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Spatial and temporal distribution of cyanobacterial soil crusts in the Kalahari: Implications for soil surface properties

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Abstract

Localised patterns of erosion and deposition in vegetated semi-arid rangelands have been shown to influence ecological change and biogeochemical cycles. In the flat, vegetated Kalahari rangelands of Southern Africa the factors regulating erodibility of the fine sand soils and the erosivity of wind regimes require further investigation. This paper reports on the spatial and temporal patterns of cyanobacterial soil crust cover from ten sites at five sampling locations in the semi-arid Kalahari and discusses the likely impact on factors regulating surface erodibility and erosivity.

Cyanobacterial soil crust cover on Kalahari Sand varied between 11% and 95% of the ground surface and was higher than previously reported. Cover was inversely related to grazing with the lowest crust cover found close to boreholes and the highest in the Game Reserve and Wildlife Management Zone. In grazed areas, crusts form under the protective canopies of the thorny shrub *Acacia mellifera*. Fenced plot data showed that crusts recover quickly from disturbance, with a near complete surface crust cover forming within 15 months of disturbance. Crust development is restricted by burial by wind blown sediment and by raindrop impact.

Crusts had significantly greater organic matter and total nitrogen compared to unconsolidated surfaces. Crusts also significantly increased the compressive strength of the surface (and thus decreased erodibility) and changed the surface roughness. Establishing exactly how these changes affect aeolian erosion requires further process-based studies. The proportion of shear velocity acting on the surface in this complex mixed bush–grass–crust environment will be the key to understanding how crusts affect erodibility.

Keywords: Cyanobacterial soil crusts; Erodibility; Surface roughness; Cohesivity; Kalahari

1. Introduction

The importance of vegetation to geomorphological processes in arid and semi-arid environments has been well-documented (e.g., Thornes, 1990; Bullard, 1997), especially in relation to aeolian erosion (Tsoar and Møller, 1986; Lancaster and Baas, 1998). In the Kalahari region of Southern Africa, geomorphological research has focused on the link between vegetation and dune mobility in the arid southwest of Botswana (Wiggs et al., 1994, 1995) and on the influence of shrubs on nebkha formation in the mixed farming areas of the dry sub-humid Molopo Basin (Dougill and Thomas, 2002). There is, however, less information on aeolian erosion

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processes in the more extensive semi-arid savanna rangelands that typify much of Botswana, Eastern Namibia and Northern South Africa and on how surface erodibility is affected by biological soil crusts. There are several reports on the occurrence of biological soil crusts in this region (Skarpe and Henriksson, 1987; Aranibar et al., 2003; Dougill and Thomas, 2004) but little information on the implications for surface erodibility. Improved understanding of aeolian erosion processes will require advances in our assessment of both surface erodibility (the degree to which a surface is susceptible to erosion) and the erosivity (the potential to erode a surface) of wind regimes.

Biological soil crusts are present in all arid and semi-arid regions (Belnap and Lange, 2003) and form from the association of soil particles and organic matter with varying proportions of cyanobacteria, algae, lichens and mosses (Belnap et al., 2003). They have been shown to reduce surface erodibility as filaments of cyanobacterial sheath material entangle surface particles and create a crust that is more resistant to entrainment than the layers below (e.g., Belnap and Gillette, 1997, 1998). Assessing the impact of crusts on surface erodibility and of crusts and vegetation on erosivity are both problematic. Erodibility is a difficult property to quantify (Geeves et al., 2000) as it depends on a variety of inter-related textural, mineralogical, chemical, hydrological and biological characteristics that vary in space and time. Shao et al. (1996) suggest one of the main limitations of contemporary wind erosion models is their inability to incorporate the evolution of surface soil conditions during wind erosion events. There is, therefore, a need to improve the information available on soil surface conditions, such as cohesive strength and roughness that affect erodibility to enable wind erosion models to be improved to incorporate the evolution of soil surface conditions (Sokolik and Toon, 1996; Shao and Leslie, 1997; Chappell et al., 2005). Similarly, improved assessments of erosivity of wind regimes and in particular how this is affected by spatial variations in the nature of vegetation cover at a landscape scale and soil surface roughness on a local scale remains an area of active research (Wiggs, 1997).

Fundamental to understanding the impact cyanobacterial soil crusts have on erodibility is a comprehension of their spatial distribution and temporal variation. Several factors are recognised as influencing crust distribution and development, including substrate, vegetation type and cover, and disturbance levels (Belnap et al., 2003) and each is considered in this study. It has been shown that vegetation and biological crust cover are inversely proportional due to competition for light (Malam Issa et al., 1999) and nutrients (Harper and Belnap, 2001). Trampling damages biological crust surfaces and consequently in grazed areas crust cover is restricted in its spatial cover and longevity. Indeed, Zaady and Bouskila (2002) describe disturbance as the key factor in determining biological crust development in areas where physical conditions are relatively constant. Given the spatial homogeneity of the Kalahari, in terms of altitude, relief and surface water (Thomas and Shaw, 1993), it is reasonable to impart a significant role to grazing disturbances in affecting the distribution of cyanobacterial soil crusts. In this context, Berkeley et al. (2005) have shown that the canopies of woody shrubs represent quasi-discrete environments where crusts can develop despite high levels of disturbance, thus displaying the importance of localised spatial heterogeneity to improved assessments of surface erodibility. Analysis of crust distribution therefore needs to account for the role of different land uses at a landscape scale; differences in grazing intensity at a farm scale; and the relationship between crusts and vegetation at a local scale.

Dougill and Thomas (2004) have documented a biological soil crust cover of between 19% and 40% at a range of regularly disturbed, communal grazing sites on Kalahari Sands. Crusts were typically 3–4 mm thick. Three morphologically distinct crusts were identified: a weakly consolidated crust with no surface discolouration (type 1); a more consolidated crust with a black or brown speckled surface (type 2); and a crust with a bumpy surface with an intensely coloured black/brown surface (type 3). Preliminary taxonomic analyses using light microscopy suggest that the crusts comprise only a few species of cyanobacteria (mainly *Microcoleus* and *Sytonema*) (Thomas and Dougill, 2006). There is no evidence of more diverse assemblages or lichen crusts forming in this environment. In this regard, the Kalahari appears different to many other drylands where with low disturbance levels crusts become dominated by lichens and mosses (Belnap and Lange, 2003).

This paper reports on the impact of cyanobacterial soil crusts on the spatial and temporal patterns of soil surface properties from a range of locations in the semi-arid Kalahari and discusses their likely impact on surface erodibility. The objectives are

1. To determine the influence of grazing levels and vegetation communities on the distribution of soil crusts at a range of sites across the Kalahari.
2. To quantify recovery of cyanobacterial crust cover after removal of disturbance impacts.
3. To determine how different types of cyanobacterial crust affect soil surface nutrients, cohesive strength

and roughness as key factors affecting surface erodibility.

2. Study area

The Kalahari Sands are ancient wind-blown deposits and the youngest unit of the Kalahari Group that cover over 2.5 million km^2 of Southern Africa, including over 80% of Botswana (Thomas and Shaw, 1991). Kalahari Sand soils typically consist of over 95% fine sand-sized sediments and are predominantly deep, structureless and nutrient deficient (Dougill et al., 1998). The Kalahari includes areas of both active sediment movement and stable surfaces, with much research focusing on the importance of surface vegetation cover (Wiggs et al., 1994, 1995) and climate change (Thomas et al., 1997; Knight et al., 2004; Thomas et al., 2005) in affecting sediment mobility, notably in the arid south west of Botswana. The importance of soil surface characteristics, especially the development of biological soil crusts, has been largely overlooked. Preliminary research on crusts has focused on their role in affecting nitrogen cycling with a number of studies in the Kalahari rangelands of western Bostwana (Skarpe and Henriksson, 1987; Aranibar et al., 2003, 2004; Dougill and Thomas, 2004; Berkeley et al., 2005). All these studies focused on highly disturbed communal rangeland sites and have estimated crust covers of between 19% and 40%. No estimates exist of crust cover in lightly disturbed sites, such as National Parks or Wildlife Management Areas that still cover large tracts of the Kalahari and where crust cover can be expected to be greater.

Pastoralism in the Kalahari has only recently been made possible by boreholes that allow access to deep groundwater reserves (Sporton and Thomas, 2002). Concentrated grazing pressure close to the boreholes adds an environmental gradient to an otherwise relatively homogenous environment (Thomas and Shaw, 1993). This leads to localised sediment mobility in a spatially confined ‘sacrifice zone’ close to boreholes (Perkins and Thomas, 1993). This zone is typically followed by a more extensive ‘bush encroached zone’ of between 2 and 8 km radius where woody shrubs, typically *Acacia mellifera*, dominate (Dougill et al., 1999; Moleele et al., 2002). The role of localised patterns of erosion and deposition in contributing to bush encroachment in the Kalahari remains unknown. However, it is logical to suppose that if significant deposition of nutrient-enriched wind-blown fine sediment and organic material occurred under bush canopies that this could contribute to an ‘island of fertility’ effect that could explain the rate and extent of bush encroachment in grazed Kalahari rangelands (Hagos and Smit, 2005).

The Kalahari has a highly seasonal summer rainfall regime with very high inter-annual variability that increases with declining mean annual rainfall (Bhalotra, 1987). The study sites investigated here (Fig. 1) form a transect between Tsabong (ca. 300 mm mean annual rainfall; 45% inter-annual variability) and Okwa (ca. 400 mm mean annual rainfall; 40% inter-annual variability).

3. Research design and methods

3.1. Spatial distribution of soil crusts

Research was undertaken during July 2003, November 2004 and August 2005 at five locations on Kalahari Sands in the Kgalagadi and Ghanzi Districts in the south and west of Botswana (Fig. 1, Table 1A). These encompassed a range of grazing intensities from the lightly grazed National Park (Mabuasehube) and Wildlife Management Zone (Okwa) to more intensely grazed communal rangelands (Tshane, Tsabong and Draihoek). Multiple plots were assessed at Mabuasehube (two), Tshane (two) and Tsabong (four) to account

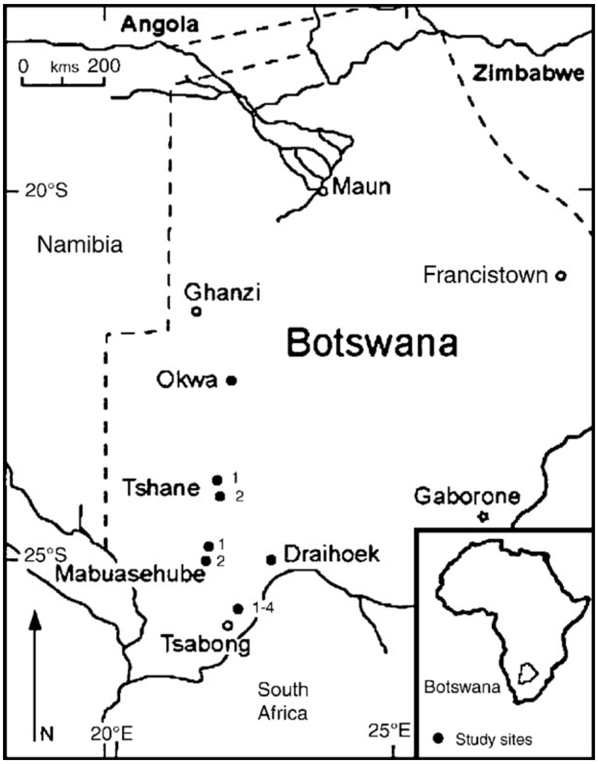

Fig. 1. Study site locations.

Table 1
Study site characteristics

(A) Vegetation cover, disturbance index and land use at each site

Site	Vegetation cover (%)		Disturbance index	Land use
	Shrubs	Grass		
Tshane 1 (T1)	27 (40)	2 (0.2)	13.2	Communal grazing
Tshane 2 (T2)	26 (40)	5 (6)	7.5	Communal grazing
Mabuasehube 1 (M1)	7 (23)	94 (20)	0.0	National Park
Mabuasehube 2 (M2)	1 (9)	17 (11)	0.1	National Park
Okwa WMZ (O1)	4 (19)	22 (22)	0.0	Wildlife Management Zone
Tsabong Mixed (Ts1)	22 (30)	–	1.6	Communal grazing
Tsabong Shrub Enc. (Ts2)	26 (28)	–	2.1	Communal grazing
Tsabong Pan (Ts3)	–	–	2.4	Pan on a commercial farm
Tsabong Sacrifice Zone (Ts4)	2 (12)	–	15.4	Water hole on a commercial farm
Draihoek Shrub Enc. (D1)	32 (44)	0.2 (0.9)	8.2	Communal grazing

(B) Percentage ground surface covered by each crust type and the amount of buried crust

Site	Cyanobacterial crust cover (%)				% of the unconsolidated surface that has buried crust below
	BC1	BC2	BC3	Total crust	
Tshane 1 (T1)	40	4	0	44 (36)	13 (24)
Tshane 2 (T2)	42	2	0	44 (38)	12 (24)
Mabuasehube 1 (M1)	75	10	1	86 (17)	1 (9)
Mabuasehube 2 (M2)	64	24	7	95 (8)	2 (12)
Okwa WMZ (O1)	80	5	1	86 (22)	5 (16)
Tsabong Mixed (Ts1)	26	39	2	68 (44)	19 (23)
Tsabong Shrub Enc. (Ts2)	24	36	4	64 (45)	17 (22)
Tsabong Pan (Ts3)	21	48	15	84 (29)	–
Tsabong Sacrifice Zone (Ts4)	11	0	0	11 (18)	11 (19)
Draihoek Shrub Enc. (D1)	55	8	1	64 (35)	–

$n=240$ 1-m^2 quadrats at each site for crust cover estimation; – = no data; standard deviation in parentheses.

for differences in vegetation community assemblages found at these locations. At each site, a representative 30 m × 30 m plot was demarcated for analysis of crust–vegetation distributions. Within each plot, measurements of crust cover were made using a series of 1 m × 1 m quadrats sampled at regular intervals of 2 m along fifteen 30-m transects aligned N–S such that a total of 240 quadrats were sampled at each site. Percentage cover was estimated for each cyanobacterial soil crust type (according to the classification system of Dougill and Thomas, 2004), unconsolidated soil and each vegetation species within each of the quadrats. At all sites except Draihoek and the Tsabong Pan, the proportion of the unconsolidated surface above a buried consolidated crust was assessed by probing under the surface to a depth of 5 cm with a thin wire. To visualise the relationship between vegetation and crust cover at sites with different grazing histories, the crust cover data were kriged and plotted using Surfer™ software.

Disturbance was quantified at each study site using counts of cattle track frequency and dung density. At each site, a 30 m × 30 m grid was established. The grid was crossed at 10-m intervals in two perpendicular directions (N–S and E–W). Cattle tracks and dung were counted along each of these gridlines, cattle tracks being defined as well-established ‘routes’, and a dung ‘count’ made of single or collections of dung pats within an arbitrary 0.5 m either side of the gridline. The data were used to produce an index of disturbance where disturbance index equals the number of cattle tracks × (number of dung pats × 0.05) (refer also to Dougill and Thomas, 2004; Berkeley et al., 2005).

3.2. Temporal changes in crust cover

Permanent monitoring plots were established to assess recovery of crust cover through time after the removal of disturbance impacts. Two 5 m × 5 m plots were established in August 2003 at a commercial farm near Tsabong, on severely disturbed soils close to a water point and farm compound where no crust cover was found. One plot was fenced to exclude all grazing animals and the other plot was left unfenced. The contrast between grazing intensity on the plots was not as marked as expected as cattle were removed from the farm shortly after plot establishment but the area was still disturbed by camels and game. Sixteen 1 m × 1 m quadrats were marked with pins in each plot and surveyed for crust type and vegetation cover in August 2003, November 2004 and August 2005.

3.3. Crusts and soil surface properties

3.3.1. Nutrient content

Extractable nutrient concentrations were measured within 24 h of sampling using a portable spectrophotometer. Extractions indicative of plant available NH_4^+–N and PO_4^{3}–P concentrations were determined according to the methods of Anderson and Ingram (1993). pH was determined using a portable probe after mixing with distilled water at a soil to water ratio of 1 g to 5 ml. Samples of all crust types (the upper few millimetres) and unconsolidated soil were air-dried prior to laboratory determination of organic matter and total N. Organic matter was determined using loss-on-ignition at 500 °C for 4 h (Rowell, 1994). Total N concentrations were determined following a Kjeldahl digestion (Anderson and Ingram, 1993).

3.3.2. Crust strength

A portable needle penetrometer was used to provide an estimate of the *in situ* surface strength of all crust types at 66 sites. The surface area of the needle was approximately 20 mm^2 and was positioned on the crust and gradual pressure applied until it failed. At each location the measurement was repeated three times and the mean value recorded. Penetrometer measurements encompass a range of soil surface properties including shear strength, friction between soil and metal and resistance to compression. McKenna Neuman and Maxwell (2002) used a laboratory-based needle penetrometer to model the breakdown of crusts in relation to the energy of impacting grains. They concluded the penetrometer gave a good approximation of the energy needed to break crusts by impacting grains during saltation and although not directly comparable to the equipment used in this study it is used to provide an indication of the likely crust resistance to entrainment.

3.3.3. Scanning electron microscopy

A JOEL 5600 LV secondary scanning electron microscope was used to capture images of the different crust types and unconsolidated surface sands. All samples were gold coated prior to analysis using a Polaron E5100 sputter-coating at 2.5 kV and 2 mA for 3 min producing coatings between 25 and 30 nm thick.

3.3.4. Surface roughness

Field measurements of soil surface roughness commonly employ a form of 'relief meter' (for example, Nash et al., 2003). The instrument used in this study comprised a stable frame onto which hung a 30 cm long adjustable bar through which 60 steel pins at 0.5 cm intervals were used to provide the profile of the surface. The bar was kept horizontal using a spirit level incorporated into the framework. Fifty three locations were sampled and at each site profiles taken in four orientations on each sampled surface. The profiles were used to provide an index of microtopography (based on analysis of mounds or depressions above a threshold value) and roughness (based on deviations of all measured pin heights from a '0' reference level). Distinct microtopography features were designated when the height of a mound, or depth of a depression was greater than 2 cm from the slope adjusted '0' reference level. A threshold value of 2 cm was chosen, due to the small number of sites at which any microtopography features above the 3 cm threshold adopted by Nash et al. (2003) were found. The high fine

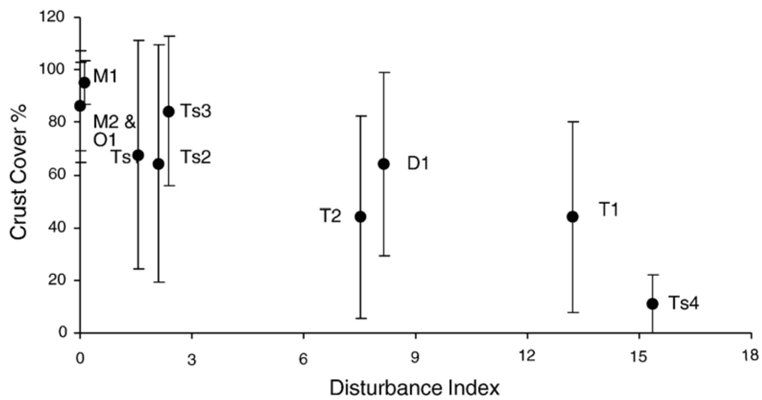

Fig. 2. Crust cover and disturbance index.

sand content of Kalahari soils and the lack of lichen or algal formation in Kalahari soil crusts explains why larger mounds or depressions are rare.

Three indices of microtopography were calculated on each of the four surfaces (unconsolidated soil, type 1, 2 and 3 crusts). These were (1) the sum of the absolute value of the depressions and mounds, (2) the frequency of depressions and mounds, and (3) the sum of the depressions and the sum of mounds. For each index, values are presented as an average for a single 30 cm transect to account for the different sample sizes on each surface. The mean heights of all deviations from the '0' reference level and the associated standard deviations were calculated for all transects and used to compare the mean roughness of each soil surface class.

3.3.5. Statistical analysis

Statistical analysis of differences between crust types in the means and distributions of all the variables was conducted using single factor ANOVA in SPSS™ where appropriate. A post hoc Scheffe's test, based on the *F*-ratio statistic, was used to test differences between

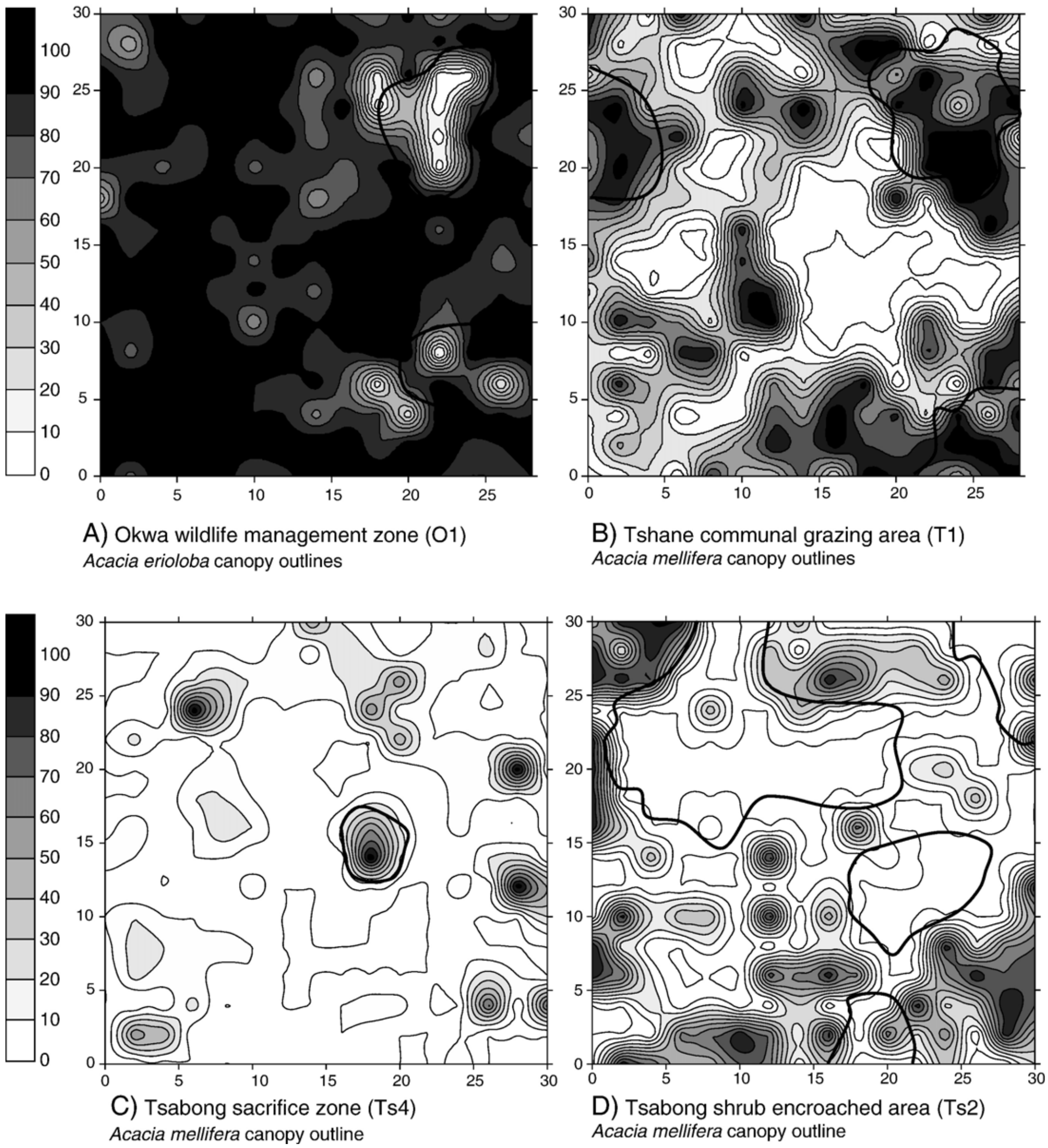

Fig. 3. The relationship between different vegetation types and % cyanobacterial crust cover within 30 m × 30 m plots at (A) Okwa wildlife management zone, (B) Tshane communal grazing area, (C) Tsabong sacrifice zone and (D) Tsabong shrub encroached area.

multiple data sets (Quinn and Keough, 2002). For all tests, statistically significant differences were only assigned to p-values of <0.05.

4. Results and analysis

4.1. The distribution of soil crusts across the Kalahari

Crust cover at communal and commercial grazing locations away from the immediate vicinity of boreholes ranged from 44% to 68% of the ground surface (Table 1B). In the absence of livestock grazing in the National Park and Wildlife Management Zone crust cover is significantly higher (84% to 95%) ($p<0.05$). Crust cover is also high on the pan site with 84% of the ground crusted. The lowest crust cover (11%) was found adjacent to a borehole where cattle frequently gather. At most locations, crust cover was predominantly type 1 (weakly consolidated with no surface discolouration), but at the pan site, the mixed bush and grass site and the shrub encroached sites at Tsabong there were also high proportions of type 2 crust (more consolidated than type 1 with a brown/black colour). There was also evidence of buried crust layers at all sites where this was assessed. The lowest amounts of buried crust (1–5% of the unconsolidated surface) were found at sites with the highest crust cover (Mabuasehube 1, 2 and Okwa sites). At the other sites buried crust ranged from 11% to 19% of the unconsolidated surface area.

The amount of disturbance at each site accounts to some extent for the amount of crust cover. Fig. 2 shows the inverse relationship between the amount of crust cover and the level of disturbance at each site. Grazing animals break the surface of the crust and therefore reduce the extent and development of crust cover, but just as important is the exposure of the unconsolidated material. This is then easily transported by wind and can be deposited onto adjacent crusts, cutting off the sunlight reaching the cyanobacteria and rendering them inactive.

The relationship between disturbance and crust cover is also affected by the amount and type of vegetation at each site. Within each of the 30 m × 30 m plots, 240 1-m quadrats were used to map crust distribution in relation to vegetation cover. Four of the plots are shown in Fig. 3 and display the species-specific relationship between crusts and vegetation. At Okwa wildlife management zone, Fig. 3A shows the high percentage of the ground covered in crust. The areas of low crust cover corresponds to areas underneath the canopy of *Acacia erioloba* trees which are used by wild animals for shade and are thus frequently disturbed, preventing crust development. The lower crust cover at Tshane is visible in Fig. 3B. Here the areas of highest crust cover correspond to the sub-canopy environments of *A. mellifera* shrubs. In regularly grazed areas these thorny shrubs provide a protective niche where crust development can occur without frequent disturbance. The leaves of *A. mellifera* are small and rarely accumulate to such a depth as to prevent light from reaching the crust surface. This protective role can also been seen in Fig. 3c from the Tsabong sacrifice zone where the only substantial crust cover occurs underneath the *A. mellifera* shrub. Under large thickets of *A. mellifera*, however, crust formation and development are restricted by the accumulation of a deep litter layer which prevent light reaching the soil surface as shown in Fig. 3D from the bush encroached Tsabong site. In contrast to locations with smaller *A. mellifera* shrubs, crust cover at the shrub encroached site was found in the plant interspaces. These data show that it is not possible to generalise the relationship between crust cover and vegetation and that it is specific to the type and size of the species. Further details on the relationship between vegetation and crusts are given in Berkeley et al. (2005).

4.2. Recovery of cyanobacterial crust cover after disturbance

Site surveys of crust distribution provide an insight into crust cover at a specific time. Crusts are, however, temporally dynamic. The cyanobacteria that form the crusts in the Kalahari are easily damaged by disturbance and are susceptible to burial by sediment and leaf litter. Cyanobacteria are, however, also highly resilient and can recover to form new crusts after extended periods of dormancy. The rapidity of this recovery is crucial to the changing erodibility of dryland soil surfaces. Crust cover in two 5 m × 5 m plots on a commercial farm near Tsabong is shown in Table 2. The plots were constructed

Table 2
Crust and vegetation cover in plots in Tsabong

Site ($n=16$ at each site)	Cyanobacterial crust cover (%)				Vegetation cover (%)	
	BC1	BC2	BC3	Total	Shrub	Grass
Open plot						
August 2003	0	0	0	0	8	0
November 2004	77 (9)	13 (10)	0.3 (1)	90 (8)	11	2
August 2005	86 (7)	6 (8)	0	93 (6)	12	5
Closed plot						
August 2003	0	0	0	0	4	0
November 2004	93 (7)	6 (6)	0	99 (5)	5	1.4
August 2005	97 (2)	1 (2)	0	98 (2)	6	3

Values in parenthesis are standard deviations.

Table 3
Selected properties of unconsolidated sands and different crust types

	Organic matter (%)	Ammonium (μg g^{-1})	Total N (μg g^{-1})	Phosphate (μg g^{-1})	pH	Strength (kg cm^{-2})
All sites	*n*=278	*n*=145	*n*=98	*n*=92	*n*=192	*n*=66
Unconsolidated	1.14 (0.93)	76.4 (48.7)	183.1 (191.1)	2.7 (1.2)	5.9 (0.4)	0
BC1	0.92 (0.49)	101.3 (52.3)	172.9 (89.2)	2.8 (1.1)	5.8 (0.5)	0.56 (0.8)
BC2	1.04 (0.4)	80.6 (44.1)	341.3 (221.3)	3.1 (1.5)	5.8 (0.6)	0.73 (0.8)
BC3	1.68 (0.53)	89.4 (51.8)	652.2 (856.5)	2.5 (0.9)	5.9 (0.3)	1.50 (0.9)

Values in parenthesis are standard deviations.

in August 2003 during a prolonged dry period and when crust cover was absent. Fifteen months later and total crust cover in the plots was 90% and 99% (Table 2) after 233.7 mm of rainfall. Most of the crust was type 1 (86% and 94%) with negligible type 3. Differences between the open and closed plot were minimal because the farmers removed their livestock after the plots were constructed. In August 2005, after a further 248.2 mm of rainfall, total crust cover was similar to November 2004. The proportion of the better developed type 2 crust was, however, lower in both plots. In the absence of livestock disturbance, this suggests that crust development was

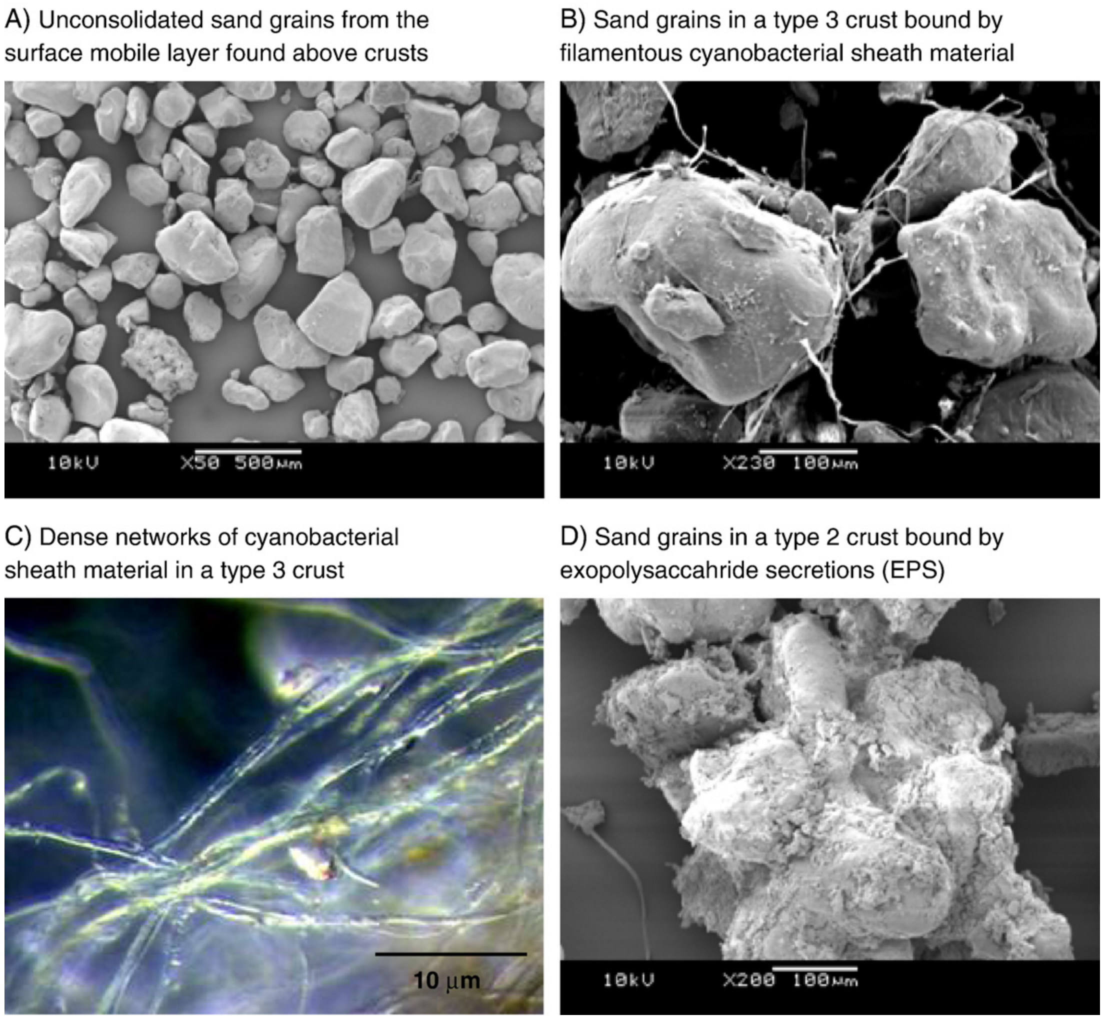

Fig. 4. Scanning electron and light microscopy images of soil surfaces.

inhibited by either sediment deposition from the adjacent soils outside the plot or that heavy rainfall over the 5–6 April 2005 damaged the crusts (84.3 mm fell in 30 h).

4.3. Implications of cyanobacterial crusts for soil surface nutrients, cohesive strength and nutrients

4.3.1. Soil surface nutrients

The presence of crusts, and in particular, the better developed type 3 crusts (well consolidated, with a black/brown bumpy surface) significantly alters the surface organic matter and total nitrogen content (Table 3). Type 3 crusts have significantly higher organic matter and total N than uncrusted and type 1 and 2 crusts ($p<0.05$). This is likely to be both because cyanobacteria in crusts fix N directly from the atmosphere and that the bumpy crust surface provides hollows for fines and organic material to collect in. There were, however, no significant differences in the pH, phosphate and ammonium in crusted and uncrusted soil surfaces (Table 3).

4.3.2. Crust strength

Crusted surfaces have significantly greater compressive strength than uncrusted surfaces ($p<0.05$). The better developed type 3 crusts also have significantly higher compressive strengths than type 1 and 2 crusts (Table 3). The scanning electron and light microscopy images in Fig. 4 show how uncrusted surfaces (Fig. 4A) have very little organic material, few aggregates and no cyanobacterial sheath material. In contrast, the type 3 crust in Fig. 4B has sand grains bound together by the filamentous sheath material of *Microcoleus* sp. The dense web of filaments typical of crusted surfaces can also be seen clearly in Fig. 4C. The distinct aggregates of sand grains in Fig. 4D are bound together by non-filamentous exopolysacharide secretion (EPS). The images show that the type of binding (EPS or filaments) is likely to influence the cohesivity of the surface and thus soil erodibility.

Table 4
Microtopography indices for each soil surface type (mean per transect values calculated as per method of Nash et al., 2003)

Soil type	Microtopography index		
	∑ depressions/ mounds	Number of depressions/ mounds	∑ depressions − ∑ mounds
Unconsolidated	21.94	1.67	12.01
Crust type 1	0.14	0.05	0.08
Crust type 2	5.92	0.41	5.06
Crust type 3	5.67	0.68	4.11

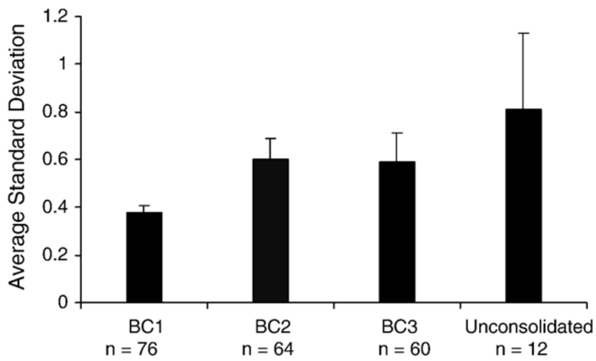

Fig. 5. Roughness measurements for each morphologically distinct crust type.

4.3.3. Surface roughness

The microtopography indices for the four different surface classifications are shown in Table 4. All indices have a consistent pattern showing that type 1 crusts are typified by a smaller number and size of microtopography features compared to either the better developed types 2 and 3 crusts, or disturbed unconsolidated soils that are typified by wider mounds and depressions typical of sandy soils that are regularly churned by livestock hooves. Types 2 and 3 crusts have a similar magnitude of total depressions/mounds over the 2 cm threshold. It is also notable that there are a greater number of depressions/mounds recorded on type 3 crusts (Table 4). This is indicative of the distinct microtopography typical of well-developed cyanobacterial soil crusts (Belnap and Gillette, 1997), rather than larger (smoother) disturbances which typify disturbed sandy surfaces.

The surface roughness index based on mean deviation from the '0' reference point of all measured pins for each of the surface types is shown in Fig. 5. Statistical analyses shows that a significant increase in surface roughness occurs as crusts develop from type 1 into type 2 crust surfaces ($p=0.04$). The lack of statistical differences for other relations is largely due to the greater variance of data, especially for the unconsolidated soils.

5. Discussion

5.1. The distribution of cyanobacterial crusts in the Kalahari

The findings presented here provide a first assessment of the spatial and temporal variability of cyanobacterial soil crusts on both local and regional scales for the Southern Kalahari. Crust cover is far more extensive than suggested in previous analyses from regularly disturbed communal rangeland sites (e.g., Skarpe and Henriksson, 1987; Aranibar et al., 2003; Dougill and Thomas, 2004).

Approximately 46% of Botswana has protected status as either a National Park or Wildlife Management Area where grazing disturbances will be minimal and crust cover can be expected to be around 90% (Table 1). Even in frequently disturbed communal and commercial grazing areas, crust cover ranged from 44% to 68% on Kalahari Sands and up to 84% on a grazed pan site. On a localised scale, crust distribution is related not only to the level of disturbance but to the density and type of vegetation cover. Large trees provide shade and attract animals thus discouraging crust development. The thorny canopy of the *A. mellifera* shrub, however, deters animals and provides an ideal environment for crust formation and development as long as the shrub size is not so large that the leaf litter produced prevents light reaching the surface (Berkeley et al., 2005).

5.2. Temporal variations in crust cover

The ability of crusts to redevelop rapidly following disturbances is clear from the plot data in Table 2. Recovery occurred despite the proximity of the plots to sparsely vegetated and disturbed surfaces (that provide a source of easily mobilised sand that could bury the crusts) and low rainfall over the first 15 months of monitoring (restricting the amount of time the cyanobacteria are active). Crust development is restricted by burial, either by dense litter layers under large shrub thickets (Fig. 3) or by mobile surface grains as displayed by the conceptual model of surface dynamics that we propose in Fig. 6. Intense rainfall is also likely to damage weakly consolidated crusts through raindrop impact and is probably responsible for the decline in the cover of the better developed type 2 crusts from November 2004 to August 2005.

Disturbance and breakage of crust surfaces will expose unconsolidated grains that will be easily entrained. The buried crust layers found at all sites (Table 1) suggest that the soil surface is highly dynamic, with crusts developing when disturbance is restricted and lying dormant under a surface layer of sand when localised disturbance provides unconsolidated material which can be entrained. The buried cyanobacteria then lie dormant under the sand layer until they are either re-exposed by further sediment movement or migrate to the surface in search of water (Garcia-Pichel and Pringault, 2001).

5.3. Implications for soil surface properties

5.3.1. Strength

Cyanobacterial crusts are capable of binding fine sand particles together, either with webs of filamentous sheaths (such as *Microcoleus* and *Sytonema*) or with exopolysaccahride secretions (EPS) (Fig. 4). The compressive strength of crusts (measured using a penetrometer) is significantly greater than uncrusted surfaces (Table 3). Crust strength also changes with crust type, and the better developed type 3 crusts have significantly higher strengths than type 1 crusts. McKenna Neuman and Maxwell (2002) found biological crust disintegration occurred by the abrasion by saltating grains during wind events. Although crust breakdown was related to the energy of impacting grains and the resistance of the crust, only low grain impact velocities were needed if key stress points in the crust were affected. They found that the longer term stability of crusts depended on the balance between growth of organisms in the crust and slow rate of abrasion under sporadic, low-energy wind events. In an earlier study, they found that resistance to breakdown depended on crust type and that fungal crusts were more stable than cyanobacterial and algal crusts (McKenna Neuman and Maxwell, 1999). Similarly, in the Kalahari, the resistance of crusts to abrasion and disintegration will depend upon crust composition and the form of the filaments or secretions binding the sand grains. More process-based studies are needed, however, to establish how the different cyanobacteria species and their associated EPS or filaments affect aggregate stability and thus resistance to particle entrainment and raindrop impact.

5.3.2. Roughness

Crust formation and development changes the surface roughness (Table 4 and Fig. 5). Initially the formation of a simple cyanobacterial crust effectively smoothes the surface and reduces roughness. The better developed types 2 and 3 crusts, however, produce a bumpy soil surface with numerous small depressions and mounds (Table 4) increasing near-surface roughness, but at a smaller scale compared to the unconsolidated surface. The implications of these changes for erodibility and erosivity are complex. The increased roughness will increase aerodynamic roughness (z_0) and thus the shear velocity ($u*$). However, it is also likely that most unconsolidated grains on the surface are below the height of z_0 and in a zone of zero wind velocity. The relatively high levels of vegetation cover that remains at all sites other than the spatially restricted sacrifice zone close to a borehole adds roughness at a landscape scale that will further increase wind $u*$ but also z_0, such that

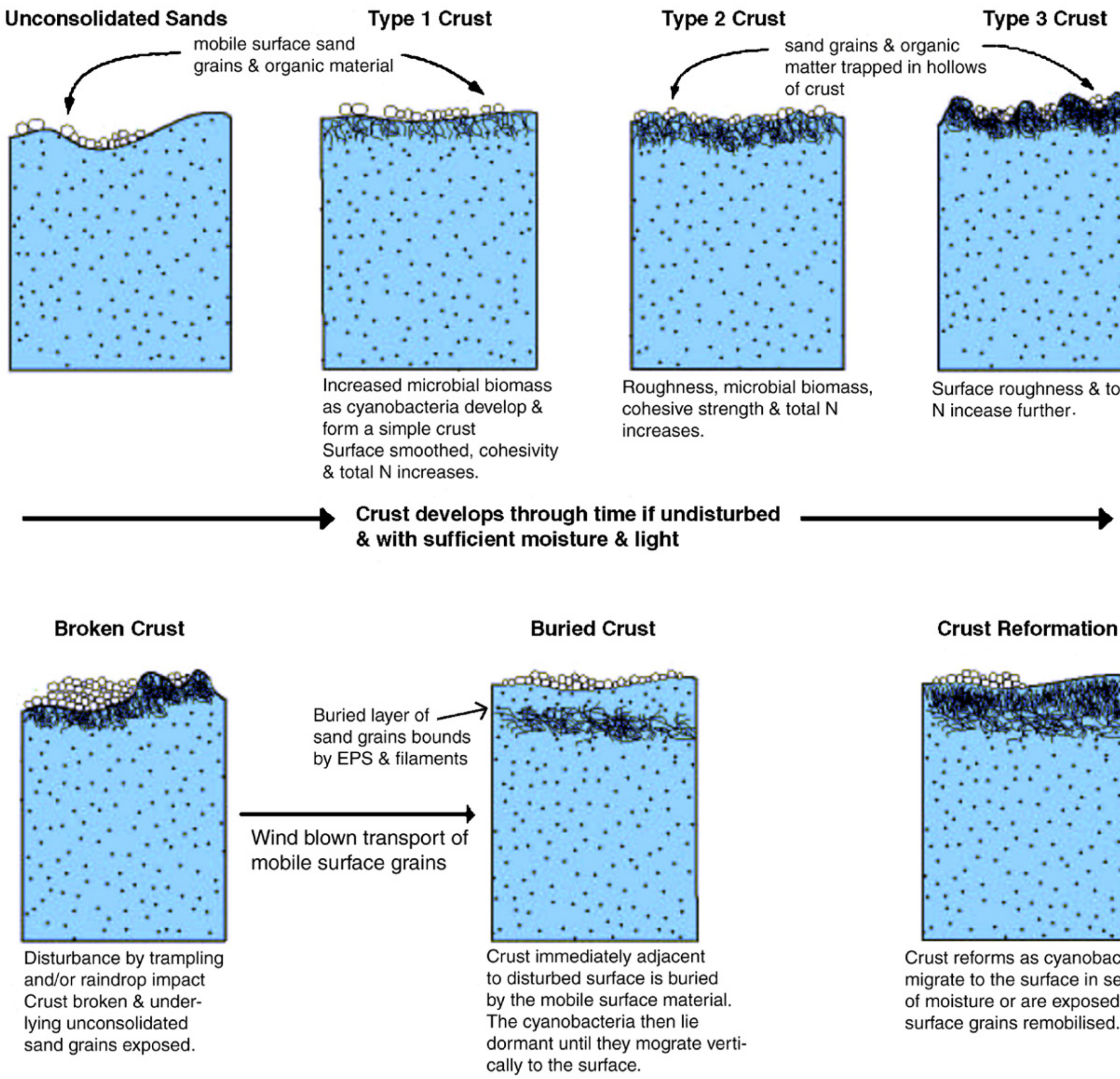

Fig. 6. A conceptual model of crust development and burial.

sediment entrainment is less likely. The hollows formed by the crust will fill with fine particles and organic matter where they will effectively be protected from entrainment. Wiggs et al. (1994) report a three-fold increase in above canopy shear velocity on vegetated compared to bare dunes in the Kalahari. However, they also found that near-surface wind velocities were reduced by 200% under the predominantly grass vegetation cover found at their study sites. Establishing what proportion of shear velocity acts on the surface in the more complex bush–grass–crust assemblages for the Kalahari rangeland sites investigated here is the key to understanding how changing roughness affects erodibility.

In grazed areas, crusts form preferentially under the canopies of *A. mellifera* (Berkeley et al., 2005). The potential of the cyanobacteria in crusts to fix atmospheric nitrogen resulting in the elevated total nitrogen in type 3 crusts (Table 3) may provide a competitive advantage to established *A. mellifera* shrubs and thus contribute to shrub encroachment (Hagos and Smit, 2005). An increase in the amount of shrubs will also significantly increase aerodynamic roughness. The interaction between the soil crusts and vegetation will be key to determining how shear velocity at the surface is affected. More work is needed to investigate the implications of this for wind erosion.

6. Conclusion

This paper presents information on the cover and characteristics of cyanobacterial soil crusts at a variety of locations in the semi-arid Kalahari of Botswana and discusses the implications for soil surface properties. We have found a far more extensive crust cover than previously reported for the Kalahari with up to 90% of the surface crusted in undisturbed areas. Crust cover was between 44% and 68% in grazed areas where woody and thorny shrubs such as *A. mellifera* provide a refuge for crust development.

Crust cover and development is restricted by grazing and intense rainfall. Broken or buried crusts, however, rapidly reform after disturbance. It is likely that buried cyanobacteria lie dormant under a mobile layer of sand until they are either re-exposed by further sediment movement or they migrate to the surface in search of water (Garcia-Pichel and Pringault, 2001). The 'pool' of dormant cyanobacteria, which will readily form crusts given the right conditions, is an important resilience characteristic of Kalahari Sand soils.

Cyanobacterial crusts significantly increase soil surface cohesion, total nitrogen and organic matter of the surface and change roughness. It is clear that crusts have an important role in surface stabilisation and erodibility. There is a need for process-based studies to determine exactly how crusts affect erodibility and in particular how this differs between filamentous and EPS bindings. This may be particularly important given the recent conclusions of Thomas et al. (2005) who predict the currently stable Kalahari dunes will remobilise during this century given even relatively small changes in climate.

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