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Morphology and microstructure of microbiotic soil crusts on a tiger bush sequence (Niger, Sahel)

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Abstract

Microbiotic crusts resulting from the colonization of soil surfaces by communities of micro-organisms dominated by cyanobacteria, eucaryotic algae or lichens are widespread in arid and semi-arid regions. In the 'tiger bush' of Niger (Sahel) microbiotic crusts occur in bare bands between densely vegetated bands. The tiger bush soils are sandy loams with pH 4.7–6.5. Three different microbiotic crusts are recognised, forming strips parallel to the vegetation banding. They are all formed mainly by filamentous cyanobacteria dominated by *Schizothrix*. Other important genera are *Scytonema*, *Lyngbya*, *Microcoleus*, *Nostoc* and *Phormidium*. The filamentous micro-organisms trap sand particles and finer particles stick on the filament surfaces. These effects enhance soil cohesion and resistance to erosion. Soil porosity is also increased by the microbial cover, with additional pores delineated by filaments on the surfaces of crusts and porous organic bodies derived from microbial remains at depth. The microbiotic crusts are essential components of the tiger bush ecosystem. Water leaving the lower sides of vegetated bands results in plant decay, and on the upslope sides vegetation grows because of increased water supply. Microbial covers help resist erosion, and increase water and nutrient retention, thus providing substrates for the expansion of plants from adjacent vegetated bands.

Author Keywords: Cyanobacteria; Microbiotic crusts; Sahel; Soil micromorphology; Soil stabilisation; Tiger bush

1. Introduction

Biological and physical crusts are the main types of soil crust in arid and semi-arid regions. Physical crusts are formed by the action of water and, to a lesser extent, wind on soil particles at the surface of bare areas. Biological crusts, also called microbiotic crusts, result from the development of communities of micro-organisms (comprising generally cyanobacteria, eucaryotic algae, and lichens, but also bacteria, mosses, liverworts or fungi) on the surface of physical crusts.

Microbiotic crusts occur in arid and semi-arid regions of USA (Rychert and Skujins, 1974; Klubek and Skujins, 1980; Cole, 1990; Beymer and Klopatek, 1991; Belnap and Gardner, 1993), in steppe environments of Australia (Eldridge, 1993a and Eldridge, 1993b), China (Reynaud and Lumpkin, 1988), in Israel (Verrecchia et al., 1995), and Sahelian Africa (Barbey and Couté, 1976; Dulieu et al., 1977; Isichei, 1980). They play major roles in soil

stabilisation against both water and wind erosion (Campbell et al., 1989; Belnap and Gardner, 1993), and in water infiltration and generation of runoff (Eldridge and Greene, 1994). Loope and Gifford (1972) report that microbiotic crusts enhance water infiltration and prevent runoff, whereas Brotherson and Rushforth (1983) and Verrecchia et al. (1995) suggest the opposite. Microbiotic crusts also enhance moisture content (Belnap and Gardner, 1993; Verrecchia et al., 1995) and increase available nutrients by concentrating essential elements, such as nitrogen, which is fixed by cyanobacteria (Harper and Pendleton, 1993).

Microbiotic soil crusts commonly occur in association with physical soil crusts, which can be divided into three main groups on the basis of their mechanisms of formation: (i) structural crusts (Fig. 1), formed in situ by water drop impact; (ii) depositional crusts (Fig. 1), formed by deposition of particles transported by water from their original location; and (iii) erosion crusts (Fig. 1), formed by water or wind erosion of the two former crusts.

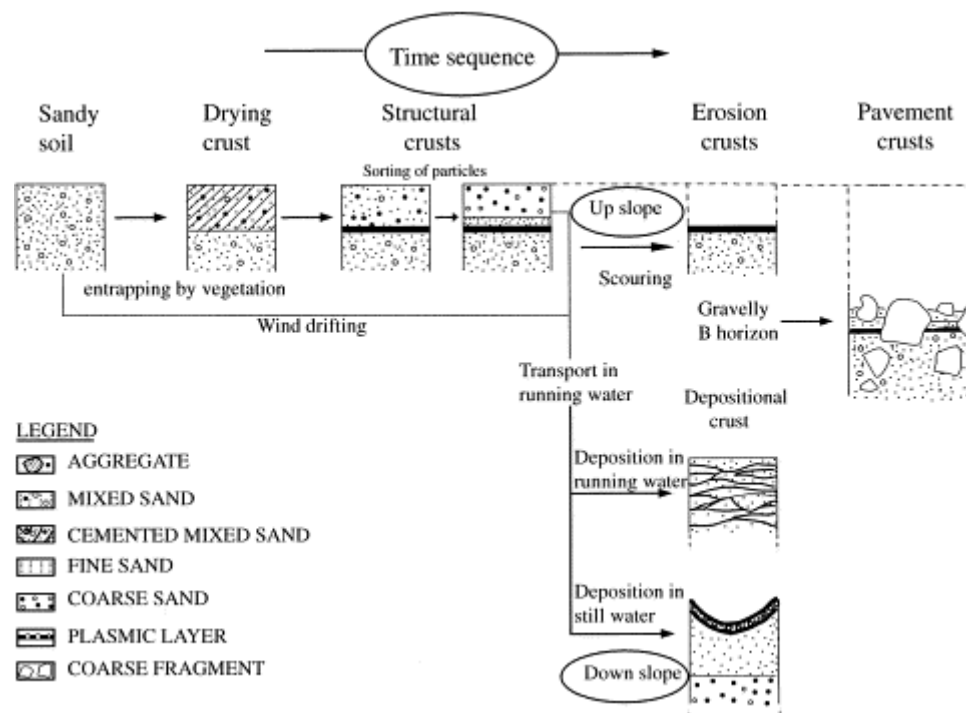


Fig. 1. Diagrammatic representation of the time sequence of soil crust formation (modified from Bresson and Valentin, 1990).

In the Sahelian zone of Niger, physical crusts comprise mainly sieving crusts, runoff crusts, still water depositional crusts and erosion crusts. Sieving crusts are structural crusts formed from two or three layers of sorted material (Fig. 1). The two-layered type is composed of a superficial layer of loose, coarse to medium sand overlying a plasmic (silt and clay) layer. The three-layered type comprises a top layer of loose coarse sand, a middle layer of fine sand, and a thin plasmic bottom layer. Pavement crusts (Fig. 1) are sieving crusts containing pebbles and gravels. Runoff crusts (Fig. 1) are very compact depositional crusts formed by deposition of particles transported by water. They exhibit submillimetric micro-layers, which are alternately coarse and fine. Still water depositional crusts (Fig. 1), also named sedimentation crusts, are formed by the deposition of particles in still water. They consist of densely packed and well-sorted particles, the size of which gradually increases with depth. The superficial

layer is usually clay-rich and breaks into curled-up plates during periods of desiccation. Erosion crusts (Fig. 1) consist of a thin, smooth, clay-rich surface layer left after erosion of an overlying sand layer.

In this paper, we report detailed micromorphological observations on microbotic crusts in the 'tiger bush' landscape near the village of Banizoumbou, in western Niger, in the Sahelian region of west Africa. The roles of these crusts in soil stabilisation and the water regime of the Sahelian environment are discussed.

2. Site descriptions, materials and methods

2.1. Site descriptions

Banizoumbou is about 70 km north-east of Niamey, the capital city of Niger. The study site lies between 13°32'N and 2°42'E, on a plateau formed by Tertiary fluvio-lacustrine deposits ('Continental terminal'; Greigert, 1966). The plateau, which is dissected in several parts by erosion, exhibits a slight slope of a maximum of 1% (Ambouta, 1997). A thick ferruginous duricrust caps the summit of the plateau (Fig. 2a), and underlies a 35–60 cm thick soil.

The climate is typical of the southern Sahel, with an annual rainfall of about 560 mm, occurring from mid-May to mid-September. Mean minimum and maximum temperatures are 22° and 34°C, respectively.

The vegetation of the plateau shows a characteristic pattern consisting of alternating densely vegetated bands comprising small trees and shrubs (Fig. 2a, arrows) and bare soil bands. From the air the resulting landscape resembles a tiger's fur (Fig. 2a), and is called 'tiger bush'. Examination of the vegetation banding reveals two distinct regions in each band (Fig. 3): a decaying section on the lower side, and a flourishing part on its upper side. This pattern is thought to be controlled by the downward movement of water (Ambouta, 1984; Cornet et al., 1992). The lower side of a band loses water, which is trapped by the upper section of the adjacent downslope band. This results in a gradual movement of the vegetated bands in an upslope direction at a rate of about 25 cm yr⁻¹ (Thiéry et al., 1995; d'Herbès et al., 1997).

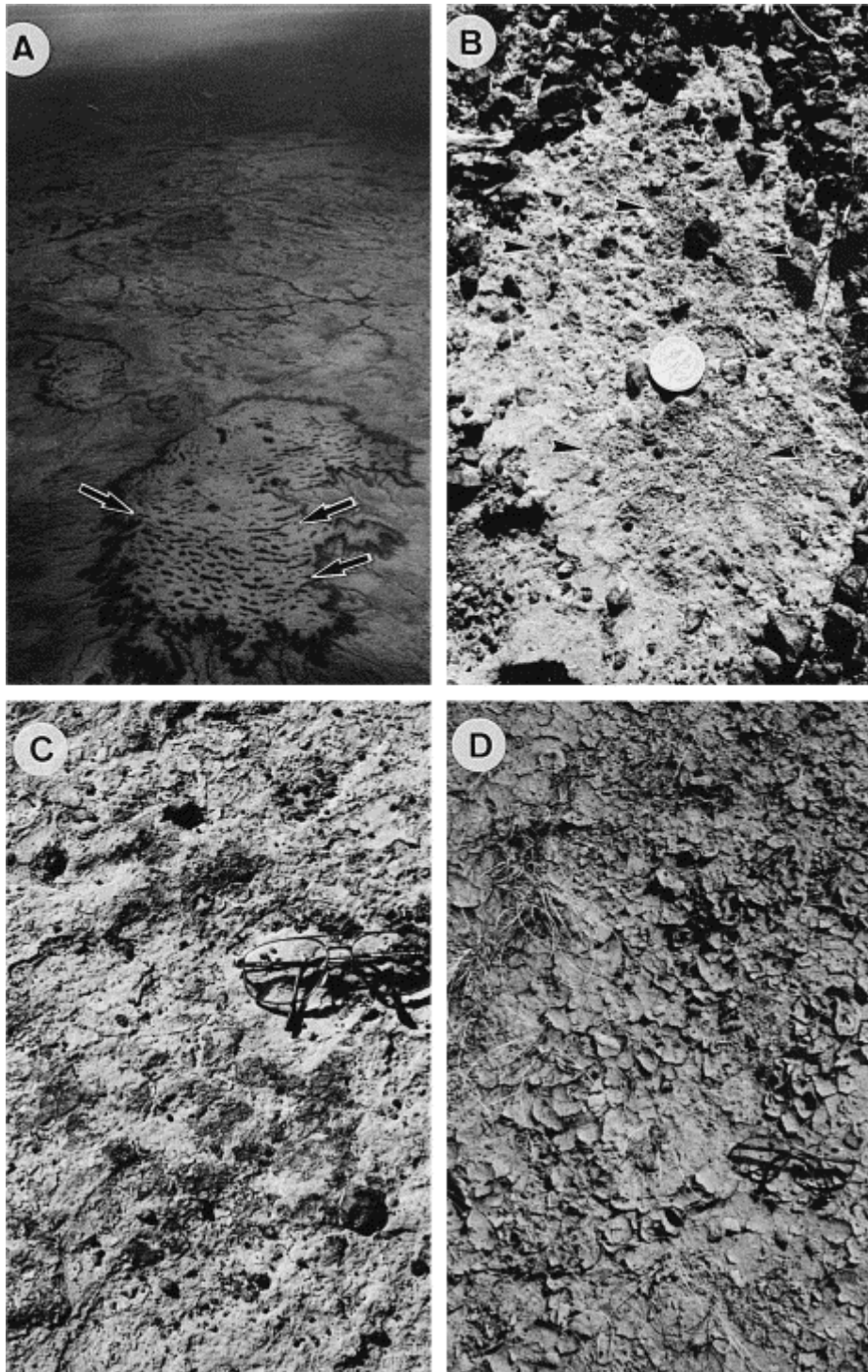


Fig. 2. Views of the sites studied. (a) Aerial view of the tiger bush landscape in western Niger on the top of a dissected plateau. Note the subparallel vegetation bands (arrowed), and the dark section of the ferruginous duricrust at the top of the cliff, approximately 15–20 m high, delimiting part of the plateau. (b–f) Views of the soil surface in the sites studied. (b) Site 1: The coarse superficial material was swept away to show the underlying fine sand layer, and vesicular pores (arrowed) at the surface of the third, plasmic layer. The superficial coarse material is visible at the top, the right, and the bottom right corner of the photograph. (c) Site 2: Darker areas correspond to patches of microbiotic crust. Lighter parts are erosion crusts. (d) Site 3: Polygonal cracking of microbiotic crust on sedimentation crust, and rare herbaceous plants. (e) Site 4: Polygonal cracking of microbiotic crust on a sedimentation crust, showing the dense herbaceous cover, and soil reworked by termites (arrowed). Scale bar is 7.5 cm. (f) Site 5: The soil is covered by a continuous litter layer.

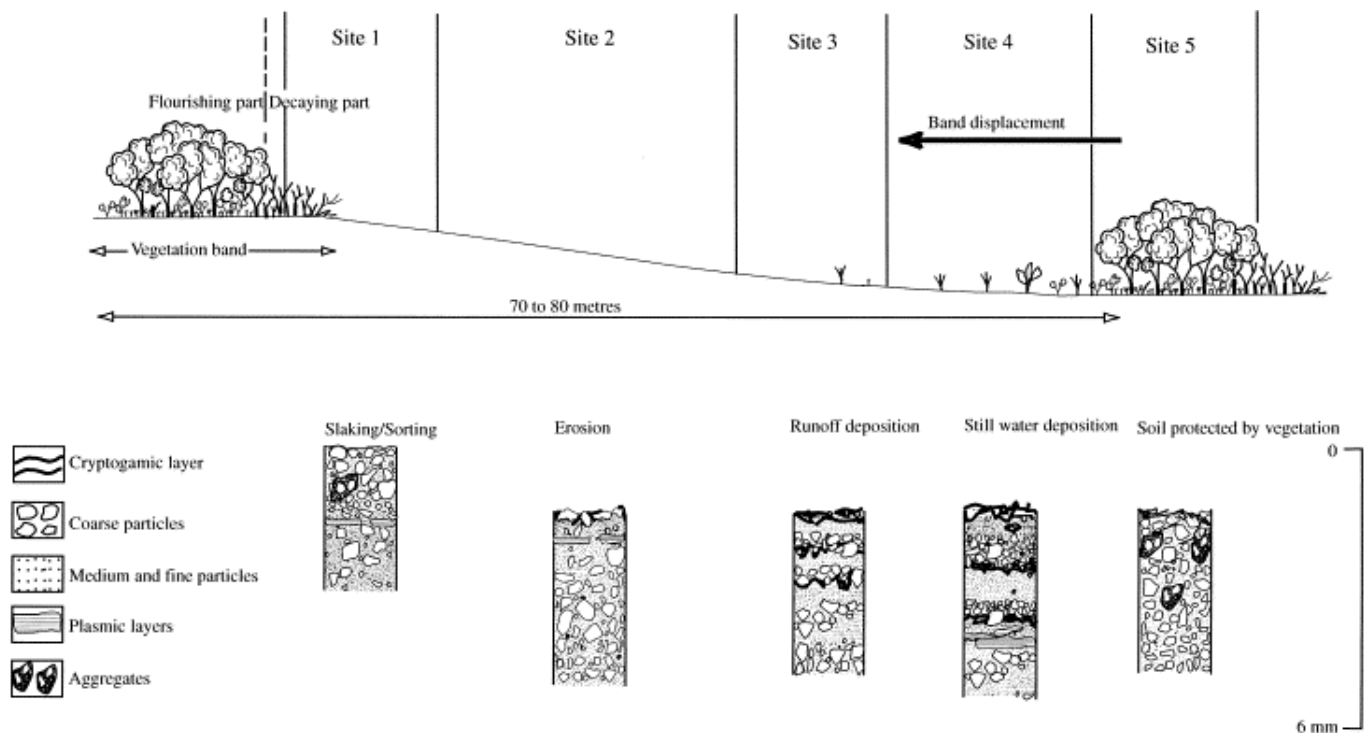


Fig. 3. Lateral and vertical patterns of a tiger bush soil sequence.

2.2. Crust sampling

Samples of soil crust approximately 7 cm thick were collected from each site (Fig. 3) in November 1994, at the beginning of the dry season. Five types of soil surface were distinguished along the slope, from the decaying part of a vegetative band to the flourishing part of the next lower vegetative band (Fig. 3).

(1) Site 1 (Fig. 2b): close to the decaying section of the band, the soil surface was a sieving crust devoid of any microbial cover. Vesicular pores formed as air bubbles were recognisable when unconsolidated coarse superficial material was swept out.

(2) Site 2 (Fig. 2c): the soil surface was an erosion crust partly capped by microbiotic crust patches.

(3) Site 3 (Fig. 2d): the soil surface was a microbiotic crust capping a still water deposition crust. Scattered herbaceous plants were present at this site.

(4) Site 4 (Fig. 2e): the soil surface was similar to that at site 3, but the grass vegetation was denser. Emerging holes of termite galleries were frequently observed.

(5) Site 5 (Fig. 2f): the soil surface under the flourishing part of the lower band was covered by a permanent litter of dead tree leaves and herbaceous plants. Scattered mosses were observed.

One sample was collected from each of the five sites. Those from sites 2 to 5 were divided into four subsamples for particle size distribution and chemical analyses. The first subsamples were the superficial organo-mineral layers, ca. 2 mm thick, which comprised most the living

micro-organisms of the crusts. The other three subsamples were taken at 10–20 mm intervals according to visible soil layering.

2.3. Methods

Observations of soil surfaces were made at two scales, on a Nacet NS 50 stereomicroscope and on a JEOL JSM 6400 Scanning Electron Microscope (SEM). For SEM observations samples were coated with gold–palladium. Vertical thin sections were examined on a Zeiss Universal light microscope and on SEM. For SEM observations the sections were coated with carbon. Micro-organisms were collected from remoistened samples with a pipette under the stereomicroscope. Particle-size distributions were determined by dry sieving of sand particles and sedimentation of finer particles (pipette method). pH was measured with a 691 Metrohm pH meter on samples dispersed in water for 24 h. Total organic carbon (TOC) was measured with a CNS-2000 Leco analyser.

3. Results

3.1. Physical and chemical analyses

All sites had similar textures (sandy loam) and pH (4.7 to 6.5) values (Table 1). TOC content shows differences between sites, in particular in the superficial layers (Table 1). Superficial samples with a microbial cover (sites 2–4) were richer in TOC (0.9 to 1.9% dry weight) than the bare sample (0.5% at site 1). Densely microbially-covered samples (sites 3 and 4) were richer in TOC (1.8–1.9%) than the litter-covered sample (1.4% in site 5). Except for the sieving crust (site 1), the TOC content of deep samples was less than the superficial layers (Table 1). At depth, microbially-covered soils (sites 2–4) had less TOC (0.3 to 0.7%) than the litter-covered soil (site 5: 0.7%) or the sieving crust (site 1: 0.6%). Among microbially-covered soils, site 4, which supported a dense herbaceous cover, was richer in TOC (0.4–0.7%) at depth than sites 2 and 3 (0.3–0.4%).

3.2. Determination of micro-organisms

Micro-organisms present in the tiger bush samples belonged to two taxonomical groups: cyanobacteria and chlorophyta (Table 2). Cyanobacteria were dominant at all sites, but Chlorophyta (two species) were present only in two sites. Eleven species of cyanobacteria were identified (Table 2). All are filamentous except *C. limneticus*. Three species are heterocystous. *Schizothrix* is the most abundant genus at all sites. The communities forming microbiotic crusts (sites 2–4) were not fundamentally different from those present in the vegetated band of the tiger bush (site 5 in Table 2). The maximum diversity of species was observed at site 3.

Table 1. Particle-size distribution, pH and total organic carbon content of the soils studied (values other than pH are dry weight percentages)

Sites	Physical crust type	Depth (mm)	Particle size distribution			pH	Total organic carbon (%)
			Sand (%)	Silt (%)	Clay (%)		
Site 1	Sieving	0–10	–	–	–		0.5
		10–15	71.0	21.0	13.5	6.4	0.6
Site 2	Erosion	0–2	57.2	34.1	12.2	6.3	0.9
		2–35	59.1	30.0	11.3	6.5	0.3
		35–55	62.7	27.7	12.2	6.5	0.3
		55–75	53.0	26.1	12.2	6.4	0.4
Site 3	Runoff deposition	0–2	54.2	29.4	13.8	5.9	1.8
		2–10	64.3	20.3	10.7	5.4	0.4
		10–20	64.5	24.8	10.0	5.0	0.3
		20–30	64.0	18.4	14.1	5.0	0.3
Site 4	Still water deposition	0–2	70.4	24.0	4.9	6.1	1.9
		2–12	59.5	34.3	7.2	5.8	0.7
		12–22	51.6	32.8	13.3	6.1	0.5
		22–42	54.9	31.8	13.4	6.1	0.4
Site 5	No crust	0–2	60.5	37.4	3.8	5.8	1.4
		2–17	64.6	20.6	11.5	5.5	0.7
		17–37	70.2	18.9	13.1	4.7	0.7
		37–57	72.6	17.5	13.5	5.5	0.7

Table 2. Micro-organisms observed in the sites studied (no micro-organism was observed at site 1)

Taxons		Site 2: erosion crust	Site 3: runoff deposition crust	Site 4: still water deposition crust	Site 5: no crust
Cyanobacteria	<i>Chroococcus limneticus</i> Lemm.	+	–	–	–
	<i>Lyngbya aerugineo-coerulea</i> (Kütz.) Gomont	–	–	+	–
	<i>L. aestuarii</i> Liebman	–	–	–	+
	<i>L. epiphytica</i> Hieron	–	–	–	+
	<i>Microcoleus sociatus</i> W and G.S. West	–	+	–	+
	* <i>Nostoc</i> Vaucher sp.	–	+	–	–
	<i>Phormidium mucosum</i> Gardner	–	+	–	–
	<i>Schizothrix friesii</i> (Ag.) Gomont	+	+	+	+
	<i>S. penicillata</i> (Kütz.) Gomont	+	+	+	–
	* <i>Scytonema javanicum</i> Bornet	–	+	–	–
	* <i>Scy. stuposum</i> (Kütz.) Bornet	–	+	–	–
	Chlorophyta	<i>Desmococcus olivaceus</i> (Pers. ex Arch.) Laundon	+	–	–
<i>Actinotaenium cucurbita</i> fo. <i>rotundatum</i> (Krieg.) Teiling		–	–	–	+

+ = Presence.

* = Heterocystous species.

3.3. Surface micromorphology

3.3.1. Site 1

Microscopic observations confirmed the absence of micro-organisms at this site. The material is composed essentially of rounded quartz grains, ca. 500 μm in mean diameter, accompanied by rare coarser sand grains (Fig. 4a). Pores probably resulting from insect activity were observed (Fig. 4a).

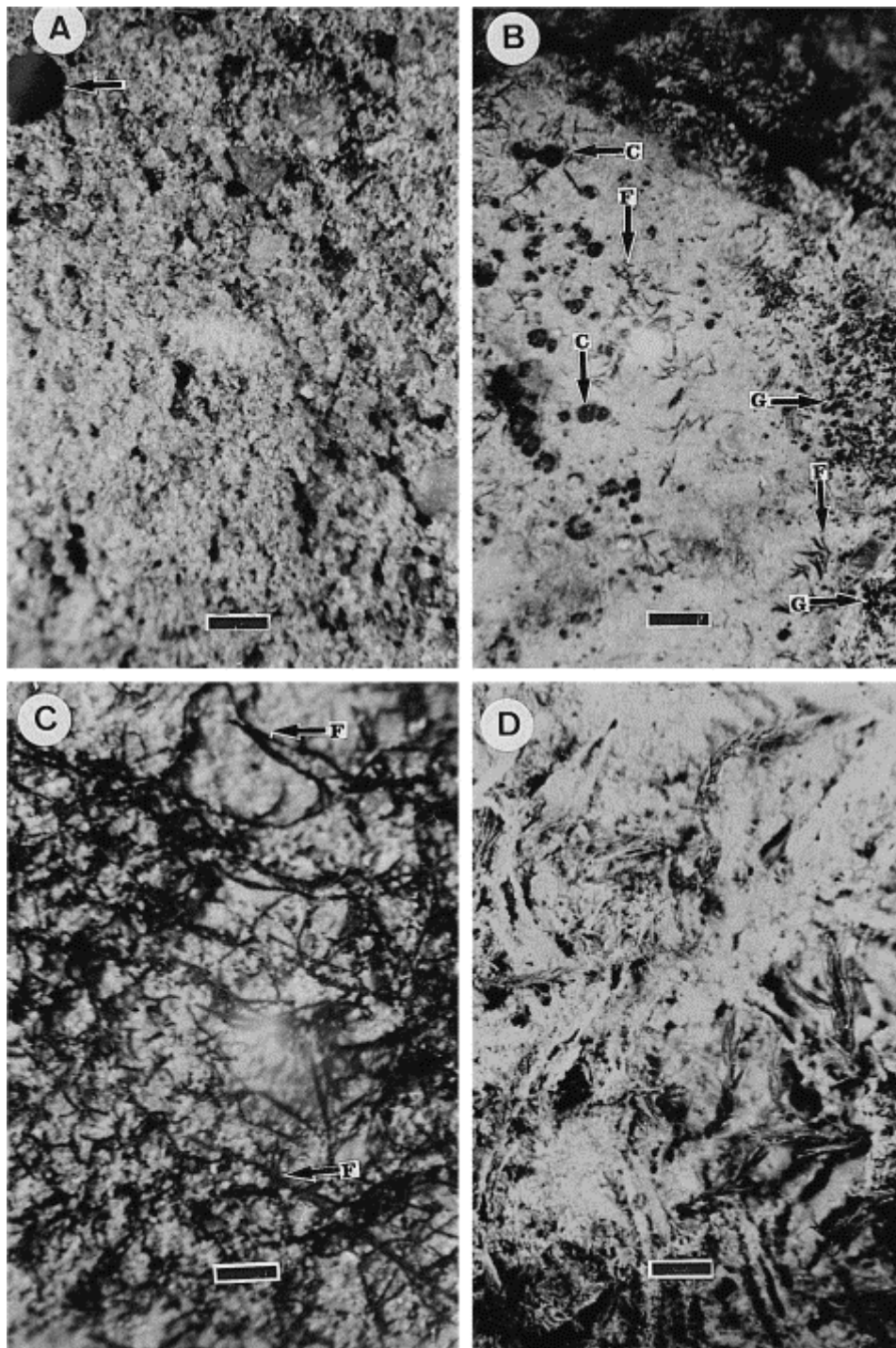


Fig. 4. Views of the soil surface under a stereomicroscope. (a) Site 1: Note the absence of any living organism or organic material, and the pore probably resulting from insect activity (arrowed) (scale bar is 0.5 mm). (b) Site 2:

Small globular colonies of cyanobacteria (*C. limneticus* Näg.; G), larger, cupular chlorophyta (*Desmococcus* Brand; C), and filamentous cyanobacteria (*Schizothrix* Kütz.; F) (scale bar is 0.5 mm). (c) Site 4: Note the network of cyanobacterial filaments (F) (scale bar is 0.1 mm). (d) Site 5: Mosses on the surface of litter. Scale bar is 0.5 mm.

3.3.2. Site 2

Stereomicroscopic observations of microbiotic crust patches revealed the presence of three different microbial colonies.

(1) Black, globular organisms, approximately 10 μm in diameter when isolated, and 250 μm when associated (Fig. 4b). These were identified as cyanobacteria of the species *C. limneticus* (Table 2).

(2) Black or reddish, filamentous organisms, 10 to 25 μm in diameter (Fig. 4b), belonging to two species of the cyanobacterial genus *Schizothrix* (Table 2).

(3) Greenish, cupular-shaped organisms, 250 to 400 μm in diameter (Fig. 4b), identified as chlorophyta belonging to the genus *Desmococcus* (Table 2).

Under SEM the *Schizothrix* filaments appeared to form a superficial network delineating pores, several tens of micrometres in diameter (Fig. 5a). Sand particles were trapped in this network, whereas finer mineral particles adhered to the surface of filaments (Fig. 5a).

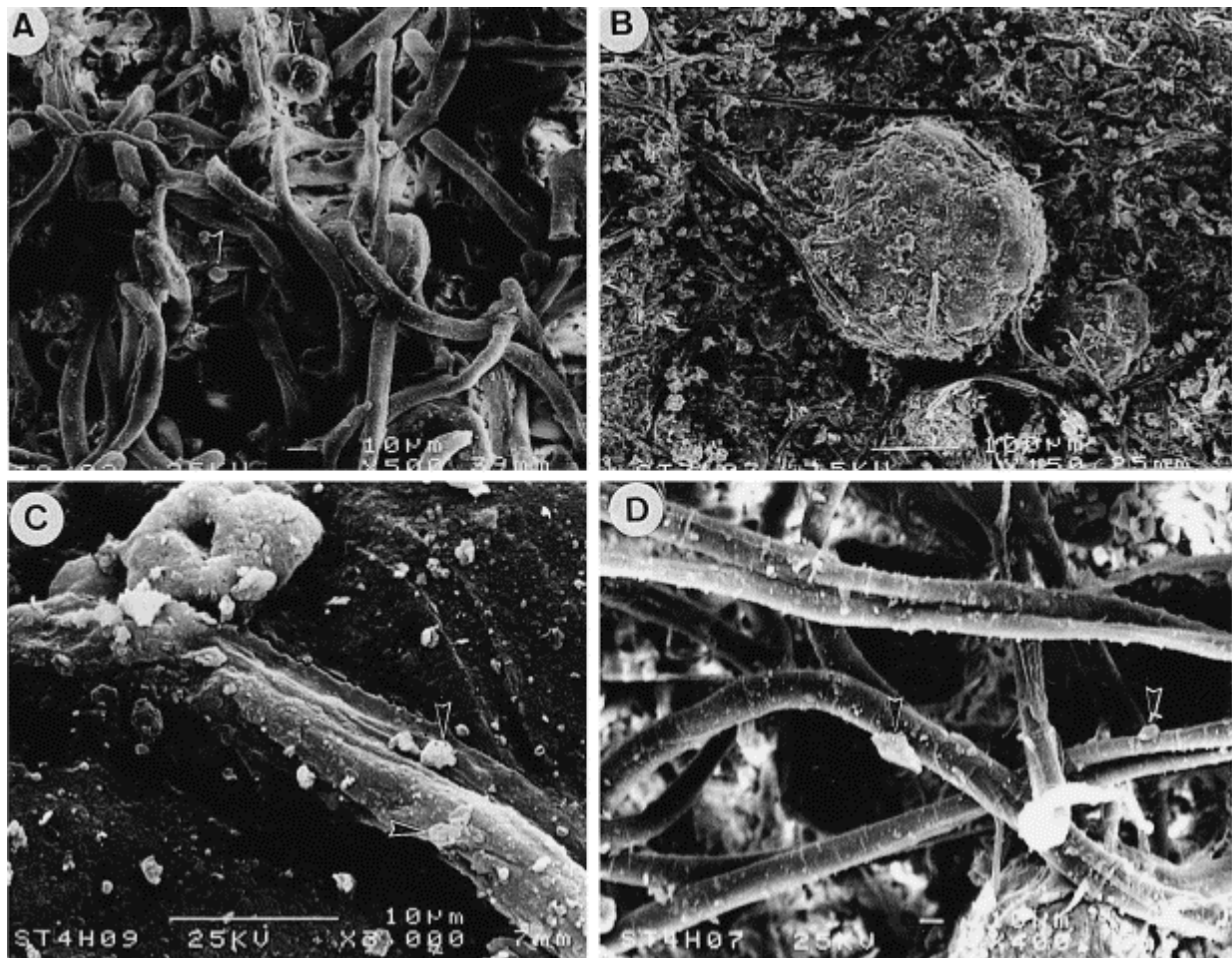


Fig. 5. SEM micrographs of the soil surface. (a) Site 2: Intertwining of filaments, which trap sand grains. Fine mineral particles stick onto the surfaces of filaments (arrowed). (b) Site 3: Network of filaments enmeshing sand grains and finer mineral particles. (c) Site 4: Contact between a filament and a sand grain. Note the filament print on the grain surface. Fine particles (arrowed) adhere to the filament surface. (d) Site 4: Filaments delineating superficial pores. Fine mineral particles adhere to the surfaces of filaments (arrowed). Bar is 10 μm .

3.3.3. Sites 3 and 4

Under the stereomicroscope there was no significant micromorphological difference between sites 3 and 4, except that the density of micro-organisms was greater at site 4. The surface of crusts appeared to be formed by a network of black or reddish filaments, 10 to 25 μm in diameter (Fig. 4c). Some filaments formed pinnacles rising above the flat surface of the crust. Under SEM the filaments appeared, as at site 2, to trap sand particles and to have finer (<5 μm) mineral particles adhering (Fig. 5b–c). The filaments delineated characteristic superficial pores, several tens of micrometres in diameter (Fig. 5d). Filament prints were observed on the surface of sand grains (Fig. 5c). Scattered liverworts were present at site 4.

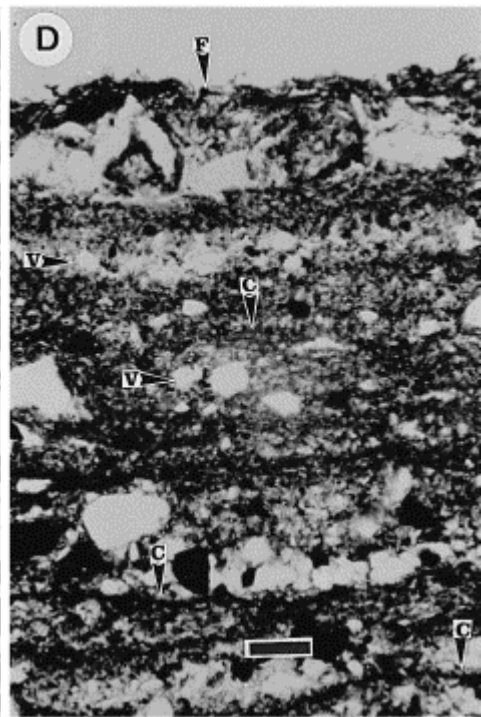
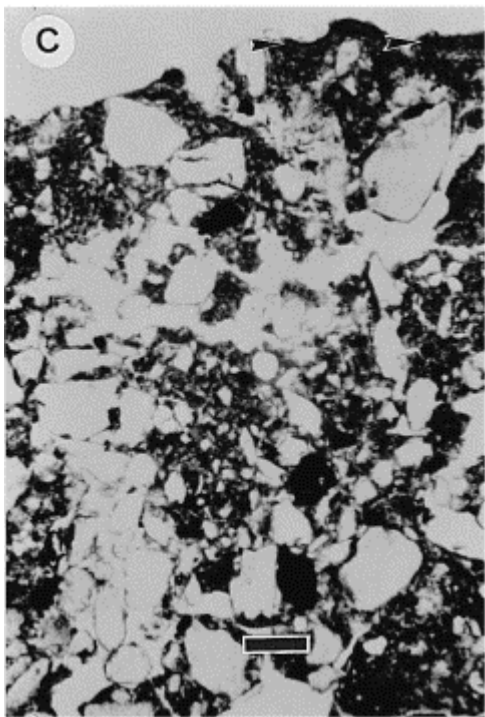
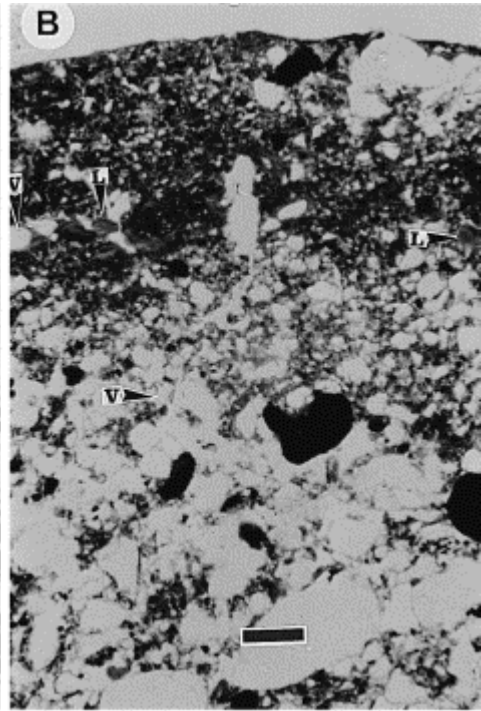
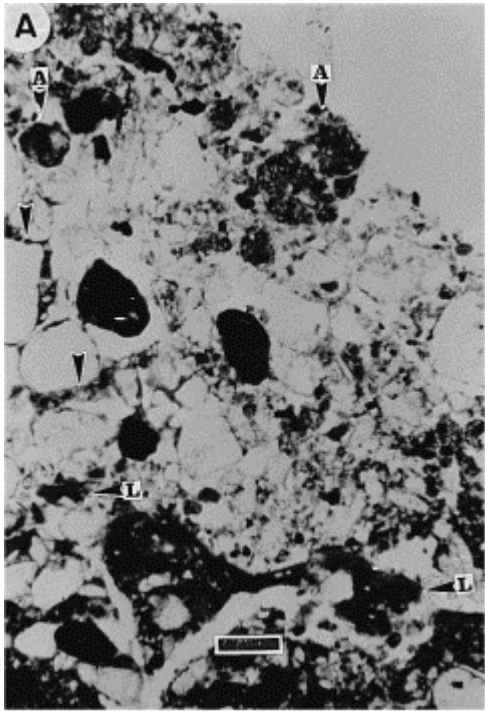
3.3.4. Site 5

At the stereomicroscope scale, the soil surface appeared to be covered by debris of higher plants, mainly tree leaves. Mosses were especially abundant (Fig. 4d) and liverworts were also present. Rare very thin, colourless filamentous micro to organisms were observed in association with rare globular micro-organisms, 100–150 μm in diameter. SEM observations indicated the presence of two species of diatoms.

3.4. Vertical cross-section observations

3.4.1. Site 1

Two different layers were distinguished at this site (Fig. 6a): a superficial layer, 0.5–1.5 mm thick, which contained sand with rare disrupted soil aggregates, and an underlying layer, >4 cm thick, which contained consolidated clay-rich material with rare sand grains. The porosities of the two layers were different (Fig. 6a): pores in the top layer were partially clogged by plasmic material, but in the underlying layer they exhibited laminated clay coatings, probably resulting from illuviation. The two layers correspond, respectively, to the medium layer of fine sand and the bottom layer of fine particles of a sieving crust (Fig. 1).



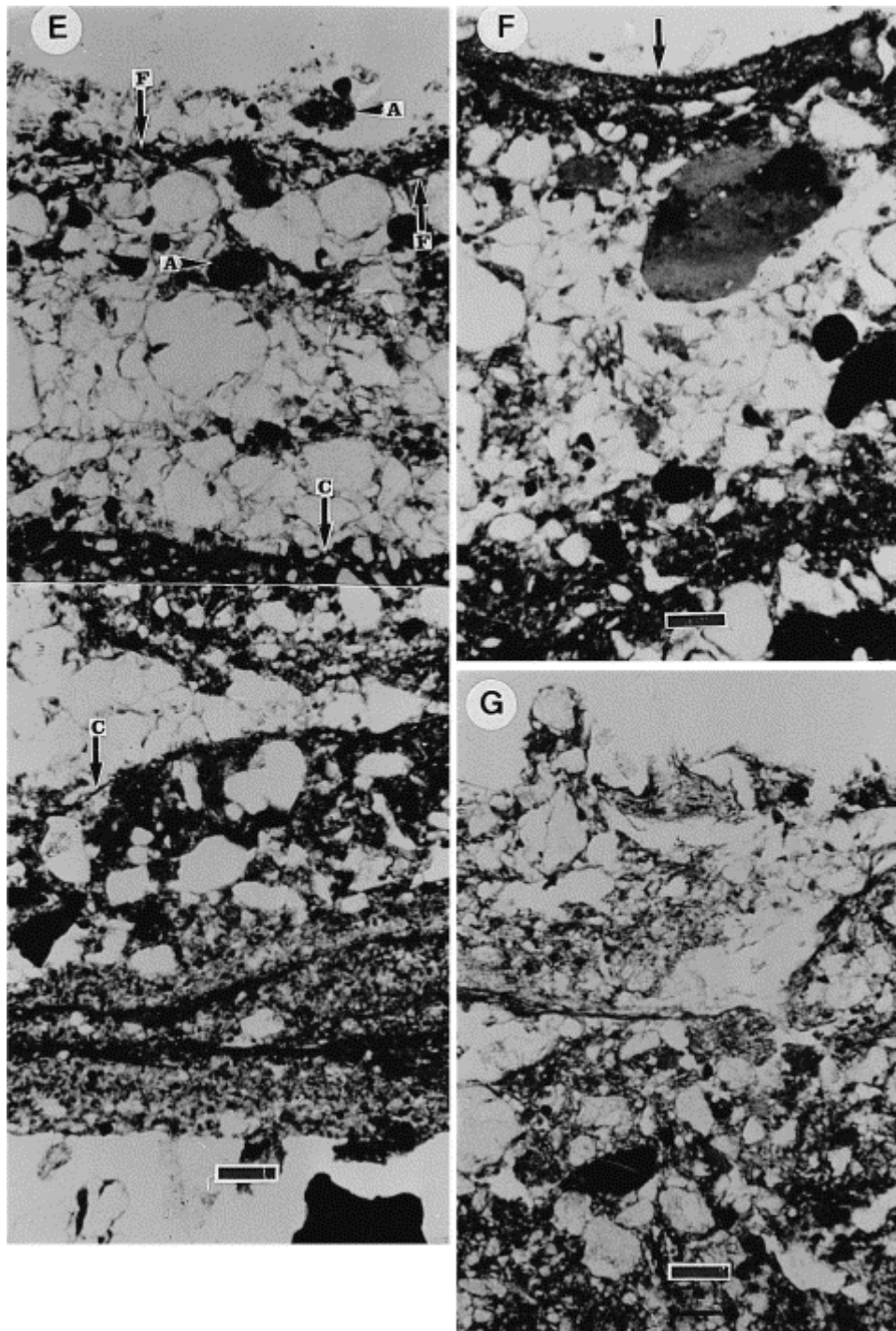


Fig. 6. Photomicrographs of vertical thin sections of soils. Scale bars are 160 μm . (a) Site 1: Sieving crust. Superficial layer of fine sand with disrupted aggregates (A) and clogged pores (arrowed), on a clay rich layer with laminated void coatings (L). The soil surface (upper right) is devoid of organisms. (b) Site 2: Erosion crust. The superficial plasmic layer exhibits laminated clay coatings (L) and rounded to vesicular pores (V). The underlying layer is formed by mixed material and exhibits polyconcave pores (V). (c) Site 2: Area covered with a discontinuous layer of living organisms (arrowed). The plasmic layer is thinner than in bare areas of the same site (b). (d) Site 3: Runoff deposition crust capped by a continuous superficial layer of living filamentous micro-organisms (F). The profile shows alternation of submillimetric sand and clay layers, and non-connected vesicular pores (V). Ancient microbiotic crusts (C) can be recognised at depth. (e) Site 4: Still water deposition crust capped by a continuous layer of living filamentous micro-organisms (F). The profile shows alternating clay and sand layers, which are thicker and better sorted than at site 3. Superficial layers include disrupted aggregates (A). Ancient microbiotic crusts (C) are seen at depth. (f) Site 4: Polygonal cracking (arrowed) of the superficial microbiotic crust. (g) Site 5: Superficial litter layer on non-layered mixed soil material.

3.4.2. Site 2

In the areas devoid of microbial cover, two layers were distinguished (Fig. 6b): a superficial layer, 0.8–1.5 mm thick, formed from plasmic material with rare sand grains, and an underlying layer, several centimetres thick, formed from mixed material. The plasmic layer was smooth and rigid and resulted from clay illuviation, as indicated by the abundance of laminated coatings (Fig. 6b). Pores were rounded to vesicular because of compaction, and partially clogged by clay washed from the soil surface. These features are characteristic of erosion crusts (Fig. 1). The lower layer contained mixed, non-sorted material, which consisted mostly of mixed sand, clay in intergrain spaces and non-living organic material (Fig. 6b).

In the areas covered with a microbiotic crust (Fig. 6c), the plasmic layer was thinner (0.1–0.2 mm thick), more structured, and contained more sand grains and non-living organic material than in bare areas (Fig. 6b). The boundary with the underlying layer of mixed material was diffuse. Pores were tubular and interconnected. Under SEM, the organic constituents of this layer, in particular the filaments, appeared to surround and bind soil particles into a coherent network (Fig. 7a,b). Organic bodies with a porous structure and comprising micron-sized spheres were frequently observed (Fig. 7a,c). X-ray microanalysis of the organic constituents revealed detectable amounts of Cl, K and Na, in addition to C.

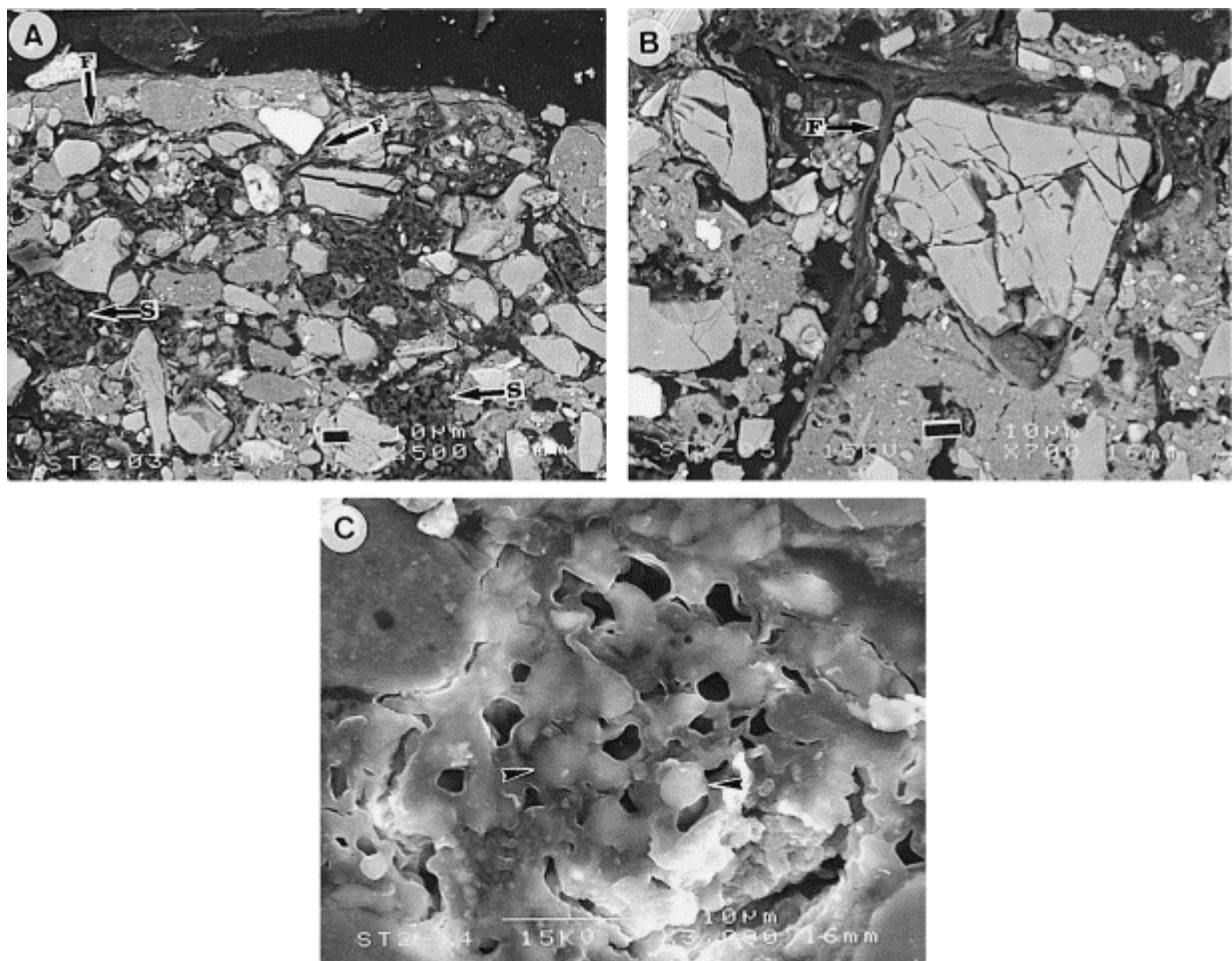


Fig. 7. SEM micrographs (backscattered electron mode) of a vertical thin section at site 2. (a) Cyanobacterial filaments (F) and dark organic bodies enmesh mineral grains. Some organic bodies appear to be micron-sized

spheres (S). (b) Enlarged view of an area in (a), showing cyanobacterial filaments (F) surrounding mineral grains. (c) Enlarged view of a dark organic body in (a). Note the porous structure of the organic matter and the presence of microspheres (arrowed).

3.4.3. Site 3

The soil profile exhibited alternating clay- and sand-rich layers (Fig. 6d) characteristic of runoff deposition crusts (Fig. 1). The soil can be subdivided into rhythmic units of variable thickness (0.2–0.4 mm), composed of a layer of sand overlying a thin layer of clay (Fig. 6d). Pores were rounded to vesicular because of compaction (Fig. 6d). The superficial microbiotic crust comprising filamentous cyanobacteria was formed at the surface of a clay layer (Fig. 6d). Ancient microbiotic crusts were recognised at depth as black organic laminae overlying clay layers (Fig. 6d). Filaments and porous organic bodies similar to those at site 2 (Fig. 7a,c) were also observed by SEM in this site, below the superficial layer of living cyanobacteria. X-ray microanalysis again indicated detectable amounts of Cl, K and Na in the organic material.

3.4.4. Site 4

As at site 3, the soil exhibited alternating layers of clay and sand (Fig. 6e). The microbiotic crust, 0.7 mm thick and made of filamentous cyanobacteria, was formed at the surface of a clay layer ca. 0.1 mm thick (Fig. 6e). Superficial polygonal cracking was observed with the light microscope (Fig. 6f). Filaments and porous organic bodies, similar to those present at sites 2 (Fig. 7a,c) and 3, were observed at depth, also with the same enrichment in Cl, K and Na.

Below the microbiotic crust, the soil profile was composed of two successive units (Fig. 6e): in the upper unit ca. 3 mm thick, the clay and sand layers were thicker (0.6–1 mm) and better sorted than at site 3, whereas the microstructure of the lower unit was closer to that at site 3. In the clay layers of the upper unit the clay was usually associated with non-living organic matter at the top, but was mixed with silt and sand particles at the bottom (Fig. 6e). The features of the upper unit are characteristic of a still water deposition crust. As at site 3, ancient microbiotic crusts were recognised at depth (Fig. 6e).

3.4.5. Site 5

Two different layers were distinguished at this site (Fig. 6g): a superficial, discontinuous layer, ca. 1 mm thick consisting of mixed higher plant debris, sand grains, and finer mineral particles and an underlying layer consisting of material of various sizes disturbed by vegetation growth.

4. Discussion

4.1. Biological composition

As observed by others, the microbiotic crusts we studied were formed by microbial communities dominated by cyanobacteria. However, they differed from most other crusts in that the prevalent genus was *Schizothrix* (Table 2). Other microbiotic crusts are dominated by *Scytonema* sp. in the N'Djamena region, Tchad (Dulieu et al., 1977) and in savanna zones of Nigeria (Isichei, 1980), by *M. sociatus* in the western Negev Desert, Israel (Lange et al., 1992) and by *Microcoleus* spp. in desert soil crusts in Idaho, Utah and Colorado (Brock,

1975; Campbell, 1979). In semi-arid and arid lands of North America, the most widespread species of cyanobacteria is *M. vaginatus*. (Vauch.) Gom. Only in hot desert regions have microbiotic crusts been hitherto reported to consist mainly of *Schizothrix* (Johansen, 1993). Chlorophyta and liverworts are also common components of the microbiotic crusts in the tiger bush.

4.2. Soil stabilisation

Micro-organisms and mineral grains are closely associated at the surface of the tiger bush microbiotic crusts. The network of filamentous cyanobacteria traps sand grains, and clay and silt sized particles adhere to the surfaces of filaments (Fig. 4c, Fig. 5a,b,d). This has already been noted in other microbiotic crusts by Cameron and Devaney (1970) and Belnap and Gardner (1993). The ability of cyanobacterial filaments to cement mineral particles to the surface of their polysaccharide envelopes is well known (Pentecost and Riding, 1986). Filament prints on the surface of mineral grains (Fig. 5c) suggest slight dissolution of the mineral at the contact with the filament.

Below the superficial layer of living cyanobacteria intermingled with mineral grains, filaments and organic bodies also appear to enmesh soil mineral particles (Fig. 6d, e, Fig. 7a,b). The porous organic bodies presumably derive from extracellular polymer secretions (EPS) of micro-organisms. Cyanobacteria and other bacteria commonly produce polysaccharide EPS which reorganize into three-dimensional networks (Défarge et al., 1996). The role of EPS in soil aggregate stabilisation has already been mentioned by Tisdall and Oades (1982). In the tiger bush soils this organic matter could be produced by the filamentous cyanobacteria or the microspheres (bacteria?) associated with the porous bodies (Fig. 7a,c).

The micro-organisms which form tiger bush microbiotic crusts thus provide cohesion to the soil through the trapping and binding effects of superficial living filaments and of microbial organic material present at depth. This cohesion enhances soil stabilisation against water and wind erosion, as was confirmed by placing bare soil samples from site 1 in water; they were completely dispersed after two days, whereas microbiotic crust samples from sites 2 to 4 remained intact after several months of immersion. In situ measurements made at other sites near Banizoumbou have shown that fewer mineral particles are removed from microbially-covered soils compared with bare soils (Malam Issa et al., 1998). These results agree with other studies, which have shown less erosion of soils covered by microbiotic crusts (Eldridge and Greene, 1994; McKenna Neuman et al., 1996; Eldridge and Kinnell, 1997).

At sites 3 and 4, the depositional crusts were interlayered at depth with ancient microbiotic crusts (Fig. 6d,e). In addition to their role in stabilisation of underlying soil, microbiotic crusts are thus probably involved in mineral particle retention and deposition on their surface, and therefore in soil accretion. Cyanobacterial mats, including *Schizothrix*-dominated mats, have been shown to control underwater particle sedimentation in shallow subtidal and intertidal marine areas (Neumann et al., 1970). In the depositional sites of the tiger bush, soil accretion occurs through a rhythmic aggradation of layers, alternately organic and mineral. The resulting structure is sedimentary rather than pedogenetic, and may be considered as a terrestrial stromatolite. Similarities between certain microbiotic soil crusts and stromatolites were noted by Campbell (1979).

4.3. Soil–water interactions

Microscopic observations of tiger bush samples revealed two features which may influence the water regime of the soil: (1) intertwining of the filamentous organisms at the soil surface delineates pores of significant sizes (Fig. 5a,d), which could favour water infiltration; (2) the presence of porous organic bodies at depth (Fig. 7a,c), which enhances the water retention capacity of the soil.

When wetted, two possible kinds of behaviour can be expected from the polysaccharide constituents of cyanobacterial envelopes and of spongy organic bodies: (1) swelling resulting from absorption of water by the polysaccharide constituents is limited and the pore field allows water circulation, or (2) swelling reduces the pore size and enhances water retention by capillary forces. According to Verrecchia et al. (1995), the absorption of water by biological material and the retention of water by strong capillary forces are the ways in which microbiotic crusts limit water infiltration and promote runoff when rain starts.

The influence on the water regime of other organisms such as termites, which were conspicuous at site 4 (Fig. 2e), should also be considered. The foraging activity of these organisms has been shown to enhance water infiltration (Ouedraogo, 1997).

Further studies are necessary to determine the interactions of tiger bush microbiotic crusts and water. Laboratory measurements have indicated that microbial crusts enhance the water retention capacity of Sahelian soils similar to those of the tiger bush. At pF 2.5, water retention was 6.8–36% for microbially-covered samples but only 2.1–3.8% for bare samples (Malam Issa, unpubl. data).

4.4. Chemical composition

The presence of photosynthetic micro-organisms may account for the organic C enrichment of the surface layer of microbiotic crusts compared with bare and litter-covered soils (Table 1). The phototrophs fix atmospheric CO₂ at rates estimated by Beymer and Klopatek (1991) for microbiotic crusts in Pinyon-Juniper woodlands (Northern Arizona, USA) to range from 43 (grazed soil) to 350 kg C ha⁻¹ yr⁻¹ (ungrazed soil). A sample from site 4 of Banizoumbou tiger bush has been shown to fix 4.3–5.3 mg C m⁻² mn⁻¹ under laboratory conditions (Malam Issa, unpubl. data).

The supply of nitrogen in microbiotic crusts is mainly from cyanobacteria and lichens (Mayland et al., 1966; Jeffries et al., 1992). Nitrogen fixation in crusts can vary from 1 to 100 kg N₂ ha⁻¹ yr⁻¹ (Jeffries et al., 1992). In the tiger bush soils, which do not support lichens, nitrogen should be fixed mainly by the heterocystous cyanobacterial species *Nostoc* sp., *Scy. javanicum* and *Scy. stuposum* (Table 2). Some other species of cyanobacteria devoid of heterocysts are also able to fix nitrogen (Stal, 1995; Bergman et al., 1997).

4.5. Microbiotic crusts in tiger bush dynamics

The microscopic features of the tiger bush sequence revealed a specific organization of the soil between successive vegetated bands (Fig. 3). From the decaying part of the upper band down to the flourishing part of the lower band, the soil surface consists successively of a sieving crust (site 1), an erosion crust (site 2), a runoff sedimentation crust (site 3) and a still water deposition crust (site 4). In site 4, the still water deposition crust caps an ancient runoff

deposition crust analogous to that at site 3 (Fig. 3). The superficial layer of the crust at site 2 corresponds to the lower, plasmic layer of the sieving crust at site 1 (compare Fig. 6a and b). The erosion crust at site 2 probably results from the evolution of a sieving crust (Fig. 3). Deposition of particles translocated from sites 1 and 2 induces the formation of depositional crusts at sites 3 and 4 (Fig. 3). These observations confirm the dynamic model of Bresson and Valentin (1990). The downward movement of water which controls the formation of the tiger bush landscape is also responsible for the organisation of soil between the vegetated bands.

The cyclic evolution which results from the upslope migration of vegetated bands also affects the soil crusts. Vegetation decay at site 5 creates a bare soil which will evolve into a structural crust (site 1 type). The structural crust will be replaced by an erosion crust (site 2 type), then by a depositional crust (site 3 and site 4 types) supplied by particles translocated from structural and erosion crusts formed above. The depositional crust will be progressively invaded by the upslope migrating vegetation and thus become a site 5 type soil.

The microbiotic crusts are essential components of the tiger bush ecosystem. The zonation of microbiotic crusts is parallel to the tiger bush banding (Fig. 3). Site 1 is devoid of any microbial cover. The density of microbial cover increases from site 2 to site 4, and the microbial communities present at site 5 are close to those forming microbiotic crusts at sites 2 to 4 (Table 2). The most extensive development of microbiotic crusts is associated with temporary accumulations of water at site 4. The microbial cover enhances stabilisation of depositional crusts and promotes retention of sand and clay particles on their surface. The continuous aggradation of mineral layers, whose surface is recolonised by micro-organisms after deposition, results in soil accretion at this site. The resulting soil provides a stabilised, well-moistened and nutrient-enriched substrate for the upslope migration of plants from the adjacent vegetated band (site 5). The microbiotic crusts are then destroyed by root and faunal bioturbation which follows the establishment of higher plants.

5. Conclusions

This study has documented further occurrences of microbiotic crusts formed by cyanobacteria, chlorophyta and liverworts on the surface of soils in semi-arid tiger bush woodlands. The results confirm the role of a microbial cover and derived organic matter in microstructure development and stabilisation of the soils.

The microbiotic crusts are essential components of the tiger bush ecosystem. The downward movement of water, which controls the dynamics of the tiger bush landscape, also controls the lateral and vertical successions of crusts in the tiger bush sequence studied. The formation of microbiotic crusts in the lower parts of bare bands helps retain water, resist erosion and accumulate soil. Microbial activity also results in C and N enrichment of superficial soil. The upslope development of trees and shrubs of the vegetated bands takes place on this substrate. The development of microbiotic crusts between the zones with higher plants appears to be a biological adaptation favourable to the preservation of the structure and nutrient level of the soil during periods of denudation.

Microbiotic crusts may thus play a specific role in the conservation and improvement of soil properties in Sahelian regions. Through increase of resistance to erosion, enrichment in essential nutrients, and control on water uptake, they can favour the establishment of farm crops.

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