BIOLOGICAL SOIL CRUSTS OF ARABIAN SABKHAT

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Abstract
Biological soil crusts are a critical component of many arid regions. Where vegetation is extremely limited, such as Arabian sabkhat, these soil crusts may play many important ecological roles. These roles include nitrogen and carbon inputs, maintaining plant-essential nutrients in a bio-available form, influencing local hydrology, affecting establishment of vascular plants, and decreasing soil erosion from either wind or water. Surface disturbance can heavily impact biological soil crusts, and often leads to reduced nutrient input and increased soil erosion. Little work has been done on Arabian sabkhat, although they may be an essential part of these ecosystems.

INTRODUCTION

Most arid and semi-arid landscapes have a limited cover of vascular vegetation. In these ecosystems, the soil spaces between the vascular plants generally contain a community of cyanobacteria, green algae, microfungi, and other bacteria. The cyanobacterial and microfungal filaments weave among soil grains in the top few millimetres of soil, gluing them together and forming a biological crust which stabilises and protects soil surfaces from erosive forces (Belnap & Gardner 1993). In regions with sufficient precipitation and soil stability, lichens and mosses colonise these spaces as well. These biological soil crusts occur in all arid and semi-arid regions and may constitute up to 70% or more of the living cover of a region. They are also referred to as cryptogamic, microbiotic, or microphytic crusts (Harper & Marble 1988).

Worldwide, biological soil crusts have many similarities in species composition, structure, and function. They occur in all types of desert and semi-desert plant

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communities. They also occur in steppes and tundra, and are frequently present in xerothermic formations in temperate regions. Despite huge differences in climate and soil in these different habitats, soil crust species within each of the above communities are often of the same genera, if not the same species. The structure of soil crusts is also similar among deserts of the same type: hot deserts of the world (e.g., Atacama, Chihuahuan, Sahara) have flat, smooth crusts, while in cool and cold deserts (e.g., Colorado Plateau, Great Basin, Arctic, Patagonia), frost-heaving gives the soil crusts a bumpy morphology.

SPECIES COMPOSITION AND COVER

Species composition of soil crusts is dependent on soil characteristics, local topography, vegetation, climate, disturbance regimes (including wind and water erosion, water pooling, as well as soil surface disturbance) and other ecological factors (e.g., hydrology). Soil characteristics that influence species composition encompass chemistry (including salinity), texture and stability. Cyanobacteria are halotolerant, with some species able to grow in NaCl-saturated solutions. However, different species have varying tolerances to salinity and the species composition of soil crusts in sabkhat is often different and more diverse at the sabkha edge than in the center (Ullmann & Büdel 2001). A sabkha in Tunisia had no cyanobacteria when Na levels were 15-19 g kg dw^{-1} soil. Once Na dropped to 7-10 g kg dw^{-1} soil, *Chroococcidiopsis* sp., *Xenococcus* sp., *Microcoleus chthonoplastes* and *M. paludosus* appeared, but were infrequent. When Na dropped further, these species became abundant, and six other species appeared. In samples from sabkhat of the United Arab Emirates, *Microcoleus* and *Nostoc* were commonly found (Belnap, pers. obs.) where salinity was low. In sabkhat with higher salinity, several genera that likely belong to the *Halothece* phylogenetic clusters were found (Garcia-Pichel, pers. comm.). These extremely halotolerant cyanobacteria have been reported from hypersaline marine mats, lagoons and inland evaporitic lakes such as the Great Salt Lake in the United States (Garcia-Pichel et al. 1998).

Crust organisms also avoid high shrink-swell clays, while preferring >10% silt (Verrecchia et al. 1995, Belnap, unpubl. data). Soil stability is also critical, as moving sediment will quickly bury crustal organisms. Where wind carries sharp sand that scours the soil surface, organisms only survive in locally-protected areas. In places of more stable sand, or with windbreaks (plant material, outcrops, local macro- or microtopography), crusts are better developed. Pole-facing slopes have greater cover compared to equator-facing slopes (Alexander & Calvo 1990). However, as sabkhat are flat, the local topography's influence on soil crusts is more through larger climate patterns than local solar radiation or evapo-transpiration rates.

Generally, crust cover is correlated with the amount of soil surface not occupied by plants, rocks or actively moving soils (Harper & Marble 1988, Johansen 1993).

This means most soil surfaces are available for crust colonisation in sabkhat. Crusts are often better developed around plants in sabkhat, as they mitigate the extreme environment by protecting crusts from wind scouring, increasing rainfall capture, providing shade, and capturing wind-blown silt.

Climate also influences crust development. Because crust organisms are only metabolically active when wet, the amount and timing of rainfall is critical in determining species cover and composition. When the potential evaporation rate (PET) is high, crust cover and species diversity are low. As the PET declines, metabolic activity times increase, with a concomitant increase in cover and diversity (Alexander & Calvo 1990, Jeffries et al. 1993, Rychert et al. 1978). As sabkhat are found in areas with high PET, crust cover is generally well below 50% and diversity limited to a few species of cyanobacteria. Timing of precipitation is also important. When rain occurs at high air temperatures, it may be available to the soil surface organisms only for a short time, which can result in net carbon losses for species that take longer to reach their net compensation point (Jeffries et al. 1993).

Disturbance regimes, including intensity, type and time since disturbance also influence crust composition. Nothing is known about the successional patterns of soil crusts on sabkhat; however, it is likely they are similar to other crusts. Newly or severely disturbed surfaces are generally bare. Colonisation by different crust species occurs in a manner analogous to terrestrial plant succession (Johansen 1993), with nitrogen-fixing species or species best able to stabilise soils appearing first. In crusts, the large filamentous cyanobacteria are first to stabilise soils, followed by smaller cyanobacteria and green algae. Further soil stabilisation (assuming salinity levels are low enough) allows the colonisation of the lichens *Collema* sp. and *Catapyrenium* sp., followed by other lichens and mosses where soil moisture or precipitation is adequate (Johansen 1993, Harper & Marble 1988).

While studies on what controls species distributions in sabkhat have been very limited, low water availability, wind-scouring and salinity appear important in determining crust composition and cover. In areas with nearby mobile sand sources and frequent winds, soil crusts are generally absent or limited to protected areas, such as rock outcrops, microtopography, or plants, and salinity controls local occurrence patterns (Ullmann & Büdel 2001, Belnap unpubl. data). In sabkhat throughout the Arabian Peninsula, as well as other hyperarid regions, cyanobacteria are generally absent from very hypersaline soils. As salinity drops, *Chroococcidiopsis* sp., *Microcoleus chtonoplastes* and *M. paludosus* are most abundant. With further declines in salinity, *Calothrix parietina*, *Nostoc* sp., and *Gloeocapsa* sp. are found. Further decreases in salinity often allow colonisation of lichens that include *Collema* sp., *Heppia* sp., and *Catapyrenium lacinulatum*. Less frequent, but sometimes seen around sabkhat are *Squamarina lentigera*, *Psora decipiens*, *Diploschistes diacapsis*, and *Fulgensia fulgens*. Worldwide, it has been observed that lichens increase with the level of carbonate, gypsum and silt in soils, and this has also been observed for sabkhat in Tunisia, Australia, and the Arabian Peninsula (Ullmann & Büdel 2001, Belnap unpubl. data).

MICROSTRUCTURE

In arid lands, most relatively undisturbed soils contain both non-biotic (physical) and biological crusts. The presence of any crust alters soil surface characteristics, and thus can play a defining role in many ecosystem functions. Physical crusts, created by raindrop impact, trampling, and/or accumulation of evaporated salts, are found in most arid soils, and their effects are often confused with those of biological crusts. They are transient soil-surface layers ranging from <1 mm to a few centimetres in thickness. They consist mostly of clays, silts, and evaporites, and thus are often structurally different from soils immediately beneath them. The presence of a physical crust provides stability to the soil surface, and the clay and silt enhance soil surface moisture retention. Consequently, the presence of a physical crust hastens colonisation of soil crust organisms. The presence of a physical crust can also seal and smooth surfaces, thus increasing the volume and velocity of water runoff, as well as often inhibiting establishment of vascular vegetation.

Worldwide, the microstructure of biological crusts is influenced by climate (frequency and depth of soil freezing and PET), species composition, soil texture, chemistry and physical crusts, disturbance history, and aeolian deposition. Unlike crusts in regions where freezing is common or lichen cover high, crusts in sabkhat are generally smooth. Smooth crusts occur in hyperarid and arid regions where rainfall is low, temperatures are high, and soils never freeze (e.g., Arabian, central Sahara, Negev, Atacama deserts). Smooth crusts consist mostly of endedaphic (living within the soil) cyanobacteria, algae and microfungi that bind together mostly mineral particles, with limited lichen cover. High carbonate or gypsiferous soils often have lichens and mosses, thus creating a rugose surface (Belnap & Lange 2001). Soils with a high content of shrink-swell clays (e.g. bentonite) are extremely unstable, and often support only large filamentous cyanobacteria (e.g., *Microcoleus*). In such soils, physical/chemical soil characteristics control crust morphology, with little contribution from biological components.

Soils crusts are dominated by photosynthetic organisms that require sunlight. Most cyanobacteria are found at 0.2-0.5 mm, where sufficient light for net carbon gain is available, but UV exposure is reduced. Well-developed crusts show a vertical layering of cyanobacterial species (Davey & Clarke 1992). Smaller, less mobile organisms (e.g., *Chroococcidiopsis, Nostoc*, *Scytonema*) are most often found at the soil surface, and contain specialised pigments for UV-protection. The larger cyanobacteria (e.g., *Microcoleus, Phoridium*), lacking UV pigments, are found below the soil surface. When soils are wetted, these large cyanobacteria glide up to the soil surface. Cyanobacteria are found closer to the surface in finer soils than coarse soils, as light is quickly extinguished by soil particles (Garcia-Pichel & Belnap 1996). Intensity, type, and time since soil surface disturbance often control the external morphology of soil crusts, as surface roughness is lost. Airborne silt and clay are trapped by sticky cyanobacterial sheaths and protruding moss stems and lichen thalli. This results in a thin layer of silt and clay on the crust surface. Silts increase soil fertility and water-holding capacity (Davey & Clarke 1992).

ECOLOGICAL ROLES

While no studies have directly addressed the ecological role of soil crusts on sabkha surfaces, there are many studies from hot desert ecosystems that are applicable to these systems.

Carbon fixation

Crust organisms respond quickly to water, with respiration beginning less than 3 minutes after wetting (Garcia-Pichel & Belnap 1996). Photosynthesis begins shortly afterwards, reaching full activity within 10-30 minutes. When soils are moist, steep oxygen gradients result in anoxic zones 1-4 mm from the surface. Recently studies of soil crust lichens (Lange 2001) showed that lichens have several different photosynthetic strategies, and that carbon (C) gains are heavily dependent on thallus hydration levels and temperature. Photosynthesis rates in most species increase with temperature up to about 26-28°C. Biological soil crusts are an important source of fixed C on sparsely vegetated areas common throughout the western United States (Beymer & Klopatek 1991). In this region, C contributed by soil crust organisms helps keep plant interspaces fertile and supports other microbial populations.

Nitrogen fixation

Soil nitrogen (N) concentrations are known to be low in deserts relative to other ecosystems, and N is known to limit net primary productivity in deserts (Romney et al. 1978). Cyanobacteria and cyanolichens can be the dominant source of N in many desert ecosystems (Evans & Ehleringer 1993). Nitrogen fixation is highly dependent on past and present water and light regimes, as well as crust species composition (Belnap & Lange 2001). Maximum N fixation occurs at soil surface temperatures of 20-30°C, with 26-28°C optimal for most non-polar crusts. Timing, extent and type of past disturbance can also be critical factors in determining fixation rates (see disturbance section). Much of the fixed N leaks into the surrounding substrate, and is available to nearby vascular plants and microbes (Silvester et al. 1996). Vascular plants growing in crusted areas show higher tissue concentrations of N when compared to plants in uncrusted soils (Mayland & McIntosh 1966; Harper & Belnap 2001). Since rainfall events in desert areas are often too small to promote plant growth, but stimulate microbial community activity, soil crusts may contribute greater N than N-fixing plant species. In addition, crusts help maintain fertility of plant interspaces, counteracting nutrients concentrating around perennial plants. Although no N fixation studies have been done in sabkhat, N-fixing cyanobacterial species are present, and are expected to increase soil N in these ecosystems.

Vascular plants

No work has directly addressed the influence of soil crusts on vascular plants in sabkhat. There have been general studies on smooth crusts in hot deserts, but results are mixed. The probability of seed entrapment on smooth cyanobacterial crusts is low compared to frost-heaved crusts of cool deserts (Belnap & Lange 2001). Smooth crusts enhance, inhibit, or don't affect seed germination, depending on the species. Plant survival and fecundity on crusted surfaces in hot deserts are either enhanced or not affected, while biomass is increased.

Vascular plants growing on crusted surfaces generally have higher tissue concentrations of N, K, Ca, Mg, P, Fe, Mn, Cl and S when compared to plants on non-crusted soils (Harper & Belnap 2001). There are several mechanisms to explain this, reviewed in Belnap & Lange (2001). Clay particles stick to the mucilaginous sheath material, which in turn bind positively-charged plant macronutrients. Crusts increase N in the upper soil layers (0-20 cm) by up to 200%. Most crust organisms bind metals and secrete powerful metal chelators; cyanobacteria also secrete peptide nitrogen and riboflavin. These substances keep P, Cu, Zn, Ni, and Fe plant-available. Cyanobacteria secrete glycollate, which stimulates uptake of phosphate, vitamins, and auxin-like substances. Crusts also secrete fixed carbon, increasing soil carbon in surface layers (0-10 cm) by up to 300%, benefitting heterotrophic microbes which are often carbon limited. C additions lower the soil C:N ratio, increasing decomposition rates. Increases in soil organic matter ameliorate compaction, reduce inorganic soil crusting, reduce nutrient leaching losses, and increase soil moisture retention. There is also a strong correlation between mycorrhizal infections of seed plants and crusted surfaces (Harper & Pendleton 1993, Belnap & Lange 2001).

Water Relations

The effect of biological soil crusts on soil water relations is heavily influenced by soil texture and structure, as well as the growth form of the crusts. In hot deserts where frost-heaving is not present and soil crusts are relatively flat, infiltration rates are heavily dependent on soil type and local features. In general, smooth crusts reduce infiltration on sandy soils and increase infiltration on finer-textured soils (Belnap & Lange 2001). On sabkha surfaces, cracking of evaporite surfaces can influence local infiltration patterns. In hyperarid regions, local reduction of infiltration can be critical in supporting plants. In the Negev, studies showed that shrubs were dependent on water run-off generated from upslope, crusted soils (Yair 2001).

Soil stabilisation

The presence of soil crusts reduces both wind and water erosion in all environments that have been studied. Polysaccharides extruded by the cyanobacteria, green algae and fungi (Fig. 1), along with the rhizins and rhizomorphs of lichens and protonemata of mosses, entrap and bind soil particles together, aggregating them into larger particles. Larger aggregates are more difficult to move, thus reducing soil loss via wind or water erosion. Soil aggregation by crusts also enables otherwise loose sandy soils to stay in place on steep slopes and in areas of shallow bedrock or caliche (Belnap & Gardner 1993).

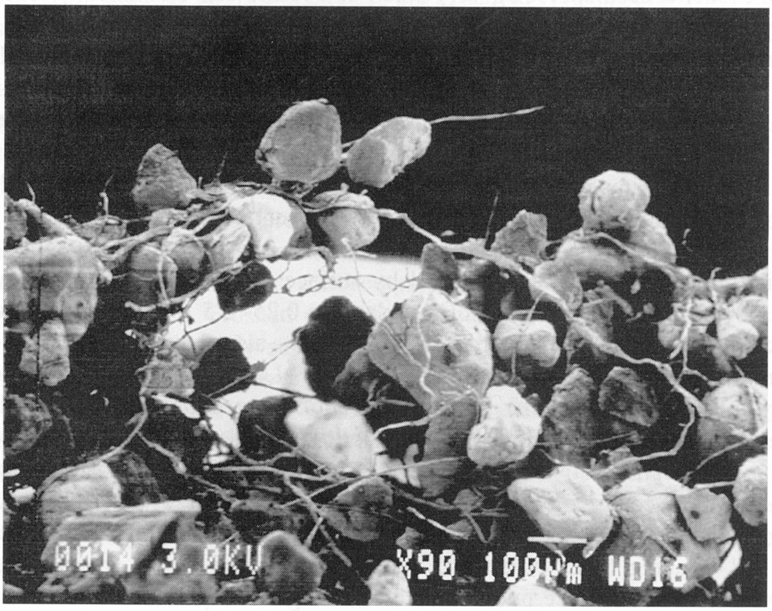

Figure 1. *Microcoleus vaginatus* in sandy soils. Sheath material binds sand grains together (note the sheaths are wound around and among sand grains [bar = 100 µm]).

EFFECTS OF DISTURBANCE AND RATE OF RECOVERY

Soils in arid regions are often highly erodible, and soil formation extremely slow, taking 5000 to 10,000 years (Dregne 1983). Animal, vehicle, and human foot traffic generate compressional and shear forces that can severely impact biological crusts. The effects of disturbance are similar worldwide, and include a reduction in species diversity, total crust cover, nitrogen and carbon fixation, as well as a reduction in soil stability. Well-developed crusts around sabkhat can contain up to 10 soil lichen, 3 moss and 10 cyanobacterial species, while disturbed areas often have only one cyanobacterial species (generally *Microcoleus*). Surface disturbance negatively affects the cohesion and coverage of cyanobacterial crusts, as crusts are brittle when dry and easily crushed (Belnap & Gardner 1993). Any compressional disturbances to these crusts leaves surfaces vulnerable to wind and water erosion (Belnap & Gillette 1998). Impacts can also be indirect: sediments from nearby disturbed areas can bury living crusts, often resulting in the death of the photosynthetic organisms (Belnap 1995). Because over 75% of the photosynthetic biomass, and almost all photosynthetic productivity, is from organisms in the top 3 mm of these soils (Garcia-Pichel & Belnap 1996), very small soil losses can dramatically reduce site fertility and further reduce soil surface stability. Consequently, trampling can greatly accelerate degradation processes through increased soil and water loss (Dregne 1983). C and N fixation is dramatically reduced in soil crusts when disturbed (Belnap & Eldridge 2001), and gaseous N loss increased (Peterjohn & Schlesinger 1990). This has large implications for deserts, where the crusts are the dominant source of C and N in plant interspaces (Evans & Belnap 1999). Decreased soil C and N alters soil food webs and thereby affects nutrient availability in these systems (Ingham et al. 1989).

Soil surface albedo is also affected by surface disturbance. Trampled surfaces have a 50% increased reflectance of wavelengths 0.25- 2.5 μm compared to crusted surfaces (Belnap 1995). Trampled surfaces can also have significantly lower temperatures than crusted surfaces, which lowers N and C fixation rates, microbial activity, plant nutrient uptake, seed germination time and seedling growth rates (Belnap & Lange 2001). Timing is often critical in deserts, and relatively small delays in germination can reduce plant fitness and seedling establishment, which may eventually affect community structure. Food and other resources are often partitioned among ants, arthropods and small mammals on the basis of surface temperature-controlled foraging times (Crawford 1991). Many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival. Consequently, altering surface temperatures can affect nutrient availability and community structure for many desert organisms.

Because crustal organisms are only metabolically active when wet, re-establishment time is slow in arid systems. Cyanobacteria are mobile and can often quickly recolonise a site. Lichens and mosses, however, are much slower, and thus underlying soils are left vulnerable to wind and water erosion for at least 20 years (Belnap & Gillette 1998). Moving sediments further destabilise adjoining areas by burying adjacent crusts, or by "sandblasting" nearby surfaces, thus increasing wind erosion rates (Belnap 1995, McKenna Neuman et al. 1996).

Recovery rates of soil crusts depend on the type and extent of disturbance, the availability of nearby inoculation material, as well as on the temperature and moisture regimes that follow disturbance events. Estimates of time for visually-assessed recovery have varied from 5 to 100 years (Harper & Marble 1988).

However, Belnap (1993) showed that many components of recovery can not be assessed visually, and recovery may be much slower. Since recovery time is dependent on presence of nearby material to colonise the disturbed area, larger disturbed areas will take longer to recover.

Recovery of nitrogen fixation appears to be quite slow, and studies suggest the negative effects on N dynamics may persist for extended periods of time after disturbance ceases (Evans & Belnap 1999). Restoration of normal surface albedos and temperatures will depend on the restoration of cyanobacteria, lichens and mosses. The use of inoculants to speed up recovery of these crusts has been used repeatedly (St. Clair et al. 1984, Belnap 1993) and is very effective in hastening recovery of all soil crust components.

CONCLUSION

Biological soil crusts are critical components of the ecosystems in which they occur. Many activities of man are incompatible with the presence and well-being of biological soil crusts. The cyanobacterial fibers that confer such tensile strength to these crusts are no match for the compressional stresses placed on them by anthropogenic activities. Crushed crusts contribute less N and C to the ecosystem. Impacted soils are left highly susceptible to both wind and water erosion. Unlike vascular plant cover, crustal cover is not reduced in drought, and unlike rain and salt crusts, these organic crusts are present during and after rain events. Consequently, they offer stability over time and in adverse conditions, factors that are often lacking in other soil surface protectors, and should be considered in any environmental management activity. Little is known about biological soil crusts of sabkhat, and it is hoped further studies will determine more specifically how soil crusts affect their ecology.

References

Alexander, R.W. & Calvo, A. 1990. The influence of lichens on slope processes in some Spanish badlands. In: Thornes, J.B. (ed), Vegetation and erosion: processes and environments. John Wiley & Sons, Ltd., Chichester, England, pp. 385-398.

Belnap, J. 1993. Recovery rates of cryptobiotic soil crusts: inoculant use and assessment methods. *Great Basin Naturalist* 53: 89-95.

Belnap, J. 1995. Surface disturbances: their role in accelerating desertification. *Environmental Monitoring and Assessment* 37: 39-57.

Belnap, J. & Eldridge, D.J. 2001. Disturbance and recovery of biological soil crusts. In: Belnap, J. & Lange, O.L. (eds.), Biological soil crusts: structure, function, and management. *Ecological Studies Series* 150. Springer-Verlag, Berlin, pp. 363-383.

Belnap, J. & Gardner, J.S. 1993. Soil microstructure of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. *Great Basin Naturalist* 53: 40-47.

Belnap, J. & Gillette, D.A. 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. *Journal of Arid Environments* 39: 133-142.

Belnap, J. & O.L. Lange (eds.) 2001. Biological soil crusts: structure, function, and management. *Ecological Studies Series* 150. Springer-Verlag, Berlin, 503 pp.

Beymer, R.J. & Klopatek, J.M. 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. *Arid Soil Research and Rehabilitation* 5: 187-198.

Crawford, C.S. 1991. The community ecology of macroarthropod detritivores. In: Polis, G. (ed.), Ecology of desert communities. University of Arizona Press, Tucson.

Davey, M.C. & Clarke, K.J. 1992. Fine structure of a terrestrial cyanobacterial mat from Antarctica. *Journal of Phycology* 28: 199-202.

Dregne, H.E. 1983. Desertification of arid lands. Harwood Academic Publishers, New York.

Evans, R.D. & Belnap, J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology* 80: 150-160.

Evans, R.D. & Ehleringer, J.R. 1993. A break in the nitrogen cycle in arid lands? Evidence from N^{15} of soils. *Oecologia* 94: 314-317.

Garcia-Pichel, F. & Belnap, J. 1996. Microenvironments and microscale productivity of cyanobacterial desert crusts. *Journal of Phycology* 32: 774-782.

Garcia-Pichel, F. Nubel, U. & Muyzer, G. 1998. The phylogeny of unicellular, extremely halotolerant cyanobacteria. *Archiv Microbiology* 169: 469-482.

Harper, K.T. & Belnap, J. 2001. The influence of biological soil crusts on mineral uptake by associated vascular plants. *Journal of Arid Environments* 47 (3): 347-357.

Harper, K.T. & Marble, J.R. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. In: Tueller, P.T. (ed.), Vegetation science applications for rangeland analysis and management. Kluwer Academic Publishers, Dordrecht. pp. 136-169.

Harper, K.T. & Pendleton, R.L. 1993. Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? *Great Basin Naturalist* 53: 59-72.

Ingham, E.R., Coleman, D.C. & Moore, J.C. 1989. An analysis of food-web structure and function in a shortgrass prairie, a mountain meadow, and a lodgepole pine forest. *Biology and Fertility of Soils* 8: 29-37.

Jeffries, D.L., Link, S.O. & Klopatek, J.M. 1993. CO_2 fluxes of cryptogamic crusts. I. Response to resaturation. *New Phytologist* 125: 165-173.

Johansen, J.R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. *Journal of Phycology* 29: 140-147.

Lange, O.L. 2001. Photosynthesis of soil-crust biota as dependent on environmental factors. In: Belnap, J. & Lange, O.L. (eds.), Biological soil crusts: structure, function, and management. *Ecological Studies Series* 150. Springer-Verlag, Berlin, pp. 217-240.

Mayland, H.F. & McIntosh, T.H. 1966. Availability of biologically fixed atmospheric nitrogen-15 to higher plants. *Nature* 209: 421-422.

McKenna Neuman, C., Maxwell, C.D. & Boulton, J.W. 1996. Wind transport of sand surfaces crusted with photoautotrophic microorganisms. *Catena* 27: 229-247.

Peterjohn, W.T. & Schlesinger, W.H. 1990. Nitrogen loss from deserts in the southwestern United States. *Biogeochemistry* 10: 67-79.

Romney, E.M., Wallace, A. & Hunter, R.B. 1978. Plant response to nitrogen fertilization in the northern Mohave Desert and its relationship to water manipulation. In: West, N.E. & Skujinš, J.J. (eds.). Nitrogen in desert ecosystems. US/IBP Synthesis Series 9. Dowden, Hutchinson and Ross, Stroudsberg, PA, pp. 232-243.

Rychert, R.C., Skujinš, J.J., Sorensen, D. & Porcella, D. 1978. Nitrogen fixation by lichens and free-living microorganisms in deserts. In: West, N.E. & Skujinš, J.J. (eds.), Nitrogen in desert ecosystems. US/IBP Synthesis Series 9. Dowden, Hutchinson and Ross, Stroudsburg, PA, pp. 20-30.

Silvester, W.B., Parsons, R. & Watt, P.W. 1996. Direct measurement of release and assimilation of ammonia in the *Gunnera-Nostoc* symbiosis. *New Phytologist* 132: 617-625.

St. Clair, L.L., Webb, B.L., Johansen, J.R. & Nebeker, G.T. 1984. Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. *Reclamation and Revegetation Research* 3: 129-136.

Ullmann, I. & Büdel, B. 2001. Ecological determinants of species composition of biological soil crusts on a landscape scale. In: Belnap, J. & Lange, O.L. (eds.), Biological soil crusts: structure, function, and management. *Ecological Studies Series* 150. Springer-Verlag, Berlin, pp. 203-213.

Verrecchia, E., Yair, A., Kidron, G. & Verrecchia, K. 1995. Physical properties of the psammophile cryptogamic crust and their consequences to the water regime of sandy soils, north-western Negev Desert, Israel. *Journal of Arid Environments* 29: 427-437.

Yair, A. 2001. Effects of biological soil crusts on water redistribution in the Negev Desert, Israel: a case study in longitudinal dunes. In: Belnap, J. & O.L. Lange (eds), Biological soil crusts: structure, function, and management. *Ecological Studies Series* 150. Springer-Verlag, Berlin, pp. 303-314.

Sabkha Ecosystems

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