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Biological Soil Crusts and Global Changes: What Does the Future Hold?

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35.1 INTRODUCTION

In arid lands of many diverse climates of the world, where vegetation is sparse or absent, the open ground is not bare but generally covered by a community of small, highly specialized organisms. Together with crustose, foliose, and fruticose, lichenized fungi (i.e., lichens), cyanobacteria, algae, microfungi, and bryophytes aggregate soil particles to form a coherent skin — the biological soil crust (see Chapter 6). Biological soil crusts play an important ecological role worldwide and are a substantial force in shaping the structure and function of many ecosystems. They increase the stability and fertility of soils and influence local hydrological cycles.

Presently, global climate is undergoing changes (Walker et al., 1999) that are likely to significantly modify the abundance, distribution, species composition, and ecological role of biological soil crusts. These changes include substantial increases in atmospheric CO_2 concentrations; increased mean temperatures and changes in extremes and annual temperature fluctuations; changes in precipitation intensity, amount, and timing; altered incident solar radiation with increased ultraviolet input; and interactions between these factors and other variables such as nutrient availability. In addition, land use change and exotic plant invasions are altering habitats on a global scale. Kates et al. (1990) estimates that almost 50% of the ice-free terrestrial land surface has been transformed by humans in ways likely to override any direct effects of changes in atmospheric chemistry (Walker and Steffen, 1997).

In this chapter we will address the likely effects of climate change and changes in land use patterns on biological soil crusts, especially the lichen component. We will examine how these future scenarios might impact the physiological functioning of both individual species and the crust community, as well as expected changes in the species composition of the soil crusts.

35.2 POSSIBLE ECOPHYSIOLOGICAL RESPONSES OF SOIL CRUST LICHENS TO CLIMATIC CHANGES

35.2.1 Increased Level of Atmospheric Carbon Dioxide

Carbon dioxide is the substrate for photosynthesis, and CO_2 response of net photosynthesis (NP) of autotrophs usually follows a saturation type function with an almost linear initial slope. Under conditions of optimal thallus water content (WC), terricolous lichens reach CO_2 saturation in the range between 1000 and 1200 ppm external CO_2 partial pressure (e.g., Nash et al., 1983; Lange et al., 1996, 1999). Lichen species possessing a CO_2 concentrating mechanism tend to have a higher carboxylation efficiency and thereby require lower external CO_2 concentrations for saturation (Palmqvist, 2000). As photosynthesis is not saturated by present ambient natural CO_2 (around 350 ppm), lichens profit from short-term experimental increases in ambient CO_2 with an almost proportional increase in their NP rate if not limited by other factors (e.g., low light or hydration; Figure 35.1). For example, low light under snow cover limits carbon (C) gains even when average CO_2 concentrations are 450 to 500 ppm with peaks to 1641 ppm (Sommerkorn, 2000). Suprasaturation of the lichen thallus by water can impede CO_2 diffusion, drastically increasing the concentrations required for CO_2 saturation (Figure 35.1).

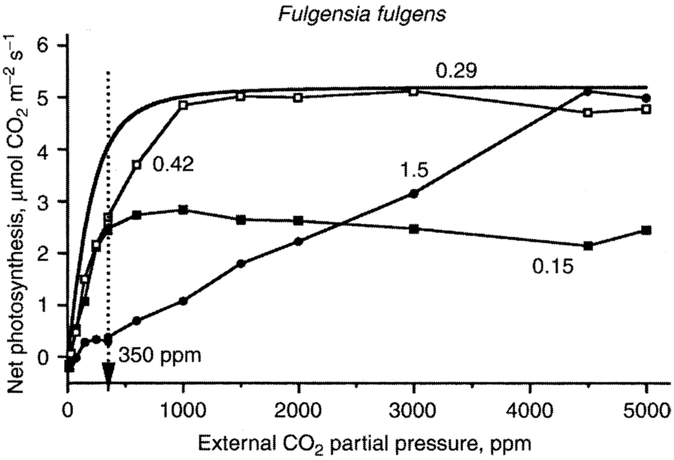


Figure 35.1 Net photosynthesis as a function of external CO_2 concentration at selected water contents (WC, mm precipitation equivalent; see numbers by each curve) of *Fulgensia fulgens* (from soil crust comunity, Hundsheimer Berg, Austria). WC of 0.29 mm denotes optimal hydration. Lower WC (0.15 mm) limits net photosynthesis at about 500 ppm. Suprasaturation changes the initial slope of response curve and increases the CO_2 concentation necessary for saturation (WC of 0.42 mm), which is reached only at 4500 ppm at a WC of 1.5 mm. Natural ambient CO_2 is indicated by dotted line and arrow. (From Lange et al., *Journal of Plant Physiology*, 154, 157–166, 1999. With permission.)

Initial responses of soil lichens to long-term experimental increases in external CO_2 have been inconsistent (reviewed by Tuba et al., 1999). Exposure of *Cladonia convoluta* (a common species in south European soil crusts) for 5 months to 700 ppm CO_2 increased net CO_2 uptake by 50%, a gain that was especially beneficial during drying cycles (Tuba et al., 1998). Tuba et al. concluded that desiccation-tolerant organisms "will be among the main beneficiaries of a high CO_2 future" (p. 39). In contrast, the epiphytic lichen *Parmelia sulcata* (also a common genus in soil crusts) acclimated after only 30 days to 700 ppm CO_2 (Balaguer et al., 1996). When subsequently exposed to 350 ppm CO_2, photosynthetic capacity was reduced, associated with less Rubisco present in the pyrenoid of the algal chloroplasts. The efficiency of photosystem II photochemistry was not significantly changed.

Balaguer et al. (1999) also studied another *Parmelia* species (*P. caperata*) around a natural CO_2 spring, where daytime CO_2 concentrations averaged 729 ppm. When compared with individuals living at 355 ppm CO_2, no evidence of a downregulation was found, in contrast to the above-mentioned laboratory study of the same genus. Carboxylation efficiency, apparent quantum yield, the light-saturated rate of NP, and total thallus Rubisco content were similar among the tested individuals, while the light compensation point of CO_2 assimilation was higher in thalli under elevated CO_2. However, no increase in lichen primary production under elevated CO_2 could be found, although enhanced accumulation of lichen substances was noted. It is not known if the photobiont or mycobiont from the two stands remains genetically identical or if differentiation has taken place under the high CO_2 that has existed for over 200 years.

Because lichen photosynthetic responses to experimentally elevated CO_2 have not been consistent, firm conclusions about the performance of soil crust organisms under future CO_2 conditions are not possible. Response variability may result from other limiting factors (e.g., nutrients) or species-specific differences. Other processes not often measured may be affected, such as nitrogen fixation (Norby and Sigal, 1989). However, it seems unlikely that dramatic CO_2-induced changes in soil crust growth are to be expected, although changes in species composition are possible.

35.2.2 Temperature Changes

Soil crust biota occur within a large gradient of habitats, ranging from hot deserts to cold steppes and polar sites. Often, identical species of cyanobacteria, green algae, and lichens can be found under extremely different temperature regimes. This may be explained by the fact that the photosynthetic carbon assimilation of soil crust lichens is adapted to a broad range of temperatures, from below freezing to temperatures higher than 40°C (see reviews in Kappen, 1988; Nash, 1996). In addition, NP of some species can be almost unaffected by temperatures between 2 and 28°C (*Psora cerebriformis*, Figure 35.2; Lange et al., 1997), or have a broad optimal temperature range (*Diploschistes diacapsis*). In general, cyanobacterial lichens (e.g., *Collema*) are better adapted to high temperatures than chlorolichens, with notable exceptions, e.g., *Squamarina lentigera* (Lange and Green, 2003) and *Acarospora schleicheri* (Nash et al., 1982). Favorable diel net primary production for species such as *S. lentigera* or *Lecanora muralis* depends more on the degree and timing of hydration than temperature, as carbon gains occur during both cold winters and warm summers (Lange, 2003; Lange and Green, 2003). Armstrong (1973) also found a strong correlation between precipitation and monthly growth in Great Britain lichens, with temperature being unimportant. However, Belnap et al. (in press) recently showed *Collema* cover declined dramatically with an increase in June average temperature ($r = 0.96$).

In addition, the photosynthetic and respiratory processes of lichens can acclimatize to wide seasonal temperature fluctuations, as discovered by Stålfelt (1939) and documented by Kershaw (1985) for arctic and boreal terricolous lichens. *Cladonia convoluta*,

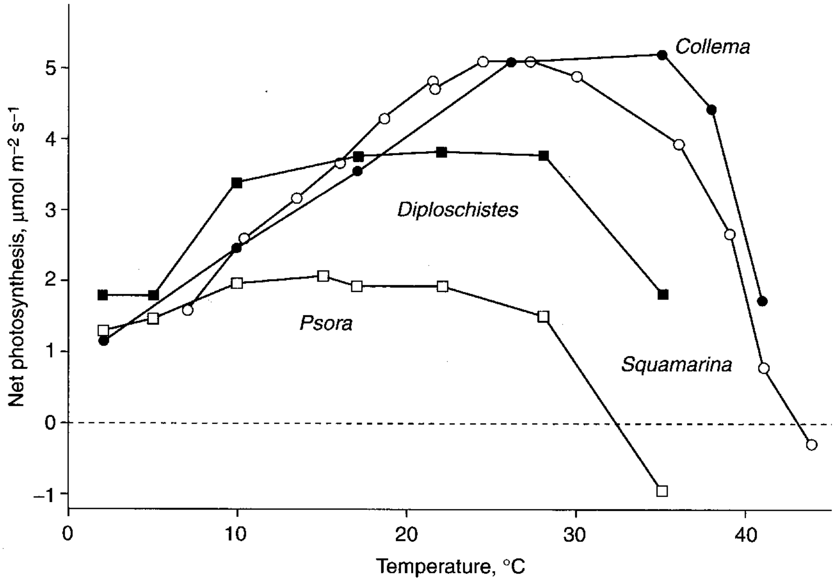


Figure 35.2 Dependence of net photosynthesis on temperature at optimal water content and saturating light for *Psora cerebriformis*, *Diploschistes diacapsis*, *Collema tenax* (from southern Utah, U.S.), and *Squamarina lentigera* (local steppe formation, Würzburg, Germany). (From Lange et al., *Flora*, 192, 1–15, 1997; Lange and Green, *Bibliotecha Lichenologia*, 88, 363–390, 2004.)

Diploschistes muscorum, and *S. lentigera* from a temperate site seasonally alter the temperature sensitivity of dark respiration such that respiratory rates are roughly equal in winter and summer (Lange and Green, 2005). This ensures a greater supply of energy at low temperatures while preventing increased loss of assimilates at higher temperatures.

Because of the low temperature sensitivity of productivity, i.e., the ability to acclimate photosynthetic and respiratory processes under different temperatures, substantial effects of increased temperature on net carbon gain of soil crust communities are unlikely. However, this does not include temperature effects on hydration (see below), nor does it consider effects on other metabolic activities such as nitrogen fixation. Increased temperatures may also stress hot desert lichens in unforeseen ways, such as during their dry-down periods, when they are especially vulnerable to heat stress.

35.2.3 Water Availability

Water availability determines the length and magnitude of metabolic activity time for poikilohydric organisms and, thus, ultimately the productivity and persistence of biological soil crust organisms. It is estimated that soil crusts are metabolically active only 10 to 12% of the year in the Namib Desert (Lange et al., 1991) and photosynthetically active 9 to 11% of the year on the Colorado Plateau, UT (Belnap, unpublished). This proportion might be even smaller for drier regions or those that lack dew or fog. Under such circumstances, even the smallest change in the length of time soils are sufficiently wet for activity will impact the function and perhaps the species composition of the crust community. This was amply demonstrated when changes in crust biota and their photosynthetic productivity were seen at neighboring sites in the Negev highlands that had almost a fivefold variance in maximal dew amounts (Kappen et al., 1980).

Individual soil crust species are also adapted to different types of precipitation. The moisture compensation point of CO_2 exchange for most green algal lichens is very low.

Diploschistes muscorum and *Fulgensia fulgens* represent extreme cases, where precipitation equivalents of 0.04 and 0.055 mm, respectively, are sufficient for activating NP. This equals a dry-weight water content of 12 to 15% and a water potential of about –200 bar, which can be attained via slight dew condensation or vapor from humid air. In contrast, free-living cyanobacteria (e.g., *Microcoleus*) or cyanobacterial lichens (e.g., *Collema*) have a much higher moisture compensation point (Lange et al., 1993, 1998). They require up to five times more water for reactivating NP, which usually occurs only after rainfall. Cyanolichens usually can store much more water than chlorolichens. They can also utilize higher levels of thallus water for photosynthesis before experiencing suprasaturation depression, compared with chlorolichens, which experience suprasaturation depression at relatively low WC (see Figure 6.3). As a consequence, cyanobacteria and cyanobacterial lichens dominate soil crusts in areas where precipitation occurs mainly as rainfall. In contrast, chlorolichens almost exclusively dominate soil crusts in regions where precipitation occurs mostly as dew, fog, or high air humidity. Therefore, changes in the type of precipitation in an area will most likely lead to alteration of the lichen community structure.

Global climate change models predict not only changes in type and amount of precipitation, but also significant changes in precipitation frequency, timing, and interannual variability (Gregory and Mitchell, 1997; Neilson, 1995). Such changes are expected to have profound consequences for soil crust physiological functioning and species composition. Application of smaller, more frequent rainfall events during summer resulted in reduced photosynthetic performance and sunscreen pigment production in *Collema*, compared with lichens receiving larger, less frequent events (Belnap et al., 2004). Summer rain can create repeated short wet–dry cycles, which often result in net C losses and negligible N fixation (Jeffries et al., 1993a, 1993b). These losses may increase mortality or even extirpation of some crust species. This may explain the sharp decreases in lichen and moss diversity observed in hot desert summer rainfall regions in the U.S., Australia, and central Asia relative to winter rainfall areas of equal precipitation. In contrast, increasing summer rainfall in the colder deserts (e.g., northern Great Basin, the Mongolian steppes, or the Arctic) is expected to increase activity time of crust species, as light levels and temperatures are optimal for C and N fixation. Increased biomass, cover, and species richness of the crusts would be expected under this scenario.

35.2.4 Altered Ultraviolet Radiation

Ultraviolet (UV) radiation can be extremely harmful to living organisms, as it interacts directly with their DNA and proteins and affects processes such as photosynthesis, respiration, N_2 fixation, and nutrient uptake (reviewed in Castenholz and Garcia-Pichel, 2000). As radiation penetrates into the soil, light fields become increasingly diffuse. However, irradiance levels are maximal at the soil surface, as both incoming and reflected light combine in this zone. Photobionts in lichens effectively use fungal tissue for protection, with a 90% reduction in UV measured in the center of *Collema coccophorum* (Büdel et al., 1997). Secreted polysaccharides with sunscreen pigments (e.g., scytonemin, mycosporine-like amino acids, melanins, phenolic compounds, and anthraquinones) protect lichens, cyanobacteria, green algae, and microfungi (Garcia-Pichel and Castenholz, 1991). In addition, some cyanobacterial species migrate below the soil surface to avoid radiation exposure, while mosses and lichens can often roll up when dry, possibly to protect sensitive surfaces from radiation damage (Frey and Kürschner, 1991; Rosentreter, 1993).

Recently, progress has been made in analyzing the function of the sun-screening orange-colored anthraquinone parietin in *Xanthoria parietina*, a pigment which protects the photobionts against excessive sun radiation (Gauslaa and Solhaug, 2004). Its synthesis is induced by UV-B (Solhaug et al., 2003), and it shows distinct seasonal acclimation with low contents in winter and high levels in summer (Gauslaa and McEvoy 2005). The same compound occurs in several typical soil crust lichens (e.g., in *Fulgensia* species) where similar performance might be expected. Although short-term laboratory studies (where organisms are watered) show that soil crust cyanobacteria and lichens respond to experimentally enhanced UV by increasing production of protective pigments, long-term field studies with enhanced UV indicate that crust organisms may often lack the resources needed for such production. In one study, cyanobacteria showed significant mortality after a summer of above-average precipitation, despite large increases in pigment production (Bowker et al., 2002). During summers of average or below-average precipitation, cyanobacteria and *Collema* often experience carbon deficits (Jeffries et al., 1993a, 1993b), and with UV additions, *Collema* showed an additional 57% decline in photosynthetic rates and declines in all measured sunscreen pigments (Belnap et al., 2004). Limited C gain or C losses require the organism to allocate C toward the upkeep of its photosynthetic machinery (e.g., chlorophyll *a*) rather than to the production of UV-protective pigments. This likely results in heightened UV damage and mortality.

As discussed above, increased UV can be expected to impact crust species under many conditions. These effects are expected to differentially affect various crust species, depending on climate factors, the species involved, and the amount and condition of their particular protective mechanisms.

35.2.5 Observed Effects of Climate Change on Soil Crust Lichen Communities

Several theoretical and experimental publications have explored the possible impacts of climate changes on terrestrial lichen performance and distribution (e.g., Bates and Farmer, 1992; Melick and Seppelt, 1994; Nash and Olafsen, 1995; Insarov and Insarova, 1996; Sveinbjörnsson and Sonesson, 1997; Insarov and Schroeter, 2002). Except for catastrophes and small-scale habitat alterations, such changes are likely to be a gradual process, given the low growth and slow successional rates of lichens. Lichen floras in Europe were impoverished by atmospheric SO_2 pollution. Studies since 1980 show a slow but continuous recovery (Nimis et al., 2002). Such slow response makes the study of climate change effects on lichens difficult.

Nevertheless, some changes in lichen species composition are already becoming apparent. A study of many sites in the Netherlands clearly demonstrates that recently increased temperature and precipitation have already resulted in floristic changes in the surveyed lichen communities (van Herk et al., 2002; see also Aptroot and van Herk, 2001). Changes over the last 22 years in the distribution of 329 epiphytic and terricolous lichens were correlated with the latitudinal distribution and ecological determinates of the different species. According to van Herk et al. (2002) and Aptroot (personal communication), in the Netherlands soil lichen species with predominantly boreal distribution are showing a decline while subtropical species are increasing. Changes in species between 1995 and 2001 appear to be positively correlated with both temperature and nutrient demand, with a recent and significant shift toward species preferring warm circumstances, independent from and concurrent with changes due to nutrient availability (van Herk et al., 2002). Soil lichen species with predominantly boreal distributions (e.g., *Cetraria islandica, Cladina rangiferina*) and those preferring somewhat cooler conditions (*Dibaeis baeomyces* and *Pycnothelia papillaria*) are declining or have totally disappeared from relatively undisturbed heathlands (Aptroot, personal communication). In contrast, soil crust lichens with a Mediterranean center of distribution (e.g., *Fulgensia fulgens* and *Endocarpon pusillum*) have not changed their distribution. *Placynthiella oligotropha*, one of the terricolous species expanding the most successfully, is a warm-temperate lichen. From these impressive analyses, it seems clear that global changes have already begun to impact the distribution of lichens, including those found in soil crust communities.

Soil crust organisms are generally unable to compete with phanerogamous plants for light and space, and they colonize the ground in the gaps of vegetation where climate conditions prevent closed plant canopies. Therefore, secondary effects of climate changes on soil crust distribution and composition due to changes in the vascular plant community also need consideration. Large increases in net primary productivity may occur in arid ecosystems due to elevated CO_2 and enhanced water availability (Melillo et al., 1993). Early results from a Mojave Desert elevated CO_2 site report an increase in cover and biomass of the invasive annual *Bromus tectorum* (Smith et al., 2000). Increased annual grass will shade soil crusts, decrease space available for colonization, and increase fire cycles. Sites dominated by *Bromus* are 10 to 500 times more likely to burn than uninvaded sites (Knapp, 1996), and fire intervals can decrease from >100 years to <5 years (Whisenant, 1990). Fire kills soil crust organisms; thus, increased fire frequency reduces crust biomass and precludes colonization of lichens and mosses. *Bromus* also increases seed availability, which then attracts burrowing rodents. Attendant soil disturbance prevents development of perennial lichens and mosses, and soil crusts are instead dominated by cyanobacteria and annual mosses. Such changes in soil crust species composition result in decreased species richness and rates of N and C inputs into soils.

Cornelissen et al. (2001) studied the interaction between phanerogamous plants and terricolous macrolichens in different arctic tundra and heath ecosystems containing fruticose and foliose lichens such as *Cladina* spp., *Cetraria nivalis*, *Stereocaulon alpinum*, and *Thamnolia* sp. The authors hypothesized that climate warming and increased nutrient availability in the more climatically mild arctic ecosystems, with relatively dense canopies, would result in a decline in macrolichen abundance as a function of increased vascular plant abundance. In contrast, they expected such a relationship to be absent in the more open high-arctic or arctic-alpine plant communities. This hypothesis was clearly supported by data from ecosystem manipulation experiments and with comparisons along natural environmental gradients.

One consequence of global climate change will unquestionably favor development of biological soil crusts. Increasing temperature and the subsequent retreat of polar and high montane glaciers (Oechel et al., 1997) will create additional substrates for the colonization of soil crust organisms. As a pioneering vegetation type, these crusts are important for stabilizing soils and increasing their fertility (Hansen, 2003; Türk and Gärtner, 2003).

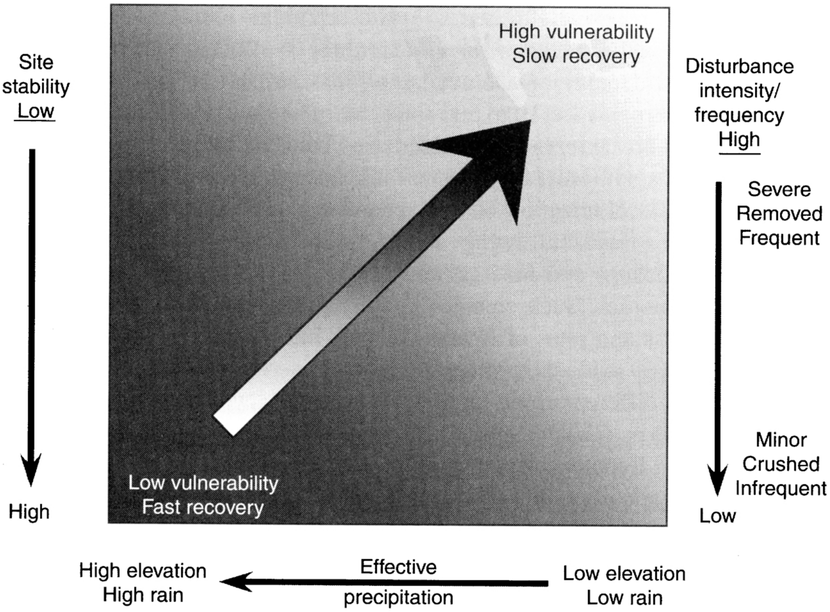
Evidence is accumulating that the global climate changes observed in the past few decades are directly and indirectly impacting biological soil crusts, including their extent, distribution, and species composition. However, it is certainly still too early to predict the direction of change or the details of these changes.

35.3 LAND USE AND LICHENS IN SOIL CRUST COMMUNITIES

While changes in land use are of global concern, increasing use of marginal lands is especially widespread in the arid and semiarid regions where biological soil crusts are most apparent. These regions are home to 35% of the world's population (Brooks and Pokshishevsky, 1986) and conversion of these lands for agricultural and recreational use is rapidly increasing (Brown et al., 1995).

35.3.1 Surface Disturbance

Compressional and shear forces are generated by both agricultural (trampling by livestock) and recreational (trampling by people, crushing by vehicles) uses. Biological soil crusts are highly vulnerable to this type of disturbance, especially when dry and therefore brittle, with lichens the most susceptible crust component. The vulnerability of a specific soil crust to disturbance is heavily influenced by soil texture, soil moisture, and the type and intensity of disturbance (Figure 35.3). Soil crust organisms on coarse-textured soils are



Factors determining site stability

	Low stability	**High stability**
Soil texture/age	Coarse/young	Fine/old
Rock/gravel cover	Rolling	Embedded
Sand deposition	High	Low
Plant spacing	Sparse	Dense
Slope	Steep	Flat

Figure 35.3 Vulnerability and recoverability of crusts depend on gradients of site stability, effective precipitation, and disturbance regimes. Top panel: Crusts at sites with the greatest stability (defined in bottom panel), greatest effective precipitation, and lowest disturbance frequency or intensity will be less impacted (dark shading) than crusts at sites with lower stability, less effective precipitation, and higher disturbance frequency or intensity (light shading). Similarly, crust recovery time is faster (dark shading) in areas of low vulnerability and slower (light shading) where vulnerability is higher. Bottom panel: Factors influencing site stability. (Adapted from Belnap and Eldridge, in *Biological Soil Crusts: Structure, Function, and Management*, J. Belnap and O.L. Lange, Eds., Springer-Verlag, Berlin, 2003, pp. 363–383.)

more vulnerable than silty and clay soils when dry, whereas clay soils are the most vulnerable when they are wet. Crusts on gravel-covered soils are the least vulnerable. Disturbance that churns the soils and buries organisms (e.g., accelerating vehicles) is much more destructive to crusts than disturbance that crushes crusts in place (e.g., slow walking). Repeated disturbance also buries crust material and, thus, is more damaging than occasional use. Lichens are the most susceptible to disturbance, followed by mosses, smaller cyanobacteria and green algae, and lastly, the large cyanobacteria.

Indirect effects of soil surface disturbance occur when destabilized soils bury or "sandblast" adjacent biological crusts, resulting in the death of the photosynthetic components of the soil crust. Direct effects occur when the brittle crust organisms are crushed and then buried, washed, or blown away (Harper and Marble, 1988; Campbell et al., 1989; Belnap, 1993). Soil crusts in undisturbed areas can have up to 20 to 30 species of soil lichens and mosses and up to 60 species of cyanobacteria, whereas adjacent disturbed areas often have no lichens or mosses and only a few species of cyanobacteria.

Resistance to wind and water erosion has been shown to parallel biological crust development, as bare soils or cyanobacterial crusts allow up to 35 times more wind and water erosion than lichen-moss crusts (McKenna-Neuman et al., 1996; Belnap and Gillette, 1997, 1998). Disturbed soil crusts are often only a few millimeters thick, in contrast to undisturbed crust that can be up to 10 cm thick (Belnap, 1995). Therefore, disturbance that results in cyanobacterial crusts leaves soils more vulnerable to erosion than those dominated by lichen crusts.

In cool regions, the cohesive soil crust is frost-heaved upward in winter and then differentially eroded downward, creating a greatly roughened soil surface. This roughened surface decreases the velocity and erosivity of wind and water. Disturbance by livestock, people, or vehicles flattens these soil surfaces, increasing erosion susceptibility. Flattening reduces residence time of the water, decreasing water infiltration. Loss of lichens and mosses also reduces the water storage capacity of the soil. Therefore, such soil surface disturbances can greatly accelerate soil loss and reduce soil moisture in these regions. In contrast, soil crusts in hyperarid regions where soils do not freeze actually smooth the soil surface. In these regions, disturbance roughens the soil surface. This increases soil erosion and increases water infiltration (reviewed in Belnap and Eldridge, 2003). However, localized infiltration in hyperarid regions is not always desirable, as it can result in the death of downslope plants (Tongway and Ludwig, 1990). Erosion is not desirable in any desert, as soils take 5,000 to 10,000 years to form in these areas (Dregne, 1983).

Disturbance to the soil crusts reduces soil fertility and moisture retention. Lichens and mosses fix more C than the equivalent surface area of cyanobacteria, and therefore their loss reduces soil C inputs. Reduction of total crust biomass also means less secretion of growth factors, chelators, and acids to free carbonate-bound phosphorus. Nitrogen fixation declines 60 to 100% immediately following disturbance (Belnap, 2003), and the subsequent death of buried N-fixing cyanobacteria and lichens results in virtual elimination of new N inputs into soils. This, coupled with continued N losses from gaseous emissions and erosion, causes decreases in soil and plant N (Ehleringer et al., 1998; Evans and Belnap, 1999). In addition, the loss of soil fine particles to which nutrients are attached directly reduces soil fertility and water-holding capacity of desert soils. Soil surface disturbance also favors invasion of annual grasses. The presence of invasive grasses leads to the replacement of lichens by mosses and cyanobacteria, with a subsequent decline in C and N inputs to soils (for a more complete discussion on invasive grasses, see Section 35.2.5).

The conversion of lichen-moss crusts to cyanobacterial crusts, with concomitant declines in C and N inputs, decreases the abundance and diversity of soil food webs and thereby affects nutrient cycling rates and nutrient availability (Belnap, 2003b). Nitrogen mineralization can decrease ~80% following the loss of lichens and mosses. Disruption of soil food webs can reverberate throughout the ecosystem, affecting vascular plants and faunal components (Coleman et al., 1992; Hendrix et al., 1992). Preventing desertification depends on maintaining stability and fertility of soils and the diversity of processes and species in ecosystems (Dregne, 1983); thus, loss of lichen-moss crusts can accelerate the desertification process.

Loss of lichens and mosses also impacts other ecosystem characteristics. Lichen-moss crusts have 50% less reflectance of wavelengths from 0.25 to 2.5 μm than bare soil (Belnap, 1995). This represents a change in the surface energy flux of approximately 40 W/m^2 and temperature differences of up to 14°C (Belnap, 1995). Soil temperatures affect many physiological process rates, including N and C fixation, microbial activity, plant nutrient uptake, and timing of seed germination. Food and other resources are often partitioned among invertebrates and small mammals on the basis of surface temperatures (Doyen and Tschinkel, 1974; Wallwork, 1982; Crawford, 1991). Many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival (Larmuth, 1978). Consequently, altering surface temperatures can affect many desert organisms.

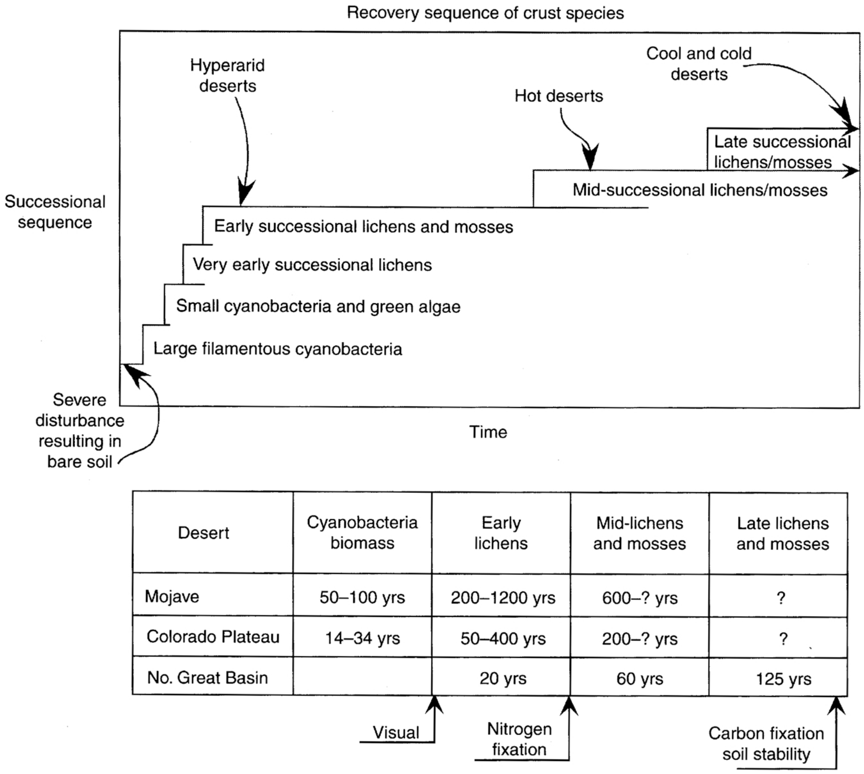
Disturbance of biological soil crusts has many detrimental effects on desert ecosystems. Conversion of lichen-moss soil crusts to cyanobacterial soil crusts means loss of fertility and stability for desert soils. These changes lead to impacts on many other aspects of desert ecosystems.

35.3.2 Recovery

Estimates of recovery times for biological soil crusts after disturbance vary widely in the literature, partially due to different assessment techniques and the lumping of different climates and crust types. Accurate assessment of recovery rates is difficult, as they depend on many factors, with the most important being soil stability and fertility; the type, intensity, and extent of disturbance; the availability of inoculation material; the predisturbance flora; and the temperature and moisture regimes that follow disturbance events (Figure 35.4; reviewed in Belnap and Eldridge, 2003). Coarse soils, with their inherent instability, low fertility, and low water-holding capacity are slower to recover than fine-textured soils with high water-holding capacity and greater fertility.

Sites receiving severe disturbance that removes crust material are slower to recover than sites receiving less intense disturbance that crushes organisms in place, leaving them to act as inoculating material. Disturbances with large surface-to-volume ratios have a slow recovery, as most colonization occurs from adjacent, undisturbed areas. Cyanolichens generally recover faster than chlorolichens, perhaps due to cyanobacterial photobionts being much more common in desert soils than green algal photobionts, thus facilitating colonization by cyanolichen spores. Because crust organisms are metabolically active only when wet, regions with low potential evapotranspiration recover much more quickly than crusts in regions with high potential evapotranspiration (Belnap and Eldridge, 2003).

In severely disturbed areas, large filamentous cyanobacteria (e.g., *Microcoleus*) generally colonize first, followed by smaller cyanobacteria, green algae, and microfungi (Figure 35.4). After soils are stabilized, early successional lichens (e.g., *Collema*) and mosses colonize. Where there is sufficient precipitation (e.g., cool deserts), these species are followed by later successional species (e.g., *Diploschistes*). Recovery of the ecological functions (e.g., C and N fixation) of the soil crusts depends on what species recolonize. Often, mosses may colonize areas previously dominated by N-fixing lichens. Consequently, N in soils and plants may take much longer to recover than expected (Evans and



Desert	Cyanobacteria biomass	Early lichens	Mid-lichens and mosses	Late lichens and mosses
Mojave	50–100 yrs	200–1200 yrs	600–? yrs	?
Colorado Plateau	14–34 yrs	50–400 yrs	200–? yrs	?
No. Great Basin		20 yrs	60 yrs	125 yrs

Figure 35.4 Colonization sequence and estimated recovery times for crustal species in the western U.S. Top panel: Arrows indicate the degree of crust development possible in a desert type; length of line indicates relative time for recovery of each successional group. Species indicative of successional groups include large filamentous cyanobacteria, *Microcoleus* spp.; small cyanobacteria, *Nostoc* spp.; very early successional, *Collema* spp.; early successional, *Placidium* spp., *Pterygoneurum* spp.; mid-successional, *Psora* spp., *Fulgensia* spp., *Tortula* spp., *Bryum* spp.; late successional, *Acarospora* spp., *Pannaria* spp. Bottom panel: Relative recovery rates for different climates. Reported estimates are averages, as sites show considerable variation in recovery times for sandy soils and are based on linear extrapolations. Recovery rates of mid- and late-successional species are not known in drier deserts, where slow recovery times have precluded estimates. Estimates are based on published rates. (Adapted from Belnap and Eldridge, in *Biological Soil Crusts: Structure, Function, and Management*, J. Belnap and O.L. Lange, Eds., Springer-Verlag, Berlin, 2003, pp. 363–383.)

Belnap, 1999). Restoration of normal surface albedos, C fixation, and soil stability require all predisturbance species to recolonize, especially lichens and mosses.

Inoculants can be used to speed up recovery of soil crusts (Tiedemann et al., 1980; Ashley and Rushforth, 1984; St. Clair et al., 1986; Belnap, 1993; Buttars et al., 1998). Cyanobacterial inoculants are being developed, but as of yet are unsuccessful for large areas. The difficulty of growing lichens and mosses in the lab will likely preclude inoculant development. The current lack of commercially available products requires that intact crusts be used as the inoculating material, limiting this technique to use in small areas.

Unfortunately, many activities associated with humans are incompatible with the well-being of soil crusts. These organisms are easily crushed, and once lost, recovery is often slow, especially for the mid- and late-successional lichen component. Therefore, reducing disturbance is the best management strategy.

35.4 CONCLUSIONS

A recent review by Hughes (2000) showed changes in the physiology, distribution, and phenology of trees, grasses, forbs, phytoplankton, butterflies, mosquitoes, oceanic and terrestrial birds, reptiles, amphibians, and insects in response to global warming. Recently, Aptroot and van Herk (2002, p. 57) concluded: "It can be safely predicted that global warming would have an influence on lichen floras." Reviews by Insarov and Insarova (1996) and Insarov and Schroeter (2002) that focused on how climate changes will affect lichens, including terricolous species, came to a similar conclusion.

Autotrophic poikilohydric organisms, such as those found in biological soil crusts, are metabolically active only when wet. Therefore, they are highly responsive to the slightest changes in water availability (both amount and timing). Temperature influences metabolic processes such as photosynthesis and nitrogen fixation, while also determining rates of water loss and thus duration of metabolic activity. Any change in these parameters will impact soil crust structure and function, as can be seen by correlating current species distributions with environmental conditions. Additionally, increases in CO_2 and UV are expected to have substantial impacts on soil crusts.

Increasing use of arid and semiarid lands, with attendant soil surface disturbance and invasion of exotic plants, will most definitely produce profound changes in soil crusts. The soil crusts are fragile systems highly vulnerable to such disturbance. Heavy livestock grazing, human trampling, and off-road vehicles crush the brittle crust, destroying its structure and changing its species composition, thus reducing soil stability and productivity. As the species composition and physiological functioning of crust components are changed through these different forces, we can expect concomitant changes in soil food web structure and function, nutrient cycling rates, vascular plants, and fauna. As these disturbances increase, crust conservation needs to become an even more important issue for land managers.

Because the photosynthetic response of lichens to elevated CO_2 has not been consistent and because information about long-term exposure is scarce, firm conclusions about the performance of soil crust organisms under future CO_2 conditions are not yet possible. Observed limitations and the variability of responses may result from factors other than elevated CO_2 (e.g., nutrients and light). The situation might be similar for mature forest trees, where little (if any) effects via CO_2 fertilization on growth are to be expected (Körner, 2003). Other lichen processes not often measured may also be affected, such as nitrogen fixation (Norby and Sigal, 1989). However, it seems unlikely that dramatic CO_2-induced changes in soil crust growth will occur. Changes in species composition might be possible, due to species-specific differences in the presence or activity of carbon-concentrating mechanisms, which will determine the CO_2 sensitivity of photobionts' photosynthesis to atmospheric CO_2.

ACKNOWLEDGMENTS

We thank Sue Phillips for assistance with graphics and Beth Roy for assistance in editing.

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The Fungal Community

Its Organization and Role in the Ecosystem

Third Edition

edited by
John Dighton
James F. White
Peter Oudemans

Taylor & Francis
Taylor & Francis Group
Boca Raton London New York Singapore

A CRC title, part of the Taylor & Francis imprint, a member of the Taylor & Francis Group, the academic division of T&F Informa plc.

Published in 2005 by
CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

© 2005 by Taylor & Francis Group, LLC
CRC Press is an imprint of Taylor & Francis Group

No claim to original U.S. Government works
Printed in the United States of America on acid-free paper
10 9 8 7 6 5 4 3 2 1

International Standard Book Number-10: 0-8247-2355-4 (Hardcover)
International Standard Book Number-13: 978-0-8247-2355-2 (Hardcover)

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Library of Congress Cataloging-in-Publication Data

The Fungal community : its organization and role in the ecosystem / edited by John
Dighton, James F. White, Peter Oudemans. — 3rd ed.
p. cm. — (Mycology)
Includes bibliographical references and index.
ISBN 0-8247-2355-4 (alk. paper)
I. Dighton, J. (John) II. White, James F. (James Francis), 1953- III. Oudemans, Peter.
IV. Mycology series.

QK604.2.C64F86 2005
579.5'17—dc22 2004061821

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