

Microbiotic Soil Crusts: A Review of their Roles in Soil and Ecological Processes in the Rangelands of Australia

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Abstract

Microbiotic crusts are assemblages of non-vascular plants (mosses, liverworts, algae, lichens, fungi, bacteria and cyanobacteria) which form intimate associations with surface soils. They play a major role in infiltration processes through changes to soil physico-chemical properties, and through their influence on soil surface roughness. Whilst some research suggests that they may restrict infiltration, Australian experience is that they are generally associated with enhanced infiltration. Unlike physical soil crusts, microbiotic crusts stabilize the soil against water and wind erosion, increasing landscape stability, particularly in areas of low vascular plant cover. Microbiotic crusts are thus useful indicators of soil surface condition, and cyanobacteria in the crusts fix nitrogen which may be utilized by developing vascular plant seedlings. Little is known, however, about how they interact with vascular plants and soil invertebrates. Their role in rangeland ecosystems has received renewed attention over the past few years with an increasing interest in ecologically sustainable development of arid and semi-arid grazing systems.

In this review we discuss the characteristics and distribution of microbiotic crusts in the rangelands of Australia, their roles in soil and ecological processes and the impacts of fire and grazing. Finally we propose a new system for classifying crusts into functional groups and identify areas requiring further investigation.

Keywords: microbiotic crusts, microbiota, cryptogamic crusts, semi-arid rangeland, soil crusts, moss, lichen, cyanobacteria.

Introduction

Microbiotic crusts are the dominant biological surface features in arid and semi-arid landscapes supporting vascular plant communities (Metting 1991). Microbiota are complex assemblages of mosses, liverworts, blue-green algae (cyanobacteria), lichen, fungi and bacteria, common non-vascular components of many landscapes. They are found in mesic environments, tropical and temperate deserts and in the polar regions of the globe. Where these complexes of plants and animals occur in association with surface soils, they are known collectively as cryptobiotic (Harper and Pendleton 1993), microfloral (Loope and Gifford 1972), microphytic (West 1990) or microbiotic (Skujins 1984; Downing and Selkirk 1993) crusts.

1993) crusts. Fig. 1 shows a typical well developed microbiotic crust found in the semi-arid woodlands of N.S.W. It comprises a mixture of mosses, lichens and algae, probably with associated bacteria and fungi. Microbiota and associated soil crusts are differentiated from other soil surface features such as vesicular horizons (Eckert *et al.* 1978; Dobrowolski and West 1991) and rain-impact and depositional crusts (Chartres 1992) by being organo-genic in nature (Evenari 1985) and by their general effect on infiltration, bulk density, water storage and chemical fertility (Chartres 1992).

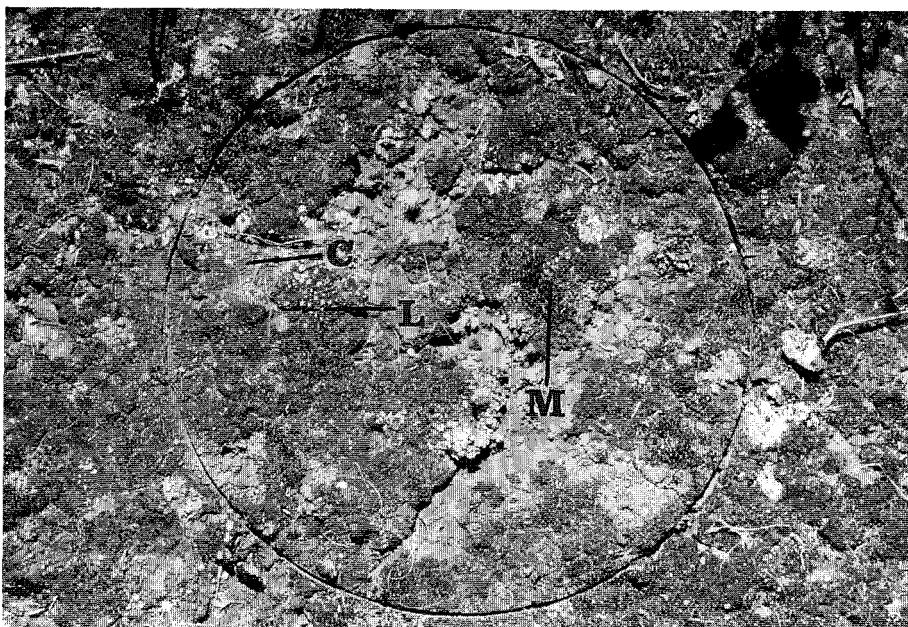


Fig. 1. A well developed microbiotic crust on a clay loam soil at Yathong Nature Reserve. Note the different types of microbiota including moss (M), lichen (L) and cyanobacteria (C). The diameter of the circle is 20 cm.

Microbiota and microbiotic crusts are integral components of the soil surface in many arid and semi-arid regions. During dry periods and droughts, they often provide the only biological form of soil cover. Although their role in hydrological processes is poorly understood, their presence is generally viewed as beneficial in maintaining rangeland stability. They are reputed to play a major role in ecosystem functioning, landscape and soil stability (West 1990), and in processes such as nitrogen fixation (Rogers *et al.* 1966), biomass production (Isichei 1990), and the regulation of infiltration in localized areas (Eldridge 1993b). Microbiota are known to be susceptible to fire (Greene *et al.* 1990), and trampling by livestock (Rogers and Lange 1971, Andrew and Lange 1986a) and are poorly developed on areas which are frequently cultivated (West 1990). An understanding of their role in ecosystem functioning and how they are affected by management is desirable if ecologically sustainable development in the rangelands is to be achieved.

The occurrence of microbiotic crusts is common in many of Australia's arid and semi-arid rangelands. These arid and semi-arid zones occupy approximately

70% of the land area of the Australian continent (Williams and Calaby 1985), and are characterized by high spatial and temporal variability in rainfall (Stafford Smith and Morton 1990). Temperatures are hot in summer and mild to cold in winter. The soils are typically ancient and highly sorted, and low in nutrients and minerals (Stafford Smith and Morton 1990), and the landscapes from which these soils were derived are often flat and highly weathered. Extensive pastoralism, predominantly the grazing of sheep and cattle on native pastures, is the principal land use over much of the rangelands. Aboriginal people own or claim large areas of rangeland in some states, and tourism, mining and conservation are predominant land uses over smaller areas.

Several recent reviews have examined the role of non-vascular plants in stabilizing the soil against wind and water erosion, influencing infiltration, enhancing the nutritional status of rangeland soils, and improving the survival of vascular plant seedlings (Harper and Marble 1989; Isichei 1990; West 1990). These reviews have drawn heavily on published literature from the semi-arid regions of North America, Europe and Israel, and to a lesser extent, Australia. Data on the role of microbiota in the Australian context is either anecdotal and therefore of limited value, or poorly documented, fragmented and hidden in unpublished reports and student theses. There is a need therefore to document, from an Australian perspective, the role of microbiota in arid and semi-arid regions of the Australian continent, particularly from the viewpoint of ecologically sustainable development. The timing of this review is appropriate because firstly, much has been published on the role of microbiotic crusts and microbiota in the past 10 years in Australia, and secondly, there is a need to resolve some of the conflicting points of view on the effects of microbiota on rangeland soils.

The purpose of this paper is to review and discuss the role of microbiota and microbiotic crusts in soil and ecological processes in Australia's arid and semi-arid rangelands. The emphasis is on the mechanisms by which microbiota and microbiotic crusts modify these processes and how they are affected by management. Where appropriate, reference is also made to overseas work. Finally, suggestions are made on the direction of future research.

Characteristics and Distribution of Microbiotic Crusts

Terminology used to describe Microbiota and Microbiotic Crusts

There has been widespread confusion over the many terms used to describe the biological components of soil crusts. The term *cryptogam* has traditionally been used to describe the diminutive members of the non-vascular plant kingdom, i.e. those plants lacking a phloem and xylem. Where these plants occur in association with surficial soils, the terms *cryptogam* or *cryptogamic crust* have been used, particularly by soil scientists and geomorphologists, to differentiate these surfaces from non-biogenic crusts. The terms *cryptogam* and *cryptogamic* are, however, not well received by biologists or ecologists, possibly because they imply that all the members are plants (*gamos* = seed *Gk.*), thereby ignoring the bacteria and algae which are not true plants. Of increasing popularity is the term *microphyte*, which although excluding non-plant components, emphasizes the more diminutive members of the non-vascular flora and separates them from

the total terrestrial vegetation (West 1990). Harper and Pendleton (1993) used the term *cryptobiota*, and Downing and Selkirk (1993) the term *microbiota*, both of which allow for the inclusion of algae, fungi and bacteria. We prefer to use the term *microbiota* which emphasizes the small nature of the organisms in the crust and does not exclude algae, fungi and bacteria. In the concluding section we attempt to eliminate the confusion over terminology by suggesting an alternative system for classifying microbiotic crusts.

In this review, we concentrate our attention on the most visible components of the crusts; the mosses and liverworts (bryophytes) and lichens. Because of problems of taxonomy and field identification of algae, fungi and bacteria, most published research refers to microbiotic crusts comprising lichens and mosses, as these are the more visible in the field.

Distribution of Microbiota

Substrate, microrelief and disturbance patterns are the most important factors determining the establishment and maintenance of microbiotic crusts (Metting 1991). Microbiota are ubiquitous in nature, being found over most of the arid and semi-arid regions of the world including Antarctica and sub-Antarctica (Seppelt 1986). In Australia, microbiota are found over extensive areas of the semi-arid and arid zones, in all vegetation communities and on most soil types. World-wide, they are commonly found in areas which are not frequently cultivated, flooded or burned, and which are not excessively stony, sandy or intensively inhabited by animals or humans (West 1990).

The distribution of microbiota is variously reported in the literature and is mainly related to the individual groups, e.g. mosses, lichens, liverworts, blue-green algae, etc., comprising the total microbiotic flora. The following discussion is a brief description of the factors affecting the distribution of some of the more visible microbiotic groups.

Mosses and liverworts

The mosses and liverworts, collectively known as *bryophytes*, are found over extensive areas of Australia in a variety of landscapes (Scott and Stone 1976; Scott 1985). Although they provide variable cover on the soil surface, they do not form true surface crusts (Richardson 1981). Despite this, some mosses such as *Gigaspermum repens* grow well on loose dune soils, probably due to their ability to produce dense networks of underground stems. This makes them important soil stabilizing agents.

Soil factors, particularly clay content and pH, appear to be influential in determining the distribution of bryophytes (Howarth 1983). Anderson *et al.* (1982) found that abundance and species diversity increased with the clay content of the substrate. In an aeolian-dominated landscape in semi-arid eastern Australia, Downing and Selkirk (1993) found that the lowest cover of bryophytes occurred on the dune sands, which were the most unstable, had the lowest pH, and were the most freely draining. They also found a remarkable similarity in the bryophyte flora between the calcareous soils on a semi-arid landscape in western N.S.W. (Mungo National Park), and that growing on a limestone substrate in humid areas of eastern Australia (Jenolan Caves).

Lichens

Lichens result from a symbiotic relationship between an alga and a fungus, with each combination producing a specific lichen. Lichens generally develop more slowly than mosses and liverworts, preferring more stable areas with minimal disturbance. Like the bryophytes, lichens are thought to be more common on fine-textured soils but not on sands nor self-mulching clays (Rogers and Lange 1972; Rogers 1977). Soil pH is also implicated in distribution with few species confined to soils with high levels of extractable calcium (Rogers 1977), i.e. highly alkaline soils.

The distribution of lichens is also strongly influenced by climatic patterns, particularly the amount and distribution of rainfall (Rogers 1971). In some areas where summer rains are not infrequent, the wet thalli of lichens may be damaged as a result of high temperatures. Rogers (1977) suggests that this controls the distribution of the lichen *Chondropsis* sp. in eastern Australia, as it only occurs in areas where winter rainfall predominates. The reduction in cover of lichens from areas subjected to increased summer rainfall, a hypothesized consequence of greenhouse and global warming, may lead to an increase in the competitive advantage of blue-green algae at the expense of lichens (Rogers 1989).

Because the development of lichen cover is restricted to stable landscapes, they have often been regarded as bio-indicators of ecological change. Landscape instability appears to limit their development. Studies from the Koonamore exclosures in South Australia demonstrated that the presence of the chenopod shrubs *Atriplex vesicaria* and *A. stipitata* was a precursor to the development of a lichen-dominated microbiotic crust (Hall *et al.* 1964).

Algae

Algae are the least visible components of microbiotic crusts and are widely distributed throughout Australia's rangelands where they occur as symbionts with crustose lichens and fungi in microbiotic crusts. Despite their ubiquitous distribution, their taxonomy is poorly understood. Algae are thought to have a preference for alkaline soils, and are more tolerant of microsites prone to regular disturbance by wind, water and grazing animals (Metting 1991). Rogers *et al.* (1966) identified 44 species of lichen growing in the central arid zone of South Australia. The crust formed by these and other free-living algae and other non-vascular flora occupy up to 30% of the total soil area.

Functions of Microbiotic Crusts in Landscape and Soil Physical and Ecological Processes

The Role of Microbiota in Landscape Processes

Microbiota are often associated with sparsely vegetated landscapes which might otherwise have high natural rates of erosion. They are thought to impart stability to these landscapes largely through their influence on soil hydrologic and erosion processes.

Hydrologic processes

Field observations of microbiotic crusts in Australia show that they are thin (1–2 mm), often discontinuous layers associated with rain-impact and depositional

crusts (Chartres 1992). Moss (1991) described a rain-impact crust [also called structural crust (Shainberg 1985)] as a surface soil layer that has been physically compacted, with little or no addition of surface solids, to a depth of 3–5 mm. Depositional crusts occur as a result of the deposition of material from both flowing and stationary turbid water (Chartres 1992).

Crusting of soil surfaces is generally thought to reduce infiltration and therefore increase runoff and the likelihood of erosion (Romkens *et al.* 1990). While the infiltration and permeability of rain-impacted and depositional crusts are generally well understood, there is conflicting evidence on the role of microbiotic crusts in regulating water flow into soils. Examples from overseas work have shown that, while increased infiltration has been observed on areas with microbiotic crusts compared with areas without crusts (Fletcher and Martin 1948; Gifford 1972; Blackburn 1975), other work (Loope and Gifford 1972; Danin 1978; Brotherson and Rushforth 1983) has demonstrated reductions in infiltration on soils with variable cover of microbiota.

Studies in Australia have also shown conflicting results on the role of microbiotic crusts in regulating infiltration. For example, in an area near Cobar, N.S.W., on degraded massive red earth soils, a patchwork pattern of non-eroded (Class 1) to seriously eroded (Class 4) soil surfaces could be identified (Greene and Tongway 1989). The coverage by microbiota on these surfaces ranged from very high on Class 1 surfaces through to zero on Class 4. Under ponded infiltration, final infiltration rates of 49 mm h^{-1} were measured on the Class 1 compared with 8 mm h^{-1} on adjacent eroded Class 4 surfaces. However, Graetz and Tongway (1986) found the opposite effect on sandy loam soils in chenopod shrublands in South Australia. When high intensity rainfall (75 mm h^{-1}) was applied to the soil surface with a lichen crust, the final infiltration rate was $<10 \text{ mm h}^{-1}$ compared with 45 mm h^{-1} on an adjacent surface where the crust had been removed by heavy grazing. Similar results were obtained at the Koonamore Vegetation Reserve in South Australia, where the presence of a lichen crust on a sandy soil reduced the infiltration rate to 70 mm h^{-1} compared with 140 mm h^{-1} in a nearby area of similar soil without crust (Rogers 1977). Several 'scalping' experiments have shown that removal of this upper 1–2 mm of microbiotic crust results in enhanced infiltration (Graetz and Tongway 1986; Greene and Tongway 1987; Yair 1990), which suggests that microbiotic crusts do cause reductions in infiltration.

These conflicting results on the role of microbiota and microbiotic crusts in infiltration are at first difficult to explain. Differences in infiltration may be due to different crust composition, or differences in the moisture status of the crusts. During small rainfall events, microbiotic crusts can be expected to enhance infiltration by absorbing water and by increasing surface retention due to their effect on increasing variation in microtopography (Eldridge and Greene 1994). However, microbiotic crusts, by forming an intimate association with surface soil particles, may actually lead to a partial or complete closing of many of the conducting pores at the surface. This effect is apparent in the scanning electron micrograph in Fig. 2 which shows that the upper 1–2 mm layer of a microbiotic crust is relatively non-porous compared with the soil below. Therefore it is probable that, during most rainfall events, microbiotic crusts will decrease hydraulic penetration and limit water entry. The probable reason for the

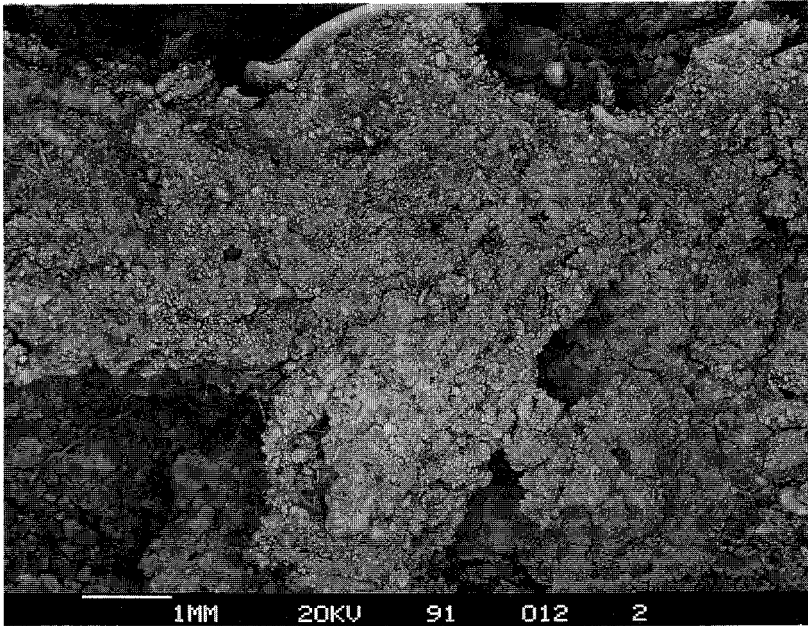


Fig. 2. A scanning electron micrograph of a microbiotic crust. Note how the upper 1-2 mm is non-porous compared with the soil below.

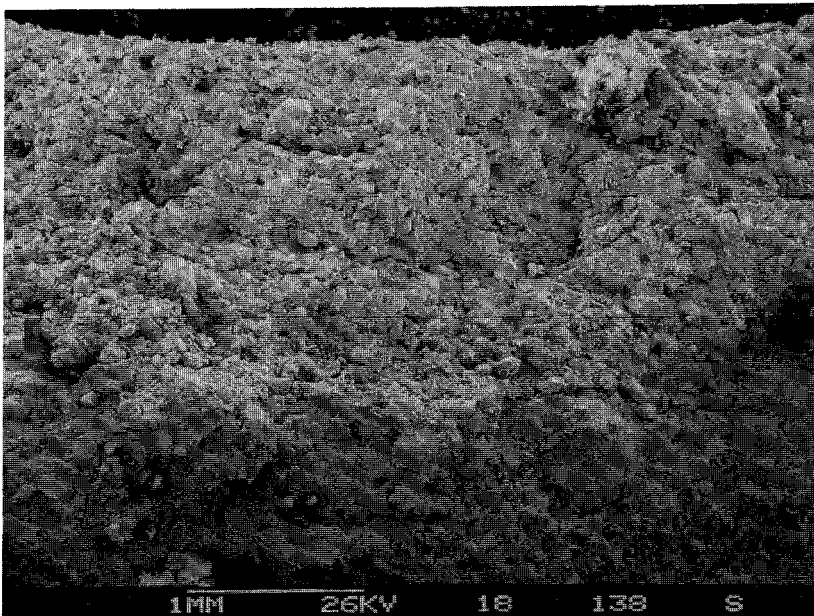


Fig. 3. A scanning electron micrograph of a Class 4 soil consisting of a dense, compacted surface.

difference in infiltration rates, measured on the massive red earth soils at Cobar, is that the surfaces without microbiota (Class 4 soils) already have an intrinsically lower infiltration rate due to the eroded nature of their surfaces (Mucher *et al.* 1988). The densely compacted nature of a Class 4 surface is shown in Fig. 3. In situations where the soil has been previously degraded, it is probable that the presence of microbiota on the soil surface increases the availability of entry points for water into the soil, thereby increasing infiltration (Eldridge 1993b).

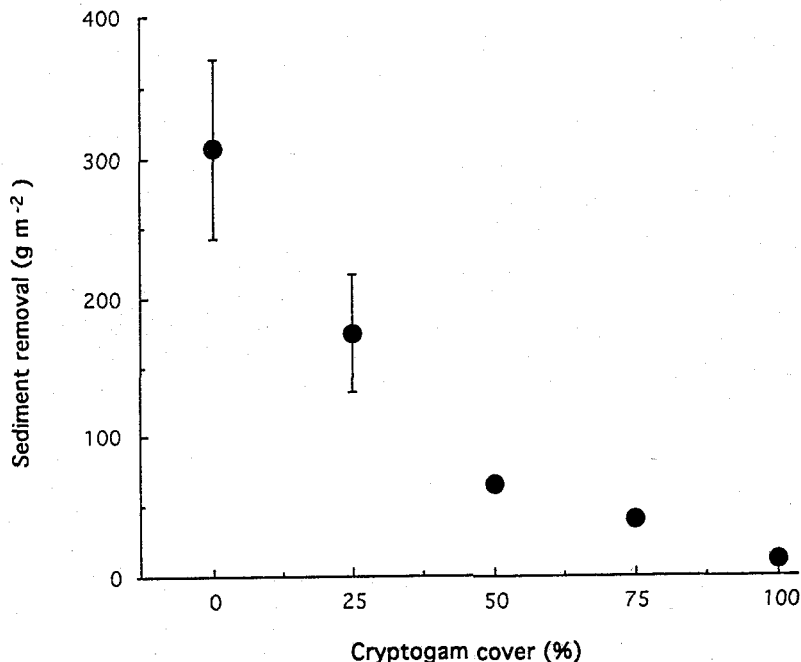


Fig. 4. Mean sediment removal for five levels of microbiotic (cryptogam) cover. Symbols fully enclose standard errors of the mean unless otherwise indicated.

Water and wind erosion processes

Most of the studies on the role of microbiotic crusts in moderating erosion processes have been related to water erosion. There are many accounts in the literature of reduced water erosion due to microbiotic crusts (e.g. Mucher *et al.* 1988; Campbell *et al.* 1989; Chartres and Mucher 1989; Kinnell *et al.* 1990; Greene *et al.* 1990; Eldridge 1993a; Eldridge and Greene 1994). In the semi-arid woodlands of eastern Australia, microbiotic crusts have been found to be quite effective at reducing sediment loss from red earth soils. Removal of the grass cover by burning, and damage to the underlying microbiotic crusts by heavy rainfalls (up to 140 mm h^{-1}), increased runoff and erosion (Chartres and Mucher 1989). Kinnell *et al.* (1990) also found that microbiota protected the soil from shallow rain-impacted flow. Sediment yield was 3–5 times greater on rain-impact and depositional crusts than microbiotic crusts. Eldridge and Greene (1994) reported a strong positive relationship between cover of microbiota and splash erosion in the absence of vascular cover. As microbiotic cover increased, there

was an exponential decline in total splash erosion (Fig. 4) and an increase in the proportion of coarse material in the sediment. Similarly, Alexander and Calvin (1990) showed that lichen-covered plots in the Spanish Badlands produced lower sediment concentrations than bare soils.

Studies demonstrating the role of microbiotic crusts in wind erosion have mainly been carried out overseas. For example, Williams *et al.* (1993) showed that higher threshold friction velocities were needed for the initiation of wind erosion where undisturbed microphytic crusts were present. West (1990) discussed how trampling by humans, livestock and vehicles breaks down microphytic crusts and allows the smaller particles to be detached and moved by erosion. In Australia there has been little direct work on the role of microbiota in wind erosion. Andrew and Lange (1986a) showed that an increase in grazing intensity near a water point in an *Atriplex-Maireana* shrubland in South Australia destroyed the lichen crust, increasing soil bulk density by up to 20%. However, the decrease in lichen cover resulted in only small increases in dust fallout. Leys (1992), working with a wind tunnel, demonstrated that surface crusts containing a large proportion of organic matter reduced wind erosion from the surface of sand dunes. Greene *et al.* (in press) showed from micromorphological evidence that these crusts with organic matter contained microbiota. If microbiotic crusts are similar in function to rain-impact crusts, then their presence should reduce wind erosion by reducing wind velocities near the surface. Leys (1990) showed with wind tunnel experiments that fragile soil crusts can reduce wind erosion at a wind speed of 48 k h^{-1} by 10-fold, and that there was 5 times the amount of wind erosion from a disrupted crust than one left intact.

The Role of Microbiota in Soil Physical Processes

Soil aggregation

Several studies have shown that the stability of soil aggregates is enhanced by microbiota. For example, Bailey *et al.* (1973) improved the aggregation of soil particles by inoculating them with algae, and Tisdall and Oades (1982) demonstrated how fungal hyphae bind microaggregates of soil $<0.25 \text{ mm}$ into stable macroaggregates $>0.25 \text{ mm}$. Aggregates from soil surfaces with microbiotic crusts have also been shown to have greater stability than aggregates from bare surfaces (Greene and Tongway 1989; Greene *et al.* 1990). Because microbiotic crusts are often only 1–2 mm in thickness, their effect on aggregation is greatest over that depth of soil. Therefore it is critical, when sampling soils with microbiotic crusts for aggregate stability measurements, to take samples at 1–2 mm depth intervals (Eldridge and Greene 1994).

Scanning electron microscope studies have also illustrated the role of fungal hyphae in microbiotic crusts in aggregating soil particles (Van der Watt and Classens 1990; Chartres 1992). Fig. 5 is a scanning electron micrograph of a microbiotic crust formed on a Typic Haplargid soil. It shows fungal hyphae under the surface of a lichen, encapsulating soil particles and physically binding them.

Microbiota also have the ability to further enhance aggregate stability by secreting gels that bind the cells and their filaments, and surrounding soil particles into small aggregates (Shields and Durrell 1964). Greene *et al.* (1990) presented micromorphological evidence that microbiota secrete amorphous gel-like organic

materials that cement mineral particles together into rounded surface aggregates. Both the physical binding of soil particles by hyphae and the secretion of gels would enhance the stability of the soil surface and help protect it from wind and water erosion. Bond and Harris (1964) and Rogers (1989) pointed out that the filamentous growth habit and production of a mucilaginous sheath can bind soil surfaces and restrict erosion. However, enhanced aggregation due to microbiota can be destroyed by fire. This effect is discussed later under the role of fire.

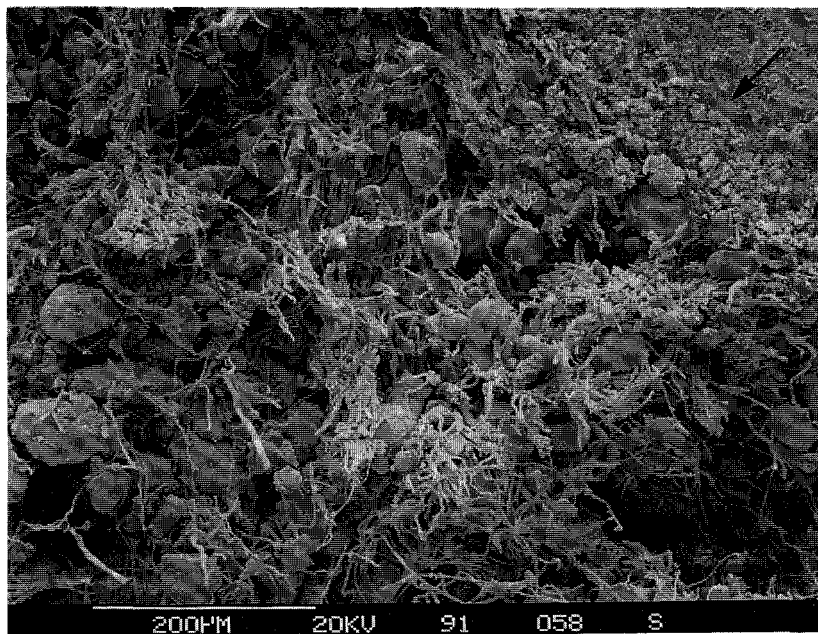


Fig. 5. A scanning electron micrograph of a microbiotic crust. Note the fungal hyphae under the surface of a lichen (arrow), encapsulating soil particles and physically binding them together.

Besides enhancing aggregation, the fungal components of microbiotic crusts have been implicated as a possible cause of water repellency in soils. For example, Bond and Harris (1964) concluded that water repellency in soil was caused by the metabolic products of the microorganisms, after observing that zones of water repellency in the soil always showed evidence of copious fungal proliferation. Savage *et al.* (1969) proposed that soil conditions conducive to fungal growth were the most important factors in inducing water repellence in soils.

The Role of Microbiota in Soil Ecological Processes

Microbiota and nutrient cycling

Australia's arid and semi-arid soils are inherently low in nutrients, especially phosphorus and nitrogen (Williams and Raupach 1983). Nitrogen fixation by blue-green algae has been considered to be important in the nitrogen economy and fertility of arid soils (Tchan and Beadle 1955; Rogers *et al.* 1966) and fixation rates quoted have varied from 2 to 41 kg N ha⁻¹ yr⁻¹ (West 1990). In

the arid zone, light showers are a more common form of rain than heavy rainfall, and microbiotic crusts may be able to capitalize on these. Charley and Cowling (1968) postulated that small falls of rain activate microbiotic crusts, fixing small amounts of nitrogen and adding it to the soil nutrient pool. These small falls, which might also include dew, are generally too transient for plants to begin actively absorbing available nutrients. Eventually, however, sufficient falls of rain following such accumulations of available nutrients would be expected to give an excellent growth response (Charley and Cowling 1968).

Using laboratory studies, Mayland and McIntosh (1966) have also demonstrated the transfer of fixed nitrogen from algal crusts to higher plants. However, some authors (e.g. West 1990, Dobrowolski and West 1991) have warned that increased nitrogen fixation does not automatically mean an increase in productivity of vascular plants. Much of the research has been based on laboratory rather than field-based experiments which may have given misleading results. Kleiner and Harper (1977) suggested that a more important role of microbiotic crusts may be in the conservation of nutrients through the prevention of sheet erosion.

Besides nitrogen, microbiotic crusts have the potential to contribute carbon to soils. Work by Beymer and Klopatek (1991) showed that microbiotic crusts consisting of blue-green algae, other terrestrial algae, lichens and mosses contributed organic carbon fixed in photosynthesis directly to the soil ecosystem. The potential of managing Australia's rangeland soils for sequestering carbon into the soil organic pool has been discussed by Walker and Steffen (1992). However, for a deliberate strategy of carbon sequestration in the rangelands to be effective and acceptable, much better knowledge of soil carbon dynamics is needed (McKeon *et al.* 1992).

Microbiotic crusts and soil invertebrates

Given the greater accumulation of nutrients and vascular plant biomass associated with microbiotic crusts, it is reasonable to expect that microbiotic crusts would enhance the occurrence and survival of invertebrates. Although we are unaware of any research in an Australian context, overseas work suggests a wide range of interactions between microbiotic crusts and invertebrates (West 1990). For example, ants have been observed eating moss capsules (Loria and Hernstadt 1980), and some species such as the desert isopod (*Hemilepistrus reaumuri*) rely on microbiotic soil crusts for energy and protein (Steinberger 1989). Other invertebrates use microbiotic crusts as a habitat (West 1990). Given the increased awareness of the role of microorganisms and invertebrates as bio-indicators of ecosystem health, more attention needs to be directed to possible links between microbiota and soil invertebrates.

Microbiotic crusts as niches for seed entrapment and germination

Although some studies have suggested that microbiotic surfaces enhance the survival of vascular plant seedlings (Harper and St Clair 1985), results are far from conclusive. Intuitively it would be expected that, by increasing surface roughness, microbiota would enhance vascular plant seedling survival by providing a greater number of 'safe sites' (Harper 1977), particularly during unfavourable times. Increased variation in microtopography might also result in small patterns

of extra water and nutrients in homogeneous and flat landscapes (Scott 1982). In some areas dominated by blue-green algae, the microbiotic crust takes on a glazed appearance due to the algal skin, which persists well into summer even when cracked (Scott 1982). This skin increases the variability in surface roughness and microtopography, and helps to prevent sand from engulfing the plants growing on it.

Micromorphological examinations of thin sections of surface crusts from the semi-arid wooded rangelands near Cobar, N.S.W., revealed layers of aggregates, litter and microbiota which could provide refugia for seeds by providing entrapment niches during wind and water erosion events (Mucher *et al.* 1988). The layers were also thought to enhance prospects for germination and establishment of plants, by increasing soil moisture availability (Mucher *et al.* 1988). Eldridge *et al.* (1992) investigated the survival of a number of cohorts of *Atriplex vesicaria* seedlings in relation to soil surface condition and landscape position on a depositional plain near Broken Hill, N.S.W. In their study, survival of seedlings growing in association with microbiotic crusts was not consistently different from that of seedlings growing on bare surfaces or those covered with gravel, sand or litter. The situation may well be different for plants with smaller seeds. Future research by the authors aims to determine whether grass seeds have enhanced germination and survival when grown in association with microbiotic crusts.

The Role of Microbiotic Crusts in Soil Surface Condition Assessment

Ground-based assessment

Because the presence of microbiota and microbiotic crusts is closely linked to enhanced soil structure and aggregation, they are recognized as essential components of soil stability and productivity in semi-arid rangelands. Tongway and Smith (1989) developed a field-based methodology to classify the surface condition of red earth soils in the semi-arid woodlands of eastern Australia. This system reflects differences in the erosional status, nutrient status and stability of the soil surface (Tongway and Smith 1989). It also provides a reliable estimate of the potential productivity of the soil surface, which is independent of any assessment of the vegetation, and is therefore applicable during periods when vascular plants are absent.

Central to this system is the cover, composition and development of microbiota and microbiotic crusts present at range sites. Using the methodology of Tongway and Smith (1989) on a degraded red earth soil near Cobar, four classes of soil in an erosional sequence were distinguished (Greene and Tongway 1989). Cover and species composition of microbiota are high on Class 1 surfaces (stable, productive), low on Class 3 surfaces (moderately unstable and unproductive), and absent on Class 4 surfaces (very unstable and unproductive; Mucher *et al.* 1988). At Yathong Nature Reserve and an adjacent grazed property, Eldridge (1993a, 1993b) studied the relationships between soil surface condition status, cryptogam cover and infiltration. On this red earth soil, three classes were distinguished. Class 1 soils were characterized by high cover, dominated by crustose lichens and moss, and the surface soils were moderately stable under wetting. This was reflected in the high saturated infiltration rates (104 mm h^{-1} ; Eldridge 1993b). The Class 3 surfaces, however, supported only sparse pasture and microbiota, and there

was evidence of considerable erosion and redeposition. The aggregate stability and organic carbon content (0–20 mm) of the Class 3 surfaces were significantly lower than the Class 1 surfaces. These features resulted in reduced infiltration rates in the Class 3 surfaces (65 mm h^{-1} ; Eldridge 1993b). The inference is that cover and composition of microbiota are useful indicators of the status of the soil surface and its capacity for infiltration.

Remote sensing

There may also be a possibility of using microbiotic crusts in assessment of rangeland soils using remote sensing. This arises because the lichen and algal components of microbiotic crusts are associated with photosynthetically active tissue. Lichens depend on moisture to hydrate the thallus and stimulate metabolic activity such as photosynthesis, which can occur rapidly on hydration (Kershaw 1985). Remotely-sensed images recorded after rain would be expected to vary due to differences in spectral response between crusted and crust-free surfaces. Even when the crusts were dry, O'Neill (1994) found that on pale clay soils at Mungo National Park, the crusts could be differentiated from their underlying soil surface due to different spectral signatures. On other soil types, however, differentiation of microbiotic crusts may be more difficult. At a selection of sites at Yathong Nature Reserve, Williamson and Eldridge (1994) reported low correlations between remotely-sensed data and cryptogam cover. This was attributed to marked similarities in the reflectance patterns of microbiotic crusts, the surface soil and senescing vegetation.

In arid and semi-arid ecosystems, therefore, where vascular plant cover is low and spatially discontinuous, crusts may be major contributors to soil reflectance signatures (Graetz and Tongway 1986). Should the hypothesized decrease in cover lichen occur, due to increases in summer rainfall as a result of the greenhouse effect (Rogers 1989), remote sensing techniques may be useful in monitoring the effects of global climatic change.

Management Factors Influencing Microbiotic Crusts

The Effect of Grazing and Disturbance

Microbiotic crusts are generally thought to be susceptible to disturbance by grazing and trampling, particularly when the soils are dry (Marble and Harper 1989). Marked changes in species composition and cover of microbiota have been observed across fence lines and between relict ungrazed areas and adjacent grazed areas. For example, differences in cover and composition of crusts at Yathong Nature Reserve and Mungo National Park and the adjacent grazed rangelands are apparent (Eldridge and Downing, unpublished data). Despite this and other anecdotal evidence, there have been few direct experiments of temporal changes in microbiotic crusts (West 1990). Andrew and Lange (1986a, 1986b), however, showed that during the development of a new piosphere in a semi-arid chenopod shrubland, the frequency of crustose lichens decreased markedly with distance from the water point, and attributed this to sheep grazing. In their study, Andrew and Lange (1986a) showed increases in soil bulk density of up to 20% but only small increases in dust fallout as a result of trampling.

In a similar study of piospheres, Rogers and Lange (1971) found that stocking pressure caused a differential destruction of lichen species close to the watering point. Unlike vascular plants, all lichens were affected to a certain extent, and decreased in frequency as stocking intensity increased. Other studies in chenopod shrublands have also indicated that over-grazing breaks up coherent microbiotic crusts that stabilize the soil at the base of perennial shrubs, allowing the dispersal of the nutrient-rich soil away from the shrubs (Hunt 1992; Williams *et al.* 1994).

Recovery of microbiotic crusts after trampling is thought to be quite slow, especially where heavy vehicular traffic is involved (Braunack 1985). On a heavily eroded soil north of Cobar, recovery of microbiotic cover took approximately 15 years (D. J. Tongway, pers. comm. cited by Mucher *et al.* 1988). After 44 years of exclosure, observations in 1969 showed that lichen cover at Koonamore in South Australia was still markedly reduced. Apart from the usual consequences of disturbance, it is possible that changes in soil texture, brought about by loss of fine material through wind erosion, will have marked effects on the ability of soil microbiota to recolonize a degraded area.

Little is known about natural rates of growth of microbiotic crusts, except that they are slow. Similarly, there are few data on growth dynamics of the individual species comprising the crusts. Glasshouse trials are currently underway to investigate the relative growth rates of microbiota on a range of surface soils found in western N.S.W.

The Role of Fire

Fire is a regular feature of many arid and semi-arid landscapes and occurs either as wildfires or as a result of prescribed burning. In many areas of the semi-arid woodlands, prescribed fire has been shown to be an economical solution for the control of woody perennial vegetation (Burgess 1988), effectively reducing shrub biomass and promoting pasture growth (Hodgkinson and Harrington 1985).

Much of the evidence on the role of fire in the dynamics of microbiotic crusts comes from studies using simulated fires on massive red earth soils in the semi-arid woodlands of eastern Australia. For example, Greene *et al.* (1990) studied the effects of fire on soil properties and demonstrated that continuous burning (annual fires for 7 years) resulted in the complete elimination of microbiota. Continuous burning also eliminated the fungal hyphae and the cementing gels and mucilaginous sheaths associated with the microbiota. This effect is shown in Figs 6 and 7 which show soil particles below a microbiotic crust before fire and after fire, respectively. Before fire, there is an abundance of hyphae compared with after fire. Fire, by removing the gels, also causes the surfaces of mineral particles to appear cleaner. The loss of microbiota and the breakdown in the integrity of the crusts by fire resulted in concomitant decreases in infiltration, increased erosion and structural decline of *in situ* soil aggregates (Greene *et al.* 1990; Kinnell *et al.* 1990). However, only 4 years was necessary for complete recovery (Greene *et al.* 1990). Other studies (Chartres and Mucher 1989) on massive red earth soils had also shown that rills are initiated by rain-impacted shallow flows when microbiotic mats were destroyed by fire.

A limited number of studies in other ecosystems have investigated the impact of burning on microbiota. Gill (pers. comm. 1993) found that the amount of

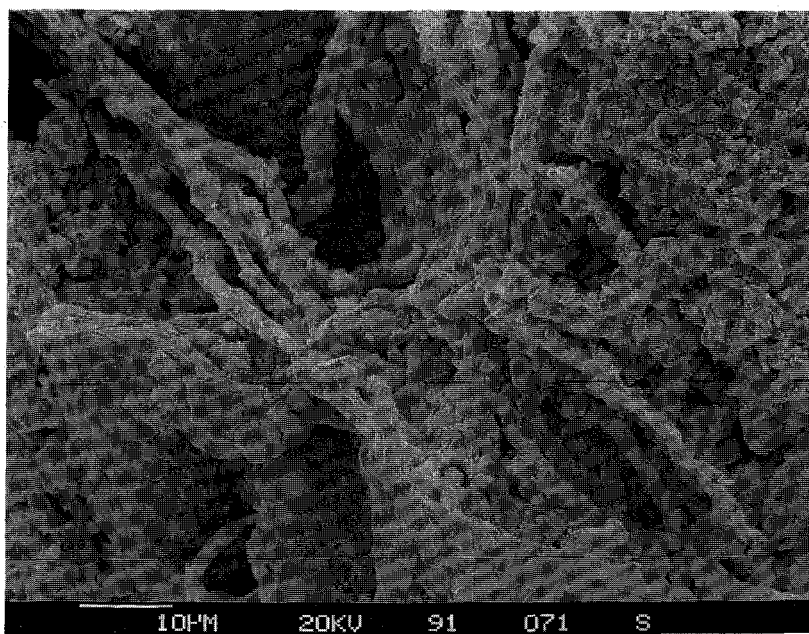


Fig. 6. A scanning electron micrograph of soil particles below a microbiotic crust prior to fire. Note the large number of fungal hyphae and the rough surfaces of the sand grains.

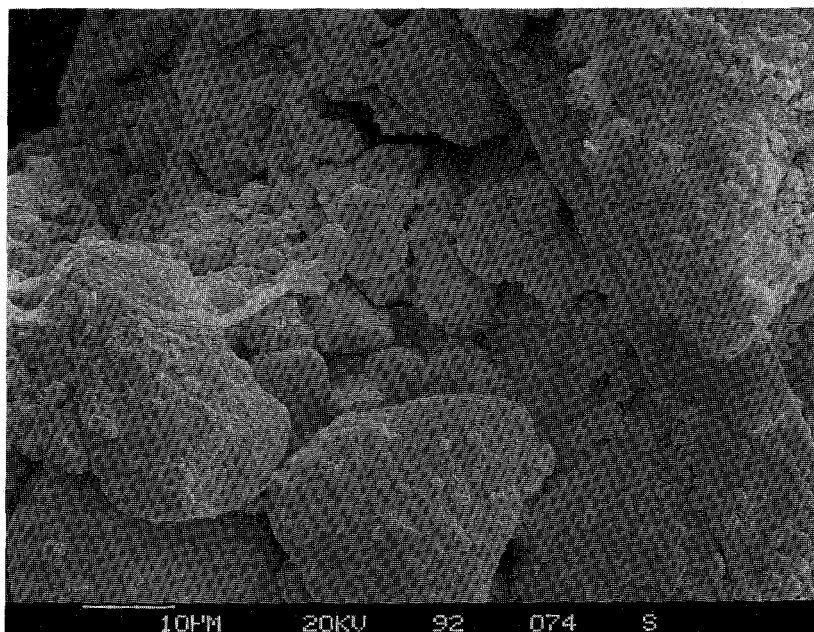


Fig. 7. A scanning electron micrograph of soil particles below a microbiotic crust after fire. Note the absence of fungal hyphae and the smooth surfaces of the sand grains.

wind-induced erosion in spinifex (*Triodia* spp.) grasslands in Western Australia increased markedly as a result of burning. In these grasslands, the soil surface was stabilized by algal crusts, and, by removing the crust, fire probably had a detrimental effect on the soil stability. Eldridge and Bradstock (1994) also studied the effects of fire on microbiotic crusts on aeolian soils dominated by mallee (*Eucalyptus* spp.). In contrast to the rapid recovery of microbiotic crusts on red earth soils (Greene *et al.* 1990), they demonstrated a slow recovery rate of microbiota after fire. Maximum cover of 43% occurred at 13 years post-fire, which coincided with the period of maximum fuel availability. This cover level probably represents the upper limit in these landscapes. An increase in the interval since last fire, increased the cover of crustose lichen and decreased the cover of algae (Eldridge and Bradstock 1994). The results suggested that frequent fires of <10 years duration lead to the predominance of a low cover of algae.

Even though overseas workers (Savage *et al.* 1969) have been able to show that fire induces water repellency in some soils containing microbiota, similar results have not been obtained in Australia. For example, Bogusiak *et al.* (1992) found that on coarse red brown sands in both woollybutt (*Eragrostis eriopoda*) and spinifex (*Triodia basedowii*) grasslands, fire failed to cause water repellency. Tongway and Hodgkinson (1992) also found that low intensity, short duration fires did not cause water repellency on massive red earth soils in a shrub-invaded woodland. Water repellency may be due to a condensation of hydrophobic layers in sandy soils and have little to do with the presence of microbiota *per se* (Gill, pers. comm. 1993).

Microbiota and Ecosystem Processes

Post-disturbance Development of Microbiotic Surfaces

Much of the semi-arid rangelands of Australia have been altered by anthropogenic activities. The original vegetation has been substantially altered, particularly by introduced herbivores and altered fire regimes, resulting in an increase in woody shrubs (Harrington *et al.* 1984), the development of a flora dominated by less-desirable perennial and annual species, and an increase in areas affected by wind and water erosion (Chartres 1992). In this environment, microbiota play a dual role as both constituents of mature arid and semi-arid ecosystems, and as pioneers in primary and secondary plant succession (Metting 1991).

Microbiota are commonly pioneering species in the revegetation of degraded soils (Bailey *et al.* 1973; Booth 1941). A conceptual model of the post-disturbance development of a microbiotic community provides some insight into the role of the various types of microbiota and their relationship to soil physical and chemical properties, and cover of vascular plants (Fig. 8).

After an initial landscape disturbance such as fire or severe overgrazing, non-vascular plants are the primary colonizers of a site. Depending on soil type, raindrop action and erosion processes lead to the formation of a rain-impact crust, throttling infiltration and interfering with seedling emergence (Moss 1991). This crust may later be colonized by biological elements to form a microbiotic crust (Scott 1982). Alternatively, a rain-impacted soil crust (Fuller 1974) bonded by silicon or carbonate may become stabilized by a layer of filamentous blue-green algae.

Apart from stabilizing the surface against erosion, algal crusts may enhance soil nutrient levels. Decaying algae supplement the organic matter store in the soil, and living algae may make essential nutrients available for uptake by pioneering vascular plants (Harper and Pendleton 1993). These added nutrients may be sufficient to provide threshold levels for short-lived pioneering vascular plants (Isichei 1990). Cover of algae reaches a peak and declines as vascular plant cover increases (Fig. 8). Short-lived plants are gradually replaced by biennials and finally perennial plants, which invest a greater proportion of their reserves in the maintenance of a favourable environment. This might include increased soil structure, facilitation of flow paths for infiltration and stability of the soil surface.

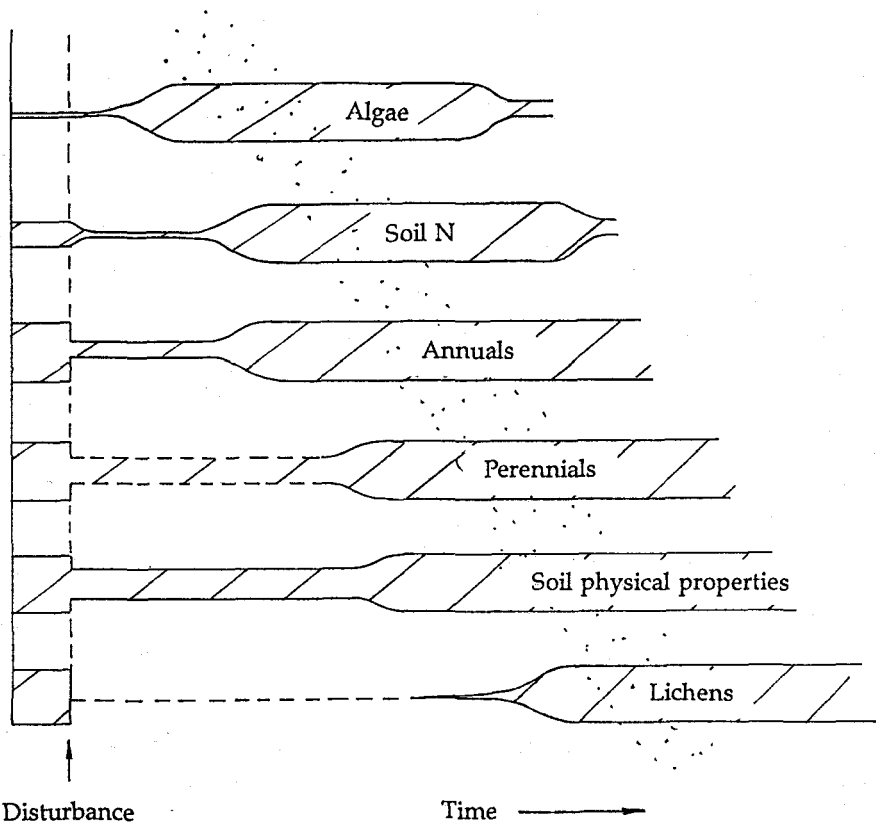


Fig. 8. An hypothesized post-disturbance development of a soil surface associated with vascular plants and microbiotic crusts. Bar thickness is proportional to cover, nutrient availability and soil condition.

Once the surface has been partially stabilized by grasses and other perennials, lichens increase in cover (Fig. 8). As they require a stable substrate on which to develop, stabilization of the surface by algal filaments is a precursor to their development. The growth of lichens results in marked increases in the capability for nitrogen fixation (Shields *et al.* 1957; Rogers *et al.* 1966; Rogers and Lange 1971; Rogers 1974). Where a strong grass canopy develops, overtopping and competition for sunlight, moisture and nutrients, and possible allelopathic effects

of litter may lead to reductions in non-vascular cover. In shrublands, however, canopies rarely reach cover levels which would eliminate microphytic crusts, and well developed crusts have been observed under dense stands of mulga (*Acacia aneura*; R. Rogers pers. comm. 1993) and under bladder saltbush (*Atriplex vesicaria*; D. Eldridge, unpubl. data). The final stage in the development of a microbiotic crust is the stabilization by the mosses and liverworts, though in some areas, mosses are precursors to lichens.

Greene *et al.* (1990) studied recolonization by microbiota on a bare soil surface that had had its original microbiotic surface removed by annual burning for 7 years. The invading microbiotic crusts were characterized into marginal, smooth and irregular surfaces. The marginal surfaces, which are characterized by small (<2 mm diam. individual microbiota), were not extensive, and presumably represented the invasion phase of microbiota on previously bare surfaces. The smooth and irregular surfaces with microrelief <5 mm and 5–10 mm respectively, were slower to colonize the soil surface than the marginal surfaces.

Microbiotic Crusts and the Development of Landscape Heterogeneity

In many arid and semi-arid environments, water and essential nutrients for plant growth are patchily distributed in the landscape. This patchy distribution leads to the development of nutrient-rich 'resource islands' (Garner and Steinberger 1989) or 'fertile patches' (Tongway 1990) within which plants and animals are concentrated. Essential nutrients arrive in pulses, such as after high-intensity rainfall or massive erosion events. This patchiness can occur at a range of scales. For example, in the semi-arid mulga woodlands of eastern Australia, groves of mulga trees occur in the runon zones of a contiguous geomorphic sequence described by Tongway and Ludwig (1990) and Greene (1992). These mulga zones contain higher levels of nutrients than the adjacent runoff zones (Tongway and Ludwig 1990). Measurement of soil water after a major rainfall event also showed that the groves contained more water (Greene 1992). Tongway *et al.* (1989) also found that throughout mulga landscapes, there are small patches, usually associated with mulga logs, that have higher infiltration rates and nutrient status than surrounding soils.

Abiotic processes have a major impact on plant distribution in semi-arid rangelands. The cycle of runon and runoff, producing zones of erosion and deposition (Pickup 1985), is fundamental to the development of patches of favourable habitat, even at a scale characteristic of microbiota. Well developed microbiotic crusts comprise a variety of non-vascular plant types (i.e. lichen, moss and liverwort), as well as blue-green algae, fungi and bacteria. Even at a scale of a few centimeters, microbiota coalesce to form roughened surfaces which affect the redistribution of rainfall and sediments. These roughened surfaces, which are shown in Fig. 1, cause water to collect in small depressions until infiltration can occur (Loope and Gifford 1972; Brotherson and Rushforth 1983). They would also be expected to reduce both water and wind erosion (e.g. Williams *et al.* 1993; Eldridge and Greene 1994) by either intercepting and trapping material eroded during rainstorms, or by supporting a sufficient pond of water to restrict raindrop detachment (Moss and Green 1983). Roughened surfaces could also act to reduce threshold wind velocities close to the surface, reducing the likelihood of wind erosion.

Many observers noted that microbiotic crusts reduce erosion, enhance soil nutrient status (particularly by nitrogen fixation; West 1990) and increase soil structure and aggregate stability (Greene *et al.* 1990), although results may vary between landscapes, soil types and vegetation communities. Although they function as fertile and stable zones, maintained at equilibrium by biotic and abiotic processes, their small size (<0.1 mm) means that their contribution to the development of landscape heterogeneity occurs on a small scale.

Studies in the semi-arid woodlands of eastern Australia have demonstrated that surfaces with an extensive cover and composition of microbiota are associated with enhanced soil structure and aggregate stability, higher infiltration, and lower rates of sediment removal compared with degraded sites with diminished cover and composition of microbiota (Greene and Tongway 1989; Eldridge 1993a, 1993b; Eldridge and Greene 1994). Simulated rainfall on surfaces of variable microbiotic cover resulted in high sediment removal rates from areas with little cover compared with areas with extensive cover (Eldridge and Greene 1994). A greater proportion of the material eroded from the degraded surfaces was silts and clays compared with coarse sand from those sites with increased cover. These finer particles of silt and clay would contain more adsorbed nutrients than the coarser sand particles (Pallis *et al.* 1990). The preferential transport of finer, more fertile soil from areas of reduced cover, and their probable deposition on roughened areas associated with increased microbiotic cover, would enhance the development of landscape heterogeneity. Ultimately, areas with sparse cover become increasingly degraded and less accessible to establishment by vascular plant seedlings (Eldridge and Greene 1994).

Interactions with Vascular Plants

The relationships between microbiota and vascular plants are poorly understood, and few experimental studies have investigated their effects on germination and establishment of vascular plants (Harper and Marble 1988). Because microbiotic crusts concentrate the two essential resources necessary for plant growth, i.e. water and nutrients within the surface 10 mm (Graetz and Tongway 1986), it is reasonable to assume that they have an effect on vascular plants. Microbiotic crusts are also likely to affect vascular plants, either through competitive effects on cover and biomass, or through changes in germination and survival, particularly through changes to soil surface condition.

Data on the relationships between microbiotic crusts and vascular plants are generally based on studies on bryophytes and lichens, because these are the most readily identifiable in the field. In Australia, numerous workers have reported positive correlations between microbiotic cover and vascular plant cover. Graetz and Tongway (1986) showed a significant positive correlation between the cover of perennial chenopod shrubs and cover of microbiota. In the semi-arid woodlands of eastern Australia, strong associations have been reported between vascular plant biomass and cryptogam cover (Mucher *et al.* 1988). In that study, biomass of biennial grasses and forbs increased as the cover of microbiota increased. Similarly, Tongway and Smith (1989) showed that a high degree of microbiotic cover and diversity on red earth soils was associated with highly productive sites, i.e. high biomass.

Other research, however, has produced conflicting conclusions. For example, strong negative relationships were found between cryptogam cover and vascular plant cover, and increases in pasture biomass were associated with decreases in cryptogam cover (Eldridge 1993a). Schofield (1985) demonstrated from studies in North America, that the area covered by mosses increased as forbs and grasses were progressively eliminated by overgrazing. Other studies from the semi-arid chenopod shrublands of South Australia showed that cryptogam cover increased as cover of herbs and trees decreased following long-term exclusion of grazing (Crisp 1975).

Differences in the interactions between microbiota and vascular plants as reported in the literature may be due to different stages of development of both the microbiota and the vascular plants, with positive relationships during early stages of development of the crusts, followed by negative correlations. The negative relationship between microbiota and vascular plants is not surprising, however. An increase in vascular plant cover through exclosure or destocking is likely to reduce microbiota cover as a result of increased competition for light and moisture and through overtopping by perennial grasses (Looman 1964).

Few studies have considered the effect of microbiota on germination and survival of vascular plants. St Clair *et al.* (1984) demonstrated enhanced seedling establishment of some grasses under laboratory conditions. Harper and St Clair (1984) showed that, even after the third growing season, survival of seedlings planted into a microbiotic crust was 1.6 times that on an adjacent scalped area. Similarly, Eckert *et al.* (1985) demonstrated enhanced establishment of a range of vascular plants on surfaces where microbiota were well developed compared with bare soils. Mucher *et al.* (1988) considered microbiota to be highly desirable components of surface crusts because of their influence on the lodgment and germination of seeds, the infiltration and runoff of water and hence of plant growth.

Eldridge *et al.* (1992), however, found no consistent relationship between surfaces dominated by microbiota and either establishment or survival of *Atriplex vesicaria* seedlings on a duplex soil near Broken Hill. Similarly, early pioneering work by McIlvanie (1942) showed that seeds of a range of plants readily germinated on bare soil surfaces, but on microbiotic surfaces failed to come into contact with the soil and dried out and died. As discussed earlier, the effect on crusts may be mediated by seed characteristics such as size and shape, as smaller seeds will have a greater soil contact area compared with larger seeds such as *A. vesicaria*. Clearly more research is needed before the role of microbiotic crusts in seedling survival is clearly identified.

An Alternative System for Classifying Microbiotic Crusts

There is confusion over the definitions of different types of microbiotic crusts (see Eckert *et al.* 1978). These definitional problems may explain the wide disparity between research results reported in the literature, particularly conflicting results on their roles in infiltration processes. One solution is to differentiate the biological components of soil crusts into functional groups based on diagnostic field traits, habitat preference and abiotic relationships. This allows the crusts to be characterized using a system which is independent of existing plant/animal classification systems. We propose a system which identifies three types or forms

of biological crusts: *hypermorphs* (above ground), *perimorphs* (at ground) and *cryptomorphs* (hidden below ground; Fig. 9).

The *hypermorphic* crusts include mosses and liverworts (bryophytes), which occur in the more moist microhabitats of semi-arid regions, such as below shrubs, often in association with algae. These crusts are more common on stable landscapes with pronounced microrelief, and are most susceptible to perturbations such as grazing and fire. Much of their influence is confined to the area above the soil surface, hence their ability to moderate the effects of wind and raindrop action.

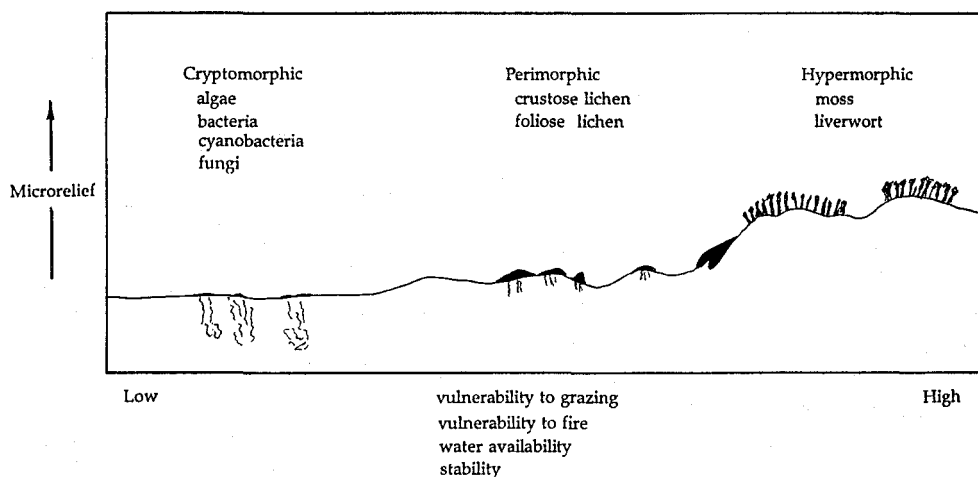


Fig. 9. A catenary sequence of surfaces dominated by microbiotic soil crusts.

The intermediate *perimorphic* crusts comprise crustose and foliose lichens, which are symbiotic associations of fungi and eukaryotic microalgae or blue-green algae (Metting 1991). Their area of influence is partitioned above and below the soil surface. As well as imparting to the surface a degree of protection against wind and water erosion, fungal hyphae associated with the lichen mats ramify the soil below the mats and enhance the development of stable soil aggregates (Bailey *et al.* 1973).

The microscopic *cryptomorphic* crusts comprise the microscopic blue-green algae, eukaryotic microalgae and filamentous fungi. They are found in disturbed sites, and are less susceptible to grazing and fire. The majority of their activity is concentrated below-ground where they enhance the aggregate structure and nutritional status of the soil.

Conclusions

Compared with the more visible vascular plants, microbiota and microbiotic crusts have been little studied in most environments, and particularly in Australia. West (1990) attributed the lack of interest they arouse to their small size, problems with identification and patchiness in time and space. Since the early ecological work of Rogers (1972a, 1972b), the bulk of Australian research into the role and function of microbiota and microbiotic crusts has been undertaken by soil scientists working in semi-arid rangelands. Their aims have been to better understand the

relationship between microbiotic crusts and soil hydrologic processes in semi-arid soils where microbiota are a significant cover component. With an increasing emphasis on ecologically sustainable development and informed management of arid and semi-arid pastoral land, a knowledge of the role of microbiota and crusts is central to our management of these areas.

This review has reinforced the notion that microbiota and microbiotic crusts are important components of arid and semi-arid ecosystems. Furthermore, their distribution and condition may indicate the health of the environment. West (1990), however, cautioned against general recommendations being made until more detailed field experimentation is forthcoming. Whilst their presence leads to reduced erosion, their role in regulating the water flow into soils, however, is not so clearly defined. For example, little is known of the link between soil condition and enhancement of infiltration by microbiotic crusts. There are few data on how microbiotic crusts interact with vascular plants and whether their presence in the rangelands indicates the health of the system. Similarly, their roles in nitrogen fixation have only really been demonstrated from laboratory studies. The extent to which fixed nitrogen is made available to developing vascular plants can only be speculated upon.

Research priorities should concentrate on the identification and classification of crust types, including the individual taxa comprising the crusts. Differences in crust composition may help to explain the disparity in infiltration rates reported in various studies. The development of an alternative system for classifying crusts is a first step in understanding the disparity in the effects of crust cover on infiltration rates. Further research is required to investigate whether the different forms of microbiotic crusts affect infiltration at varying levels of cover. Attention also needs to be focussed on the interrelationships between microbiotic crusts, vascular plants and soil biota, given the increased interest in biodiversity and ecologically sustainable development. Finally, research should address the impacts of fire and grazing on semi-arid rangelands where crusts are a predominant ground cover.

Microbiotic crusts are markedly different in form and function from physical soil crusts, such as rain-impact and depositional crusts which are generally regarded as undesirable. Thus, the first step in understanding crusts is to determine whether or not they are biological in nature. It is then necessary to examine how they are distributed in the landscape, and to develop techniques to identify types of microbiotic crusts, at least to functional group level. Both ground and remotely-sensed methods may need to be developed. Secondly, we need to know whether the development of a stable microbiotic surface is a prerequisite to the development of higher plant cover, or *vice versa* (West 1990). This has implications for grazing management, as some argue that high intensity grazing and destruction of the crust's integrity are necessary to allow vascular plants to establish (Savory 1988). Thirdly, information is required on the recovery of microbiotic crusts after disturbance, and the likely effects of different land uses and management practices such as pastoralism, fire and tourism on their sustainable use.

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