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5866

5866

Micro-arthropods associated with *Welwitschia mirabilis* in the Namib Desert

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Significantly more micro-arthropods were found under *Welwitschia* plants than in unvegetated areas. Densities varied considerably with locality of plant ranging from a mean ± *SE* of 1 710 ± 720 micro-arthropods m^{-2} in the Northern Namib to 145 700 ± 95 930 micro-arthropods m^{-2} in the southernmost locality. The same taxa were found at all sites and these are also common to North American and Australian deserts. The structure of the micro-arthropod community varied considerably with locality and sex of the plant. Tarsonemid mites were numerically dominant at some sites while Collembola were dominant at others. Prostigmatids were the most abundant group of mites, and mites were generally the most abundant micro-arthropod.

Daar word merkbaar meer mikro-artropode onder die *Welwitschia*-plante aangetref as in plekke waar geen plante voorkom nie. Die digtheid het heelwat gewissel met plant-lokaliteit en het gestrek vanaf 'n gemiddelde ± standaardfout van 1 710 ± 720 mikro-artropode m^{-2} in die noordelike Namib tot 145 700 ± 95 930 m^{-2} mikro-artropode in die mees suidelike gebied. Dieselfde taksa is op elke plek gevind, en hulle is ook algemeen in die Noord Amerikaanse en Australiese woestyne. Die struktuur van die mikro-artropoodgemeenskap het aansienlik verander met die lokaliteit en geslag van die plant. Tarsonomied-myte is getalsdominant op sekere plekke terwyl Collembola op ander plekke weer dominant is. Prostigmatiede is die volopste groep van die myte, en myte is in die algemeen die volopste mikro-artropode.

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Productivity in desert ecosystems is limited not only by moisture but also by nutrient levels (Hadley & Szarek 1981). For example Seely & Louw (1980) consider Namib dune sands to be deficient in both nitrogen and phosphorous. Nutrients accumulate in dead organic matter, and in many arid shrub communities litter and dead wood may exceed alive above-ground biomass (Noy-Meir 1974). Factors affecting decomposition and nutrient turnover are therefore of particular interest in deserts.

Mineralization and decomposition of litter are due primarily to bacteria and fungi (Seastedt 1984), while soil fauna are seen as regulators of the rate of decomposition and nutrient flow rather than direct movers of energy (Chew 1974). Since microbial decomposition of litter and wood at or near the soil surface is limited to short periods when this layer is moist, detritivorous arthropods (i.e. millipedes, nematodes, mites and termites) may play a particularly important role before and between microbial and fungal decomposition in desert ecosystems (Noy-Meir 1974). Indeed, when micro-arthropods were eliminated from soil in the Chihuahuan Desert, decomposition of litter was significantly reduced (Whitford, Repass, Parker & Elkins 1982).

Although an increasing interest has been shown in the soil fauna of deserts (Wallwork 1982), work has been restricted mainly to North American and Australian deserts. The soil fauna of the Namib Desert is poorly known and studies have been largely of a taxonomic nature (Coineau & Theron 1983), concerned with specific groups (Wallwork in prep.) or restricted to the dune sea (Coineau & Seely 1982). Before assessing the importance of micro-arthropods in the decomposition cycle it is necessary to establish the identities and relative abundances of the component groups (Franco, Edney & McBrayer 1979). As an introduction to the soil micro-fauna of the gravel plains in the Namib Desert, the micro-arthropod community associated with *Welwitschia mirabilis* plants was investigated. In American deserts highest densities and diversities of micro-arthropods are associated with shrubs where litter accumulates (Santos & Whitford 1983) and micro-arthropod densities are directly correlated with amounts of surface litter (Santos, Depree & Whitford 1978). *Welwitschia mirabilis* acts as a 'litter trap', the large straplike leaves curl down to the ground and collect large quantities of litter below them (Figure 1). I investigated the micro-fauna found in litter collected around *Welwitschia* and in the soil beneath the plants. In particular I asked the following questions:

(i) Does the soil below *Welwitschia* plants harbour more micro-arthropods than soil of nearby unvegetated areas?

(ii) What is the composition of the soil fauna and the relative abundance of the various groups and how do these compare with other deserts?

(iii) Does the structure of the micro-fauna community change with geographic locality of the plants?

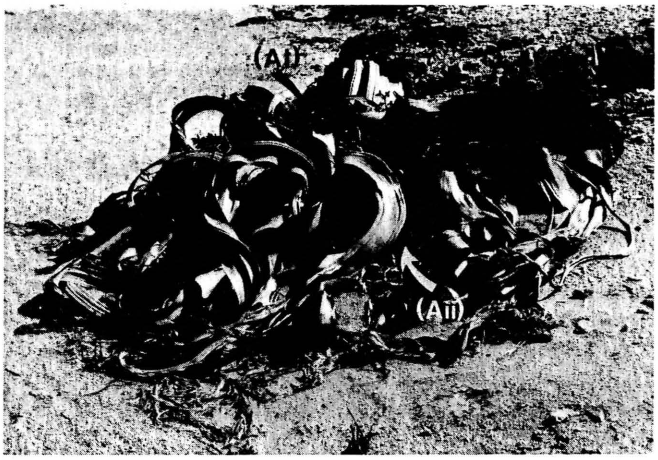

Figure 1 A male *Welwitschia mirabilis* showing litter in the stem depression [A(i)] and litter below the leaves [A(ii)].

Materials and Methods

Soil and litter samples were collected from *Welwitschia* plants at four localities on the Namib gravel plains (Figure 2). Samples were taken from the following positions at each plant:

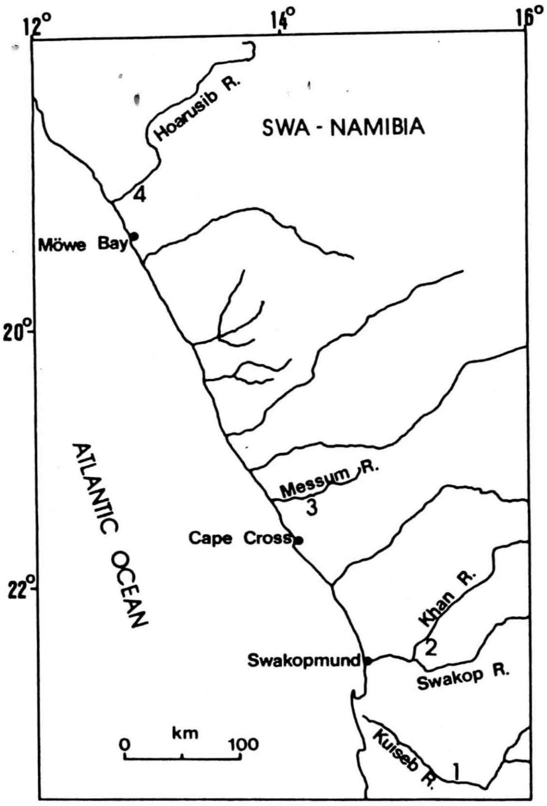

Figure 2 Geographic position of study sites. 1 = Welwitschia Wash, 2 = Swakopmund Fläche, 3 = Messum River, 4 = Northern Namib.

A — approximately one litre of litter was collected from
A(i) the depression in the *Welwitschia* stem
A(ii) under the *Welwitschia* leaves;

B — one litre of soil (or all the soil if less than one litre was present) was taken from the depression of the *Welwitschia* stem;

C — a core of soil, 16 cm deep and 15,5 cm in diameter, was taken under the *Welwitschia* plant close to the stem;

D — a core of soil, 16 cm deep and 15,5 cm in diameter, was taken 3 m south of the plant in an unvegetated area.

Samples were taken from five female and five male plants at Welwitschia Wash and from three female and three male plants at the other study sites. Samples were collected between 09h00 and 12h00 at Welwitschia Wash, Swakopmund Fläche and the Northern namib and between 15h00 and 18h00 at the Messum River. All sampling took place between 20 – 29 January, 1983.

Samples were kept in sealed plastic bags in a cool place. Within 40 h of collection, litter samples (A) were sieved to separate most of the soil from the litter, and then extracted for 96 h on Tullgren funnels using 60 W light bulbs. Animals were collected in 70% alcohol. The litter was then oven dried at 70°C for five days and weighed.

Soil from the litter samples was weighed and processed in a similar manner to soil samples B – D. Soil samples were processed within four days of collection. Each sample was well mixed and 500 ml removed for processing. In the case of litter soil, the entire sample was used. Micro-arthropods were extracted from soil samples using the grease film extraction method (Aucamp & Ryke 1964) as modified by Coineau (in prep.). In the modified technique, micro-arthropods were washed off the vaseline-greased slides using a fine paintbrush and xylol. Samples were then centrifuged, the liquid drawn off and replaced by 100% alcohol; this procedure was repeated using 100%, 90% and 70% alcohol.

Where possible the extracted micro-fauna were sorted into families. Densities were expressed as number/100 g sample for litter (A), number/500 ml soil for B samples and number/m^2 for C and D samples.

Results and Discussion

Soil in unvegetated areas supported a less numerous and less diverse fauna than soil below *Welwitschia* plants (Tables 1 and 2). Tarsonemid mites were the only arthropod present at all sites in unvegetated soils, and no more than four families of mites were present at any one site. There were significantly fewer micro-arthropods in unvegetated soil than in soil below *Welwitschia* plants (Mann-Whitney *U* test, $p < 0{,}001$ for Swakopmund Fläche, Messum River and Welwitschia Wash; $p < 0{,}02$ for Northern Namib). Santos *et al.* (1978) found a direct correlation between micro-arthropod densities and surface litter accumulation in North American deserts. Surface litter is thought to enhance water retention and to moderate surface temperatures in the upper 20 cm of soil; factors which promote micro-arthropod growth. The microclimate below *Welwitschia* litter was found to be more equable than nearby exposed areas (Marsh in prep.).

Micro-arthropod densities reported in this study varied considerably within and between sites (Tables 1 – 4). Total micro-arthropod densities for samples in which tarsonemids were dominant were far in excess of densities reported for other deserts and more in line with forest and grassland ecosystems; in the other samples, however, densities fell within the range reported for other deserts (Table 5).

As in other deserts (Franco *et al.* 1979; Wallwork 1982) mites were the numerically dominant micro-arthropod, constituting at least 85% of the micro-fauna at Welwitschia Wash, the Messum River and the Northern Namib; at Swakopmund Fläche, however, Collembola dominated the soil fauna below *Welwitschia* plants and were numerically abundant in stem soil and litter (Figure 3). Collembola dominate the soil fauna in Australian deserts (Greenslade 1981) and have been recorded in low numbers from North American deserts (Franco *et al.* 1979; Santos *et al.* 1978). Collembola have the ability to undergo anhydrobiosis and certain collecting techniques (notably the use of Tullgren funnels) would not extract Collembola in inactive forms (Greenslade 1981, 1982; Greenslade & Greenslade 1983). Greenslade (1982) found increased numbers of Collembola after wetting litter in Australian deserts and in New Mexico, Whitford, Freckman, Elkins, Parker, Parmalee, Phillips & Tucker (1981) found that litter was dominated by Collembola one hour after wetting although no Collembola were extracted from dry litter controls. Coineau (unpublished data) collected *Welwitschia* litter from the Messum River in May 1983 and extracted 1 290 Collembola from 1,5 kg female plant litter and 1 000 Collembola from 1,5 kg male plant litter two weeks after wetting the litter. In the present study, only 2 Collembola were found in an equivalent amount of female litter and no Collembola were found in male litter at the Messum River. Collembola, in inactive forms (either anhydrobiotic or as drought resistant eggs) may be present in large numbers in *Welwitschia* litter. The large number of Collembola collected at Swakopmund Fläche may have been due to frequent heavy fogs or a recent rainfall event. Unfortunately meteorological records are not kept in this area.

D

Table 1 Densities (×10^{-2})m^{-2} of various micro-arthropod taxa in soil of unvegetated areas (mean densities ($\bar{X}$) ± standard errors (*SE*) are given for each group)

	Welwitschia Wash	Swakopmund Fläche	Messum River	Northern Namib
Micro-arthropod group	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*
Mites				
Prostigmata				
Tarsonemidae	8,8 ± 4,8	0,7 ± 0,7	0,3 ± 0,3	1,3 ± 0,7
Nanorchestidae	–	–	–	1,3 ± 0,7
Raphignathidae	–	–	–	–
Tydeidae	–	–	–	0,3 ± 0,3
Bdellidae	–	–	–	–
Neophyllobiidae	–	–	–	–
Others[a]	–	–	–	–
Cryptostigmata				
Oribatulidae	0,2 ± 0,2	–	0,3 ± 0,3	–
Haplochthonius	–	–	–	–
Cosmochthonius	–	0,3 ± 0,3	–	–
Palaeacaridae	–	–	–	–
Astigmata				
Acaridae	–	0,3 ± 0,3	–	0,3 ± 0,3
Mesostigmata	–	–	–	–
Other arthropods				
Pseudoscorpionidae	–	–	–	–
Collembola	–	–	–	0,2 ± 0,2
Thysanura	–	–	–	–
Psocoptera	–	–	–	–
Thysanoptera	–	–	–	–
Coccidae	–	–	–	–
Insect larvae	–	–	–	0,2 ± 0,2
Polyxenidae	–	–	–	–
Total mites	9,0 ± 4,7	1,3 ± 0,8	0,7 ± 0,7	3,2 ± 1,5
Total arthropods	9,0 ± 4,7	1,3 ± 0,8	0,7 ± 0,7	3,6 ± 1,5

[a] Caeculidae, Smarididae, Cunaxidae, Trombidiidae, Cheyletidae, Anystidae

C

Table 2 Densities (×10^{-2})m^{-2} of various micro-arthropod taxa in soil below *Welwitschia* plants (mean densities ($\bar{X}$) ± standard errors (*SE*) are given for each group)

	Welwitschia Wash	Swakopmund Fläche	Messum River	Northern Namib
Micro-arthropod group	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*
Mites				
Prostigmata				
Tarsonemidae	1452,7 ± 959,3	12,6 ± 8,6	152,7 ± 100,0	3,4 ± 1,3
Nanorchestidae	–	1,4 ± 1,1	0,7 ± 0,4	8,4 ± 7,2
Raphignathidae	0,6 ± 0,3	1,3 ± 1,0	1,7 ± 1,3	0,7 ± 0,7
Tydeidae	–	1,7 ± 1,0	0,7 ± 0,7	–
Bdellidae	–	–	1,2 ± 0,7	0,3 ± 0,3
Neophyllobiidae	0,2 ± 0,2	–	–	–
Others[a]	0,2 ± 0,2	1,1 ± 0,7	2,7 ± 1,2	–
Cryptostigmata				
Oribatulidae	0,8 ± 0,4	3,8 ± 1,1	5,5 ± 3,3	1,0 ± 0,7
Haplochthonius	1,2 ± 0,9	1,2 ± 0,9	3,2 ± 1,6	–
Cosmochthonius	0,4 ± 0,4	–	1,0 ± 1,0	1,2 ± 1,0
Palaeacaridae	–	–	0,5 ± 0,4	–
Astigmata				
Acaridae	0,8 ± 0,8	0,9 ± 0,4	0,5 ± 0,4	0,9 ± 0,6
Mesostigmata	–	0,3 ± 0,3	–	–
Other arthropods				
Pseudoscorpionidae	–	2,2 ± 1,2	–	0,3 ± 0,3

Table 2 Continued

	Welwitschia Wash	Swakopmund Fläche	Messum River	Northern Namib
Micro-arthropod group	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*
Collembola	0,2 ± 0,2	151,6 ± 138,2	0,3 ± 0,3	0,9 ± 0,4
Thysanura	–	–	–	–
Psocoptera	–	0,9 ± 0,9	0,2 ± 0,2	–
Thysanoptera	–	–	–	–
Coccidae	–	–	–	–
Insect larvae	–	–	–	–
Polyxenidae	–	–	–	–
Total mites	1456,9 ± 959,5	24,3 ± 8,1	170,3 ± 100,5	15,9 ± 7,2
Total arthropods	1457,1 ± 959,3	179,0 ± 13,9	170,8 ± 100,4	17,1 ± 7,2

[a] Caeculidae, Smarididae, Cunaxidae, Trombidiidae, Cheyletidae, Anystidae

Table 3 Densities of various micro-arthropod taxa in 500 ml soil taken from *Welwitschia* stems (mean densities ($\bar{X}$) ± standard errors (*SE*) are given for each group)

⑧

	Welwitschia Wash	Swakopmund Fläche	Messum River	Northern Namib
Micro-arthropod group	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*
Mites				
Prostigmata				
Tarsonemidae	493,7 ± 194,4	158,7 ± 103,0	12,5 ± 6,6	145,8 ± 91,2
Nanorchestidae	0,2 ± 0,2	0,3 ± 0,2	0,8 ± 0,5	1,8 ± 1,3
Raphignathidae	0,6 ± 0,3	1,3 ± 0,9	2,3 ± 1,3	1,5 ± 1,2
Tydeidae	1,5 ± 1,0	6,2 ± 3,8	3,7 ± 2,7	–
Bdellidae	–	–	1,0 ± 1,0	0,2 ± 0,2
Neophyllobiidae	–	–	–	–
Others[a]	–	–	1,0 ± 1,0	–
Cryptostigmata				
Oribatulidae	1,1 ± 0,5	0,5 ± 0,3	1,0 ± 0,4	0,5 ± 0,5
Haplochthonius	1,3 ± 0,5	4,8 ± 3,1	2,0 ± 1,6	1,5 ± 1,0
Cosmochthonius	2,2 ± 1,5	0,2 ± 0,2	0,2 ± 0,2	0,5 ± 0,5
Palaeacaridae	–	–	0,3 ± 0,2	–
Astigmata				
Acaridae	0,3 ± 0,2	0,2 ± 0,2	0,3 ± 0,2	0,5 ± 0,34
Mesostigmata	–	–	0,3 ± 0,3	–
Other arthropods				
Pseudoscorpionidae	0,1 ± 0,1	0,5 ± 0,5	1,0 ± 1,0	–
Collembola	12,2 ± 11,9	103,5 ± 90,0	0,7 ± 0,7	0,2 ± 0,2
Thysanura	–	–	–	–
Psocoptera	–	–	0,5 ± 0,5	–
Thysanoptera	–	–	–	0,2 ± 0,2
Coccidae	–	–	–	–
Insect larvae	–	0,5 ± 0,3	–	0,2 ± 0,2
Polyxenidae	–	–	–	–
Total mites	501,0 ± 195,3	172,2 ± 105,0	25,4 ± 9,7	152,5 ± 93,5
Total arthropods	513,3 ± 192,0	276,7 ± 190,2	27,6 ± 10,1	153,1 ± 95,0

[a] Caeculidae, Smarididae, Cunaxidae, Trombidiidae, Cheyletidae, Anystidae

Prostigmatids were the dominant order of mite at all four localities, comprising 12 of the 18 families found. The remainder of the mites comprised four cryptostigmatid families, one family of Astigmata and a few unidentified mesostigmatid mites (Tables 1 – 4). Although cryptostigmatid and astigmatid mites occurred in low numbers they were found at all study sites and in all sampling positions (Tables 2 – 4). The dominance of prostigmatid mites within the acari is consistent with findings in other deserts where prostigmatids are dominant in arid soils with a high mineral content (Elkins & Whitford 1982; Santos *et al.* 1978; Santos & Whitford 1981; Wood 1971).

Tarsonemids, minute fungivorous prostigmatid mites, were abundant at most study sites and were often the dominant group of micro-arthropods associated with *Welwitschia*. Tarsonemids are also a dominant micro-arthropod group in some North American desert ecosystems (Elkins & Whitford 1982; Santos & Whitford 1983) where they appear to be important regulators in the later stages of decomposition (Whitford, Freckman, Parker, Schaefer, Santos & Steinberger

A

Table 4 Densities of various micro-arthropod taxa in 200 g *Welwitschia* litter [100 g litter from stem + 100 g litter from under plant] (mean densities ($\bar{X}$) ± standard errors (*SE*) are given for each group)

	Welwitschia Wash	Swakopmund Fläche	Messum River	Northern Namib
Micro-arthropod group	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*	$\bar{X}$ ± *SE*
Mites				
Prostigmata				
Tarsonemidae	201,2 ± 147,0	0,9 ± 0,5	8,8 ± 3,5	1,0 ± 0,3
Nanorchestidae	–	4,7 ± 1,6	2,4 ± 1,1	7,1 ± 6,7
Raphignathidae	0,6 ± 0,3	9,2 ± 1,7	17,4 ± 9,6	1,2 ± 0,8
Tydeidae	0,2 ± 0,1	49,6 ± 18,7	19,8 ± 17,9	0,3 ± 0,2
Bdellidae	0,6 ± 0,3	0,2 ± 0,2	7,7 ± 1,7	0,8 ± 0,3
Neophyllobiidae	0,3 ± 0,3	2,8 ± 1,4	1,1 ± 0,6	0,2 ± 0,2
Others[a]	0,1 ± 0,1	1,5 ± 0,6	1,2 ± 0,4	0,3 ± 0,2
Cryptostigmata				
Oribatulidae	2,6 ± 0,4	11,2 ± 4,6	17,3 ± 8,4	3,9 ± 2,5
Haplochthonius	1,1 ± 0,5	7,8 ± 4,6	1,2 ± 0,5	0,2 ± 0,1
Cosmochthonius	0,1 ± 0,1	–	0,8 ± 0,4	0,7 ± 0,5
Palaeacaridae	–	2,9 ± 2,8	0,1 ± 0,05	–
Astigmata				
Acaridae	0,5 ± 0,2	2,0 ± 0,4	1,9 ± 0,9	1,0 ± 0,7
Mesostigmata	–	–	0,5 ± 0,5	–
Other arthropods				
Pseudoscorpionidae	0,2 ± 0,1	2,6 ± 1,5	0,8 ± 0,3	–
Collembola	0,6 ± 0,5	29,0 ± 23,5	0,1 ± 0,03	–
Thysanura	–	0,4 ± 0,3	0,7 ± 0,3	0,1 ± 0,1
Psocoptera	0,8 ± 0,4	8,2 ± 2,5	3,8 ± 1,6	1,4 ± 1,4
Thysanoptera	1,2 ± 0,9	–	0,1 ± 0,0	0,2 ± 0,2
Coccidae	0,2 ± 0,2	0,3 ± 0,3	6,2 ± 4,2	0,3 ± 0,3
Insect larvae	0,1 ± 0,1	2,4 ± 0,7	2,1 ± 0,8	0,1 ± 0,1
Polyxenidae	–	–	–	0,9 ± 0,9
Total mites	207,0 ± 147,4	93,9 ± 24,0	79,4 ± 19,0	16,7 ± 10,9
Total arthropods	210,0 ± 141,0	136,8 ± 35,0	93,2 ± 38,0	19,7 ± 8,6

[a] Caeculidae, Smarididae, Cunaxidae, Trombidiidae, Cheyletidae, Anystidae

Table 5 Comparative densities of soil arthropods in various environments

Habitat	Description	Density (m^{-2})	Source
Various forest soils	Total arthropods	154 000 – 834 500	Various authors in Wallwork (1970)
Lowland grassland	Acari and Collembola	32 000 – 298 000	Wallwork (1970)
Australian desert	Micro-arthropods	2 000 – 3 000	Wood (1971)
Chihuahuan Desert USA	Micro-arthropods:		Santos *et al.* (1978)
	under shrubs	3 100	
	unvegetated area	146	
New Mexico USA — gypsum sand dunes (interdune area)	Micro-arthropods:		Santos & Whitford (1983)
	under shrubs	18 345 (Max Oct)	
	open spaces	89 (Min July)	
Southern Mojave Desert USA	Micro-arthropods:		Wallwork (1972)
	under Juniper trees	1 600	
Northern Mojave Desert USA	Micro-arthropods:		Franco *et al.* (1979)
	around perennial plants	12 400 (Max Dec) 1 200 (Min July)	
Namib Desert Namibia	Micro-arthropods:		Present study
	under *Welwitschia*	1 495 – 823 357 (WW) 522 – 87 403 (SF) 600 – 62 468 (MR) 0 – 4 722 (NN)	
	Unvegetated areas	70 – 900	

NN = Northern Namib, WW = Welwitschia Wash, SF = Swakopmund Fläche, MR = Messum River

1983). Nanorchestids, the other fungivorous prostigmatids present in *Welwitschia* samples, were only dominant in the Northern Namib samples, where tarsonemid numbers were low. The nanorchestid, *Speleorchestes*, is widespread and

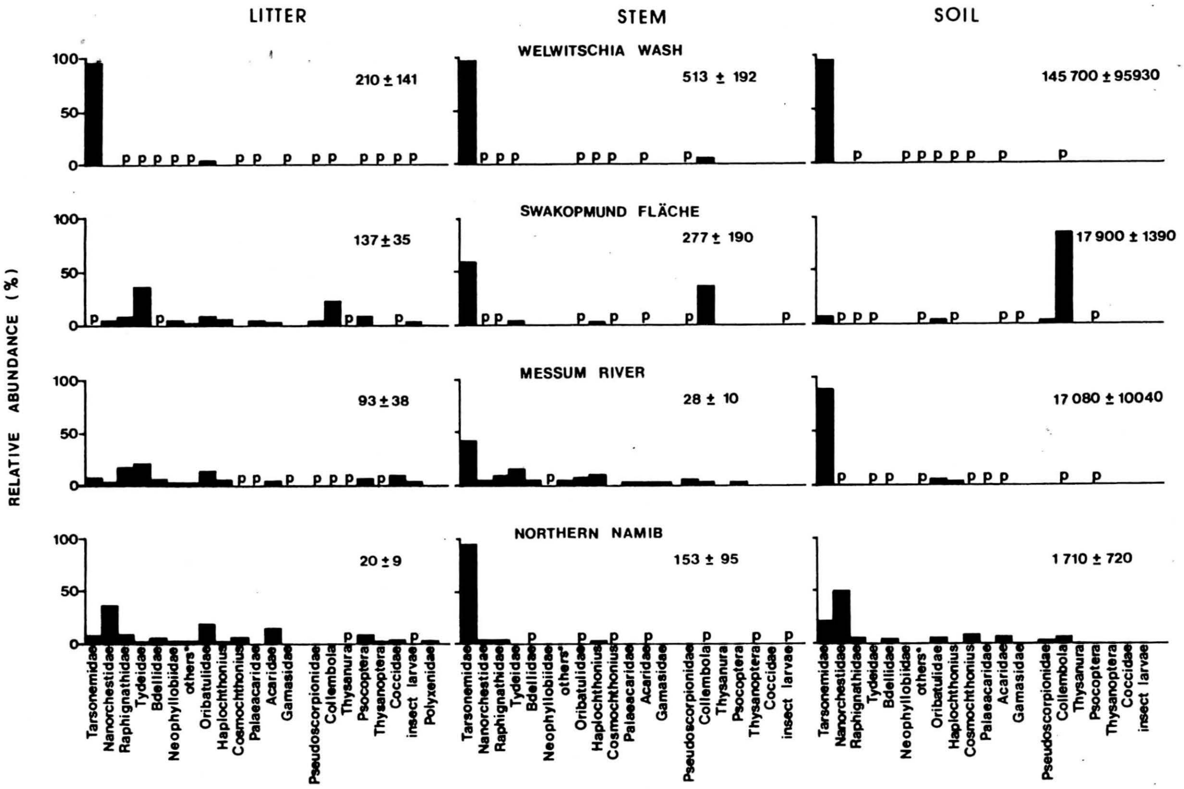

Figure 3 Relative abundance of micro-arthropod taxa at four study sites. Mean density ± *SE* of total micro-arthropods is given for: litter (number 200 g^{-1} litter), stem soil (number 500 ml^{-1} soil) and soil below *Welwitschia* plants (number m^{-2}). 'p' indicates relative abundance < 1%. *Others includes the following prostigmatid families: Caeculidae, Trombidiidae, Smarididae, Cheyletidae, Cunaxidae and Anystidae.

abundant in Australian deserts (Wood 1971) and has been found in all North American hot deserts (Santos & Whitford 1983). The predatory prostigmatids found in this study are also common to North American deserts (Franco *et al.* 1979; Santos & Whitford 1981; Wallwork 1982). Tydeid mites were often the most numerous predatory mite in *Welwitschia* litter samples. In North American deserts, these predatory mites play an important role in the initial stages of decomposition by preying upon and thereby regulating the numbers of bacteriophagous nematodes (Santos, Phillips & Whitford 1981; Santos & Whitford 1981). Nematodes in arid soil are generally anhydrobiotic (Freckman & Mankau 1977) and probably not preyed upon in this form. Large numbers of nematodes have been extracted from soils below *Welwitschia* plants (Procter 1982) and may be preyed upon by tydeid mites when they become active during moist conditions.

There appears to be a reciprocal relationship between the relative abundance of prostigmatid and cryptostigmatid mites depending on the nature of the soil (Wallwork 1982). Cryptostigmatid mites are normally abundant in moist organic soils but certain groups have the ability to colonize arid areas; *Haplochthonius* and *Cosmochthonius* are two such groups which were found in the present study and occur in many deserts and arid regions throughout the world. These mites are small and delicate and their cuticles are not heavily sclerotized. They appear, however, to have some form of drought resistance since they are not uncommon in above-ground habitats (Wallwork 1982) and were found in litter samples in this study.

Mesostigmatid mites thrive in moist organic soils and are not usually abundant in deserts (Wallwork 1982). They were rare in the present study. Although astigmatid mites are generally not abundant in the soil fauna, members of this order often occur in dry environments (Wallwork 1972) and acarids, the only astigmatids which occurred in *Welwitschia* samples, are locally abundant in certain habitats of the Chihuahuan desert (Wallwork 1982).

In *Welwitschia* soil and litter, mites and Collembola constituted at least 85% of the microfauna, the remainder comprised pseudoscorpions, various insect groups and, at the Northern Namib site, polyxenid diplopods. None of these remaining groups made up more than 7% of the total fauna.

It has been suggested that relatively few groups of micro-arthropods are adapted to arid conditions; for instance in the deserts of south-western United States only a few varieties of mites occur, and these are common to most deserts (Elkins & Whitford 1982; Franco *et al.* 1979). The results of this study support this suggestion, since the same taxa of micro-arthropods occurred at all four sites in the Namib and most of these taxa have been found in North American and Australian deserts.

Owing to the large variation in micro-arthropod numbers between *Welwitschia* plants at each study site, it was difficult to ascertain whether the various taxa have habitat preferences favouring male rather than female plants or litter to soil. Nevertheless certain trends were apparent in this study. I tested for differences in density of the more common micro-arthropod groups (Tarsonemidae, Oribatulidae, Tydeidae, Bdellidae, Raphignathidae, Haplochthonius, Psocoptera and Collembola) between stem litter and litter below plants. Raphignathidae were significantly more numerous in litter below plants than in stem litter ($p < 0,02$, Wilcoxon matched pairs signed-rank test) and Caeculidae and Anystidae were only found in litter samples and not in soil samples; similarly, Santos & Whitford (1981) found that these latter two predatory groups were found only in surface litter and not in buried litter and Raphignathidae only in buried litter.

Litter below *Welwitschia* plants consists largely of the previous season's reproductive structures. The nature of litter collected at male and female plants will therefore differ, and nutritional and structural differences in litter may affect the composition of the micro-fauna. No group of micro-arthropods was associated only with male or female plants; however, at Swakopmund Fläche there were significantly more tarsonemids in stem soil and soil below male plants than at female plants ($p < 0{,}05$, Mann-Whitney *U* test). Furthermore, at the Northern Namib site, tarsonemids were significantly more numerous in the stem soil of male plants than female plants ($p < 0{,}05$, Mann-Whitney *U* test). A further statistical test was performed on the data from all sampling positions at all sites and tarsonemids were then found to be significantly more numerous in samples from male plants than in those from female plants ($p < 0{,}02$, Wilcoxon matched pairs signed-rank test).

Although the same taxa of micro-arthropod were present at most study sites, their densities and relative abundances varied considerably with geographic locality. Population densities of soil micro-arthropods appear to fluctuate in response to factors such as the quantity of litter present; moisture; long-term rainfall of the area and season of the year (Steinberger & Whitford 1984; Steinberger, Freckman, Parker & Whitford 1984). Since long term weather data at the four study sites in the Namib are scanty and differences in soil and litter moisture and litter quantities are unknown, the nature and importance of factors affecting distribution and abundance of micro-arthropods in the Namib cannot be resolved until further research is carried out. The relatively low numbers of micro-arthropods collected in the Northern Namib, however, may be due to the smaller size of plants at this site, which resulted in a significantly shallower stem soil ($p < 0{,}005$, Mann-Whitney *U* test) than at the other sites, and a smaller collection area for litter below the plants.

Conclusions

Steinberger *et al.* (1984) emphasize that the energy and nutrient source (litter) of desert soil fauna is the principal regulator of population size rather than water. Noy-Meir (1973, 1974), however, proposes that most desert ecosystems are primarily regulated by rainfall. Biologists (Santos, Elkins, Steinberger & Whitford 1984; Steinberger *et al.* 1984; Wallwork, Kamill & Whitford 1984; Whitford *et al.* 1983) investigating micro-arthropods in North American deserts have, however, suggested that the 'pulse-reserve' paradigm proposed by Noy-Meir (1973, 1974) does not apply to desert soil micro-arthropods. Certain taxa appear to be relatively independent, above a certain moisture threshold, of environmental constraints (Santos *et al.* 1984; Whitford *et al.* 1983). Furthermore, fluctuations in population densities are largely seasonal and mites do not respond to artificial watering outside of the 'predictable' rainy season (Steinberger & Whitford 1984; Wallwork *et al.* 1984). The area of the Namib Desert in which the present study was carried out, receives a substantially lower rainfall (< 100 mm p.a.) than North American deserts. Furthermore, rainfall is patchy in distribution and unpredictable (Seely 1978). A major, and more predictable, source of moisture for many Namib animals and plants is advective fog which may be blown inland at night (Seely 1984). However, soil moisture below *Welwitschia* plants did not increase following fogs (Marsh in prep.) and it remains speculative whether micro-arthropods associated with *Welwitschia* obtain fog moisture. Owing to the lower, more unpredictable and different nature of precipitation in the Namib, micro-arthropods in this desert may react more opportunistically to moisture inputs than their North American counterparts. Coineau (unpublished data) found large numbers of oribatid nymphs in samples two weeks after watering *Welwitschia* litter from the Messum River, yet no nymphs and relatively few adult oribatids were found at this site in the present study. Clearly, further experimental work is required to elucidate whether micro-arthropod population densities fluctuate seasonally in the Namib Desert or if they respond opportunistically to any moisture input as the pulse-reserve model (Noy-Meir 1973, 1974) would suggest.

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