1 ab | 1 ab | 0 ab | 2 a |
| OC | % | 0·43 a | 0·27 a | 0·47 a | 0·86 a | 0·56 a | 0·90 a | 0·70 a | 0·27 a | 1·02 a |
| N | % | 0·05 ab | 0·04 ab | 0·05 ab | 0·09 ab | 0·07 ab | 0·10 a | 0·08 ab | 0·03 b | 0·10 a |
| P | mg kg$^{-1}$ | 11·60 ab | 14·03 ab | 11·82 ab | 15·62 ab | 16·56 ab | 22·17 ab | 18·49 ab | 11·21 b | 25·47 a |
| Ca | cmol kg$^{-1}$ | 2·32 a | 2·19 ab | 2·26 a | 2·16 ab | 2·26 a | 2·14 ab | 2·18 ab | 2·30 a | 2·04 b |
| Mg | cmol kg$^{-1}$ | 0·59 b | 0·40 c | 0·48 bc | 0·60 b | 0·61 b | 0·76 ab | 0·63 b | 0·46 bc | 0·80 a |
| Na | cmol kg$^{-1}$ | 0·05 a | 0·13 a | 0·08 a | 0·10 a | 0·04 a | 0·08 a | 0·09 a | 0·21 a | 0·89 a |
| K | cmol kg$^{-1}$ | 0·54 ab | 0·25 ab | 0·18 b | 0·25 ab | 0·29 ab | 0·42 ab | 0·50 ab | 0·46 ab | 0·59 a |
| ECEC | cmol kg$^{-1}$ | 3·50 a | 2·97 a | 3·00 a | 3·13 a | 3·19 a | 3·40 a | 3·40 a | 3·42 a | 4·32 a |
| ESP | % | 1·60 a | 4·60 a | 2·78 a | 3·60 a | 1·45 a | 2·74 a | 3·10 a | 6·89 a | 18·35 a |
| Mn | mg kg$^{-1}$ | 11·11 ab | 7·42 b | 6·41 b | 9·05 ab | 10·49 ab | 17·10 ab | 12·47 ab | 9·27 ab | 31·97 a |
| Zn | mg kg$^{-1}$ | 0·58 a | 0·44 a | 0·56 a | 0·63 a | 0·87 a | 0·92 a | 0·66 a | 0·85 a | 1·04 a |
| Fe | mg kg$^{-1}$ | 20·20 b | 21·44 ab | 28·17 ab | 33·92 ab | 39·99 ab | 48·90 a | 44·36 ab | 21·25 ab | 43·72 ab |

* Distance from headwaters.

**Table 5.** *Average soil characteristics among the Hoanib, Huab and Kuiseb rivers. Means in a row followed by different letters are statistically different at* $p < 0{\cdot}05$ *level*

| | Units | Hoanib*,† | Huab*,† | Kuiseb‡ |
|---|---|---|---|---|
| pH | | 7·52 a | 7·48 a | 7·06 b |
| EC | $\mu S\ cm^{-1}$ | 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 | $mg\ kg^{-1}$ | 7·37 b | 8·00 b | 16·49 a |
| Ca | $cmol\ kg^{-1}$ | 2·11 a | 2·13 a | 2·20 a |
| Mg | $cmol\ kg^{-1}$ | 1·28 a | 0·88 ab | 0·59 b |
| Na | $cmol\ kg^{-1}$ | 0·17 a | 0·18 a | 0·19 a |
| K | $cmol\ kg^{-1}$ | 0·43 a | 0·70 a | 0·38 a |
| ECEC | $cmol\ kg^{-1}$ | 3·99 a | 3·89 a | 3·37 b |
| ESP | % | 4·64 a | 4·94 a | 5·15 a |
| Mn | $mg\ kg^{-1}$ | 5·29 b | 5·39 b | 12·97 a |
| Zn | $mg\ kg^{-1}$ | 0·34 b | 0·77 a | 0·73 a |
| Fe | $mg\ kg^{-1}$ | 8·31 b | 9·81 b | 33·93 a |

*Excluding wetland sites (Hoanib-Dubis; Huab-Opdraend).
† $n = 12$.
‡ $n = 36$.

## Discussion

Variation in levels of micro- and macronutrients among the rivers is partly attributable to differences in catchment geology. For example, while the Kuiseb catchment is composed largely of micaceous schists, the Hoanib catchment is underlain by significant amounts of dolomite, a source for the greater amount of magnesium within its alluvium. Despite such variation, the river's ephemeral hydrologic regime gives rise to soil characteristics common to all three systems. Chief among these are the 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 (Jolly *et al.*, 1993; Busch & Smith, 1995), 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 leaching and evaporative concentration, may be responsible for the increase in soluble salts observed at the lower-most sampling sites on the Huab and Kuiseb rivers (Tables 3 and 4) (Jacobson *et al.*, in press). 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 & Munns, 1987).

Soil salinization does occur at wetland sites, however, where capillary movement of water from a shallow groundwater table 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 were saline (Tables 2 and 3), often exhibiting 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 (pers. obs.). 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 & 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. Biologically-significant soil salinization in the Namib's rivers appears to be limited to isolated sites with shallow ($<1$ m) water tables. Of far greater significance to soil properties within these rivers is the effect of floods and their downstream discharge decay upon patterns of material transport and deposition.

### *Hydrologic decay, alluviation, and the ecology of silt*

Transmission losses in the lower Kuiseb River are high, ranging from $\sim 0{\cdot}4$–$1{\cdot}7\%\ \mathrm{km}^{-1}$, resulting in a rapid downstream decrease in stream power and capacity (Jacobson, 1997). As stream power and capacity decrease, alluviation must increase (Bull, 1979). The downstream increase in silt percentage observed in the Kuiseb River, paralleling the downstream reduction in mean discharge, reflects this relationship. The longitudinal profile of the Kuiseb River is convex in its lower reaches (Fig. 2) and delimits an alluviation zone, as was 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 remain 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 may also directly influence the nutrient status of the 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.

An important consequence of silt alluviation patterns in ephemeral rivers is their influence upon moisture dynamics within floodplain soils, and in turn, their 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 (Jacobson *et al.*, 1995; Shelley & Crawford, 1996; Jacobson, 1997).

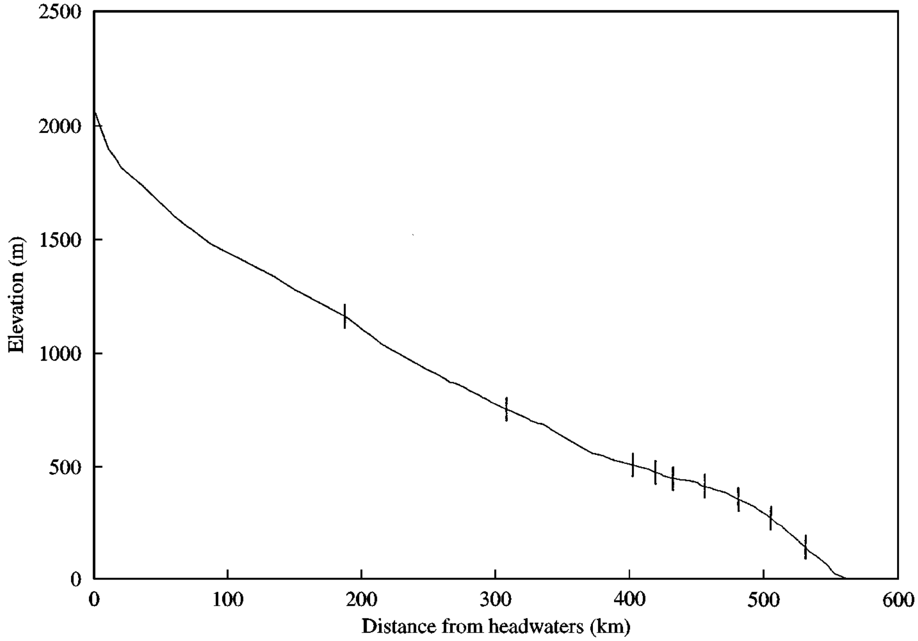

**Figure 2.** Longitudinal profile of the Kuiseb River, showing the alluviation zone ( ~380–480 km) within the lower river and sampling site positions (vertical bars).

In addition to inorganic sediments, floods also deposit large amounts of organic matter (Jacobson, 1997). Variations in channel morphology, such as meanders or mid-channel islands, influence deposition patterns, often resulting in large accumulations. Organic matter is commonly deposited over large areas on the outside of channel bends or point bars in mats of several centimeters or more in depth. Organic matter (litterfall) also accumulates under riparian vegetation. Finally, riparian vegetation, both on the floodplain and within the channel, is an important retention structure during floods, accumulating large amounts of organic matter. All of these deposits may be mobilized in subsequent floods or incorporated into the soil profile when overbank floods bury them under inorganic sediments. Once buried, organic accumulations are exposed to more constant regimes of temperature and moisture than surface organic matter, which dries quickly in the arid environment.

Silt caps on the floodplain surface act to retard the desiccation of underlying sediments, favouring a higher and sustained level of decomposition relative to that experienced by surficial organic matter. While exposed sands can dry to depths of more than 30 cm within weeks of a flood, several cm of silt can maintain subsurface soil moisture levels of 4–6% (by weight) for several months or more following recession (pers. obs.). 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 organic matter by an unusual assemblage of Basidiomycetes, including the fungus *Battarrea stevenii* (Liboshitz) Fr. (Jacobson *et al.*, 1999*b*). This large fungus fruits from subsurface silts, breaking through the surface silt crust several months to a year after a flood has inundated the floodplain. Thus, flood pulses, in addition to depositing nutrient-rich sediment, also trigger the activity of soil micro-organisms, directly influencing decomposition and mineralization rates (Jacobson *et al.*, 1999*b*). The pulse of carbon and nitrogen mineralization associated with drying and rewetting cycles has been described from soils across a range of climates (Cabrera, 1993; Van

Gestel *et al.*, 1993), although the effect may be particularly pronounced in the water-limited ecosystems associated with ephemeral rivers.

Riparian trees appear to track the vertical heterogeneity in moisture and nutrient availability within the soil profile. 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 advantageous 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.

An important source of organic matter is the physical processing of woody debris and *Faidherbia albida* fruits during floods, which yields a large amount of highly-labile organic matter (Jacobson *et al.*, 1999*a*, in press). More than a dozen species of fungi, including several species of lignin-decomposing fungi typically found only on logs and other woody debris, are commonly found fruiting from surficial silt deposits within one to two weeks of flood recession. Excavations have confirmed that silt-associated FPOM (fine particulate organic matter) is the principal nutrition source for these fungi (K. Jacobson, unpublished data). The presence of similarly-derived FPOM deposits has been noted previously from other dryland rivers. Minckley and Rinne (1985) provided a historic review of the dynamics of large woody debris in desert streams, detailing the many references to fine particulate organic matter in desert floodwaters. 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. Finally, Forbes (1902) noted that Arizona floodwaters are rich in organic matter, and noted the ‘fertilizing value’ of these materials.

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, 1997). Soil enrichment occurs in association with woody debris piles retained on in-channel trees, as the 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, 1997). 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 centimetres. The silt plates also curl slightly at the edges, separating from underlying sands. This highly dissected surface and subsurface creates a unique microhabitat within the riparian zone (pers. obs.). Moist microclimates within cracks and under silt plates provide refugia for frogs (*Tomopterna delalandei*) and various invertebrates, including millipedes and isopods. In addition, the cracks are foraging sites for insectivores, including scorpions (*Parabuthus villosus*) and shrews (*Crocidura cyanea*).

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, appear to be the most biologically productive reaches within ephemeral river ecosystems. Preliminary data on the density of *F. albida* along the

Kuiseb River 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 (P. Jacobson, unpublished data). We suggest that the hydrologic regime, through its control of soil characteristics, particularly nutrient and moisture availability, is the principal factor controlling both the structural and functional characteristics of ephemeral river communities, including their spatial distribution along the river. In turn, any alteration of the hydrologic regime will produce a concomitant shift in the structure, productivity, and distribution of these fluvial ecosystems.

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