27 Disturbance and Recovery of Biological Soil Crusts

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27.1 Introduction

Disturbance can profoundly affect the cover, species composition, and the physiological functioning of biological soil crusts. The disturbances we discuss include air pollution; exposure to oil, herbicides, and pesticides; invasion by annual exotic weeds; mechanical disturbances such as human and livestock trampling (see Chap. 29), off-road driving, mining, and hiking; and, briefly, wildfire (for extensive discussion, see Chap. 28). Studies on disturbance have generally been limited to the western US and Australia, with limited work done in China, Israel, South Africa, and Zimbabwe.

Methods of assessing impacts of, and recovery from, disturbance have been highly variable in the past. Generally, measurements have been limited to visual estimates of crust cover. However, Belnap (1993) showed that visual assessment can accurately assess only moss and lichen cover, and cannot be used to measure recovery of cyanobacterial biomass, soil stability, and/or physiological functioning of crustal organisms. In addition, some studies have only considered total crust cover but have not delimited the relative cover of cyanobacteria, mosses, and lichens. The relationships between total crust cover and impacts of disturbance can be weak, as cyanobacterial cover generally increases, while moss and lichen cover decreases, after disturbance. This often makes total crust cover a poor measure of the dynamics of soil-crust recovery. Differentiating between crustal components is also important because alteration of species composition can heavily influence ecological functioning of the crusts (Eldridge 1998).

Comparing recovery rates from different studies can be problematic, as factors known to control recovery rates (such as site stability and precipitation following disturbance) are often not reported. More importantly, severity of disturbance is seldom quantified. Studies generally report disturbance levels as "light", "moderate", or "heavy" without any definition of these categories; thus, what is "moderate" in one study may be considered "heavy" in another. As studies cover a large range of climatic zones, soil types, levels of

disturbance, and ways to calculate recovery, and because there has been no standard for measuring crust recovery, it is not surprising that recovery rates in the literature have ranged widely (2 years in cool deserts to over 3000 years in very dry deserts), and either show no pattern or often appear contradictory (Anderson et al. 1982; Callison et al. 1985; Jeffries and Klopatek 1987; Cole 1990; Belnap 1995,1996; Belnap and Warren 1998).

27.2 Disturbance Effects

The impact of a given disturbance depends on the soil, plant, and climate characteristics of the site, and the severity, frequency, timing, and type of the disturbance (Fig. 27.1). While most disturbances result in similar types of impacts, severity can vary widely. For instance, vehicles and trampling exert both compressional and shear forces; however, these forces are much greater for vehicles than trampling. In addition, vehicles often turn soils over and bury crustal organisms, while trampling tends to only compress the surface. Vehicle tracks often channel water and thus slow or prevent recovery (Webb and Wilshire 1983). Intensifying physical impacts (such as high-intensity, short-duration grazing) is deleterious to the cover and species richness of biological soil crusts (Johansen 1993). Disturbance that removes or kills crustal organisms results in greater impact and slower recovery than disturbance that leaves crushed crust material in place (see Sect. 27.3.3). As lichens and mosses are less tolerant of disturbance than cyanobacteria, frequent disturbance can maintain the biological soil crust at a low successional stage (e.g., cyanobacterially dominated; Harper and Marble 1988).

   Timing of disturbance can affect the degree to which the cover and species richness of the crust is reduced. The intrinsic strength of soil varies with moisture content (Fig. 27.2). Soils with little tendency to form aggregates, such as sands, are more susceptible to compressional stresses when dry. Fine-textured soils or those with inorganic crusts are more vulnerable to compressional disturbance when wet (Webb and Wilshire 1983). Crust components are brittle when dry, and the connections they make between soil particles are easily crushed. Thus, compressional disturbances can severely affect the ability of crusts to stabilize soils, especially in dry sandy and silty soils. For instance, grazing in the early wet season (winter) has been shown to have less impact on crust cover and species composition than late winter or spring grazing. As crustal species are only metabolically active when wet and are brittle when dry, disturbance in dry seasons is more destructive, and organisms are less able to recover, than when disturbed in wet seasons (Harper and Marble 1988).
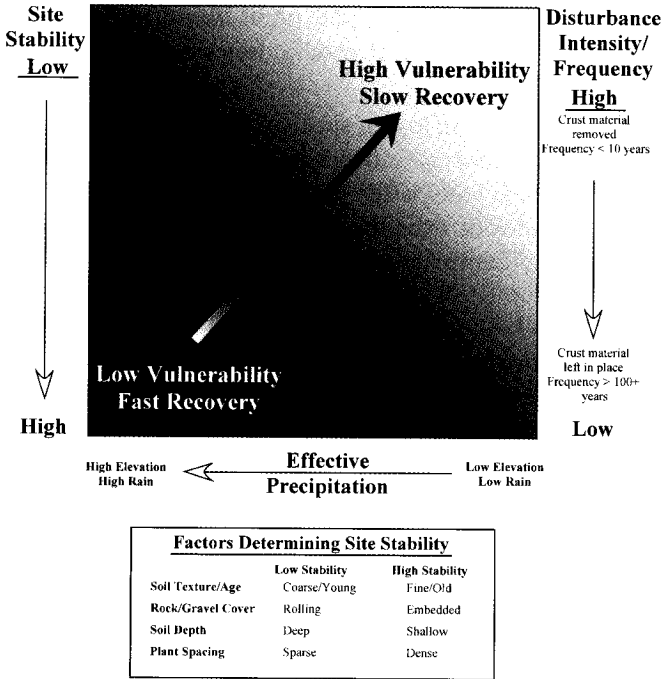
Site Stability

Low

Disturbance Intensity/ Frequency

High Vulnerability Slow Recovery

High

Crust material removed
Frequency < 10 years

Crust material left in place
Frequency > 100+ years

Low Vulnerability Fast Recovery

High   **Low**

High Elevation
High Rain   **Effective Precipitation**   Low Elevation
Low Rain

Factors Determining Site Stability		
	Low Stability	High Stability
Soil Texture/Age	Coarse/Young	Fine/Old
Rock/Gravel Cover	Rolling	Embedded
Soil Depth	Deep	Shallow
Plant Spacing	Sparse	Dense

Fig. 27.1. Vulnerability and recoverability of crusts depends 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 sites with lower stability, less effective precipitation, and higher disturbance frequency or intensity (*light shading*). Similarly, 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

		Soil Texture		
		Sand	Clay	Silt
Soil Moisture Content	Frozen	Low	Low	Low
	Wet	Medium-High	High	Low
	Moist	Medium-High	Medium	Medium
	Dry	Very High	Low	Very High

Fig. 27.2. Vulnerability of crusts to disturbance varies according to soil texture and moisture. Note crusts on sandy soils are more susceptible to disturbance when wet than when dry, while crusts on clay soils have the opposite response

27.2.1 Disturbance Effects on Species Composition of Biological Soil Crusts

Overall, disturbance generally results in loss of species diversity, biomass, and surface cover of cyanobacteria, lichens, and mosses. The more severe the disturbance, the greater the loss. Thus, after severe disturbance, the crust community with multiple species of cyanobacteria, lichens, and mosses is often simplified to a community dominated by one or a few species of cyanobacteria.

Air Pollution. A few studies have addressed the impact of air pollutants on soil lichens in desert environments. No differences have been found in species composition near pollution sources when compared to control sites. It is reasoned that lichens with thalli closely appressed to the soil surface, as found in most desert soil-crust lichens, are less susceptible to damage by air pollutants than lichens whose tissue is more exposed to air. In addition, most desert soils are very alkaline, and thus thought to buffer acidic pollutants (Nash and Sommerfeld 1981).

Oil Spills, Insecticides, and Herbicides. We know of no study that directly addresses the effects of oil, oil dispersants, insecticides, or herbicides on species composition of intact soil crusts. However, much work has been done on individual species of cyanobacteria, green algae, and mosses isolated from soil crusts. Tested species were differentially affected, both positively and negatively, depending on the compound and the species tested. Thus, exposure to these agents could either kill or potentially alter species composition of crusts (Metting 1981; Youtie et al. 1999).

Annual Plant Invasion. Invasion of exotic annual plants into perennial plant communities can impose a long-term threat to biological soil-crust communities because the crust-dominated interspace between perennial plants is often heavily invaded. Surveys in invaded communities show that rich perennial moss/lichen communities are quickly replaced with only a few species of annual mosses and cyanobacteria (Kaltenecker 1997; Belnap and Phillips 2000). The mechanism by which this shift occurs is not known, but probably results from increased plant material shading the soil surface, increased soil turnover by elevated rodent populations, and/or increased fire frequency.

Fire. The effects of fire are covered extensively in Chapter 28. In summary, the main effects of fire are loss of cover, biomass, and species diversity of soil crusts (Johansen et al. 1993). Damage to, and recovery of, soil crusts depends on the prefire composition and structure of the vascular plant community and distribution of fuel, fire intensity, and fire frequency. Hotter and more

frequent fires result in more damage to the crusts. Frequent fires prevent the recovery of lichens and mosses, resulting in crusts containing only a few species of cyanobacteria.

Mechanical Disturbance. Mechanical disturbance includes activities such as vehicle traffic (military and recreational), trampling by livestock (Chap. 29) and people, and land-clearing (such as mining). Such uses are intensifying exponentially in arid and semiarid areas of the world. Effects of mechanical disturbance are especially noticeable at sites with highly erodible soils and large topographic relief (Harper and Marble 1988).

Over 30 studies on four continents document that livestock grazing, vehicles (both recreational and military), and human trampling dramatically reduce lichen-moss cover and species richness of crusts. Resistance to disturbance generally decreases in the following order: cyanobacteria > gelatinous lichens > squamulose, crustose lichens; mosses > foliose lichens (reviewed in Harper and Marble 1988; West 1990; Johansen 1993; Eldridge and Greene 1994; Ladyman and Muldavin 1996). Cyanobacteria, being relatively mobile, are the most resistant to disturbance. Lichens use a combination of thallus structures, pigments, water storage capacities, tolerance of inundation, and/or an ability to fix atmospheric nitrogen (N) to increase resistance to disturbance. For example, Rogers and Lange (1971) showed that the lichens *Collema coccophorum* and *Heppia lutosa* (*H. despreauxii*) were the lichen species least affected by sheep trampling around a watering point. These lichens are able to fix atmospheric N, and to store greater amounts of water than phycolichens (Galun et al. 1982). In a comparison of species inside and outside a grazing exclosure, cover of most lichen species was significantly reduced with grazing (Table 27.1). In addition, most soil-surface disturbance compacts soils. Compaction influences soil water and nutrient-holding capacity, which can lead to changes in the species composition of soil-crust communities. These subtle compositional changes often occur before changes in cover are apparent (Eldridge 1996).

Burial. Disruption of crusts often destabilizes underlying soils, leaving adjacent crusts vulnerable to burial by wind and water-moved sediments. Large filamentous cyanobacteria can respond to limited burial by moving up to 5 mm every 24 h if wet. Mosses can also cope with limited burial (Fig. 15.2). However, when burial is too deep, these organisms will die. Burial often kills other photosynthetic components of the crust, including lichens, green algae, and smaller cyanobacteria (Campbell 1979), and thus generally results in a greatly simplified crustal community.

Table 27.1. Frequency (%) of lichens and a liverwort on loamy and sandy soils inside (ungrazed) and outside (grazed) exclosures at Koonamore Vegetation Reserve, South Australia in May 1972. Species extirpated by grazing (frequency = 0) were not evaluated statistically. Frequencies of all other species were significantly reduced with grazing ($p<0.10$). (After Crisp 1975)

Species	Type	Loamy soil		Sandy soil	
		Ungrazed	Grazed	Ungrazed	Grazed
Acarospora smaragdula	Crustose	2.2	0.4	0.2	0.0
Aspicilia calcarea	Crustose	27.4	18.0	11.3	2.1
Aspicilia calcarea	Fruticose	12.1	0.7	1.0	0.0
Collema coccophorum	Squamulose	46.7	40.2	36.4	17.4
Fulgensia subbracteata	Crustose	16.4	4.6	3.1	0.1
Psora decipiens	Squamulose	32.6	12.7	5.0	0.7
Eremastrella crystallifera	Squamulose	9.5	0.4	1.6	0.2
Toninia sedifolia	Squamulose	9.4	2.8	3.0	0.2
Riccia lamellosa	Liverwort	3.7	0.3	0.4	0.0

27.2.2 Disturbance Effects on Nutrient Inputs and Retention

Carbon inputs. Cyanobacterial crusts near coal-fired power plants have greater chlorophyll *a* per unit soil surface area than crusts away from the plant. This is partially a result of fertilization by nitrogen (N) and sulfur compounds from the effluents (Sheridan 1979; Belnap 1991). Photosynthesis-inhibiting herbicides show significant impact on *Nostoc* growth and N fixation (Gadkari 1988). In general, herbicides inhibit growth and reproduction in culture (Metting 1981). However, effects appear to be more pronounced in the laboratory than in the field, and may be transitory (Prasad et al. 1984).

Alteration in species composition of the crust will affect the total carbon (C) fixation of crusts, as lichens and mosses fix more C per unit soil surface area than cyanobacteria (Phillips and Belnap 1998). As much of the C fixed by crustal species is released into the surrounding soils (Lewin 1956), reduction in crust cover is expected to reduce soil C available for often carbon-limited microbial populations. This, in turn, may affect decomposition rates and soil-nutrient levels (Paul and Clark 1996).

Nitrogen Inputs. Effluents from power plants have been shown to decrease N fixation in *Collema* and *Microcoleus-Nostoc-Scytonema*-dominated crusts (Sheridan 1979; Belnap 1991). Atmospheric N deposition may offset reduced N inputs from crusts; alternatively, anthropogenic N deposition may aggravate N loss through increased ammonia volatilization and denitrification. In addition, biological soil crusts release ammonia in the soils, while anthropogenic N deposition contains large amounts of nitrate (F. Garcia-Pichel et al.,

unpubl. data). Microbial and vascular plant species differentially use ammonia and nitrate; thus, deposition of additional nitrates may alter ecosystem dynamics (Binkley et al. 1997).

Free-living or lichenized *Nostoc* show stimulation of N fixation at low concentrations or short exposure to arsenic, nickel, lead, palladium, and zinc. However, longer-term exposure to cadmium, lead, and zinc inhibit fixation (Henriksson and DaSilva 1978). The impact of insecticides, herbicides, phenolics, and oil compounds on N fixation is highly variable, as can be expected, given the vast array of these compounds. Exposure to crude oil and oil dispersants decreases N fixation in *Nostoc* (Marowitch et al. 1988). Nitrogen fixation is significantly inhibited in *Nostoc* by many insecticides, herbicides, and phenolic compounds tested (Megharaj et al. 1988; Bhunia et al. 1991).

Mechanical disturbance can result in large decreases in soil N through a combination of reduced input and elevated losses (Peterjohn and Schlesinger 1990; Evans and Belnap 1999). In all soils tested, disturbance by vehicles, human foot traffic, mountain bikes, and raking immediately reduces N input from crusts (25–40 % on silty soils; 76–89 % on sandy soils). Over time, nitrogenase activity can drop to 80–100 % of controls, due to subsequent death of buried material (Belnap et al. 1994; Belnap 1995, 1996).

Changes in species composition also affect N inputs, as cyanobacteria fix an order of magnitude less N than the equivalent soil surface area of cyanolichens such as *Collema* (see Chap. 16). Thus, the shift from a lichen crust to a cyanobacteria crust can result in less N entering the ecosystem, as has been shown in multiple studies. Jeffries et al. (1992) showed that heavy grazing reduced N fixation in sandy soils by 95 %. Terry and Burns (1987) measured a 64 % reduction of N fixation in a silty loam soil in burned areas, 85–94 % reduction in grazed areas, and 99 % reduction in a tilled area. *Collema* cover was reduced 50–80 % in grazed areas relative to adjacent ungrazed areas (Brotherson et al. 1983; Johansen and St. Clair 1986); thus, N inputs would be expected to be reduced accordingly. Evans and Belnap (1999) showed N fixation in an area released from grazing for 25 years was still 2.5 times less than an adjacent, never-grazed area due to a reduction in *Collema* cover.

Decreased N inputs from crusts can have long-term impacts on soil N levels (see Chap. 20). Jeffries (1989) found 50 % less N in grazed soils compared to adjacent ungrazed soils. Evans and Belnap (1999) found a 42 % decrease in soil N and 34 % decrease in plant tissue N when comparing a previously grazed to an adjacent ungrazed area. In the same area, stable N isotopes showed that both soil and plants in the grazed area contained less newly fixed N than the ungrazed area, and N mineralization potential decreased almost 80 % (Rimer and Evans 1997). This has large implications for ecosystems that are dependent on soil crusts for N inputs, such as found on the Colorado Plateau (Evans and Ehleringer 1993).

27.2.3 Disturbance and Vascular Plants

As discussed extensively in Chapter 21, crusts can affect vascular plant germination, survival, and nutrition. Lichen-moss crusts in areas with frost-heaving (as in cool and cold deserts) increase perennial vascular plant seed entrapment, germination, establishment, survival, biomass, and nutritional status (Belnap and Harper 1995). In these deserts, disturbance that flattens frost-heaved surfaces and/or eliminates mosses and lichens can have a negative effect on some or all of these characteristics. However, germination and survival of some exotic annual grasses can be enhanced with soil-crust disturbance.

In hot deserts, seed entrapment, biomass, and fecundity of annual plants is generally increased when smooth cyanobacterial crusts are disturbed (Prasse 1999), though there are some exceptions (Gutterman 1994). Disturbance of smooth cyanobacterial crusts enhances germination of some annual species, while decreasing germination of other annual species (Zaady et al. 1997). Rugose crusts in hot deserts have received little study. We found no work that addressed the effects of disturbance on seed entrapment in rugose crusts in hot deserts. Effects on germination in rugose crusts appear to be species-dependent. In contrast to smooth crusts, disturbance to hot-desert rugose crusts lessens survival and biomass of perennial plants (McIlvanie 1942; Crisp 1975).

Biological soil crusts have been shown to influence availability of many plant-essential nutrients, and the loss of crusts can result in less plant-available Mg, K, Fe, Ca, P, Mn, and S (Chap. 21). Spatial distribution of nutrients is also affected with disturbance, as lichen-moss crusts are more patchily distributed across the landscape than cyanobacterial crusts (Klopatek 1992).

27.2.4 Disturbance and Surface Albedo

Trampling of dark-crusted surfaces exposes underlying, lighter soils, thus increasing albedo (reflectance) by up to 50 % at most wavelengths measured. This represents an energy loss from the soil surface of approximately 40 W m^{-2}, and can reduce soil temperatures by up to 14 °C (Belnap 1995). Such changes in reflectance are especially evident with remote platforms, as can be seen in the Negev Desert, along the US-Mexico border and in Australia (see Chap. 31). Much of this difference is attributed to loss of biological soil crusts (Graetz and Tongway 1986). These large-scale changes in surface color may lead to changes in regional climate patterns (Sagan et al. 1979).

27.2.5 Disturbance and Soil Hydrology

The effect of crust disturbance on soil hydrology is very site-specific (see Part V). Water infiltration, runoff, and resultant soil moisture are influenced by soil surface roughness, soil texture, microtopography, surface albedo and temperature, vegetative cover (both vascular and nonvascular), and climatic conditions. All these factors can be altered when soil crusts are disturbed. In general, disturbance flattens rolling and pinnacled crusts, decreasing water infiltration and increasing runoff. Disturbance to smooth and rugose lichen- or cyanobacterial-crusted surfaces in hot deserts can increase overall infiltration rates (Greene et al. 1990; Eldridge et al. 2000). However, this increase in infiltration may negatively affect nearby vascular plants that depend on interspace runoff for survival in hyperarid regions (see Chaps. 21, 22). Alteration of soil structure as a result of soil compaction can also reduce infiltration rates. Available soil moisture is a complex interaction of many soil and plant characteristics, such as infiltration, soil moisture-holding capacity, albedo, and plant root density. Only three studies were found that addressed the combined effects of crusts on available soil moisture, with disparate results. Two studies found increased soil moisture under intact crusts, while the other found soil moisture increased under disturbed crusts (reviewed in Harper and Marble 1988; D. George, unpubl.).

27.2.6 Disturbance and Wind and Water Erosion

Compressional disturbance damages soil-stabilizing cyanobacterial sheath material both on the surface and at depth. The damage at depth is nonrepairable, as living cyanobacteria are not present to regenerate their sheaths. As more than 75 % of photosynthetic biomass and productivity are from organisms living in the top 3 mm of soils, disturbance that results in even small soil losses can dramatically reduce site fertility and further reduce soil-surface stability (Garcia-Pichel and Belnap 1996).

Water Erosion. Globally, studies consistently show that crust cover significantly decreases water erosion of both coarse-textured and fine-textured soils (see Chaps. 22–26). Continuous tracks have a greater impact than nonconnected disturbances (such as hoof prints) due to increased volume and velocity of water flow along the tracks (Webb and Wilshire 1983). Crushing of cyanobacterial connections between particles results in smaller, unconnected soil aggregates, which are then more easily moved by water. In addition, surfaces flattened by compressional disturbances are less able to reduce water velocity, thereby allowing movement of larger soil particles.

Wind Erosion. All studies of wind erosion indicate that disturbed soils are more susceptible to wind erosion than undisturbed soils. Soil particle movement is initiated at lower wind speeds when crusts are crushed or absent. Resistance to wind erosion varies with the development of biological soil crusts. Crusts with lichens and mosses, on both silt and sandy soils, have 2–130 times the resistance to soil erosion than less well-developed crusts or bare soil. Vehicle tracks result in greater damage than hoof prints on a given soil type. Decreased resistance of soils to wind erosion is directly associated with increased sediment movement. Experimental disturbances applied to crusts increased sediment production up to 35 times compared to adjacent undisturbed crusts (Belnap and Gillette 1997, 1998; J. Belnap, unpubl. data). Nearby soil crusts are often buried by blowing sediment, resulting in the death of photosynthetic organisms (for extensive discussion, see Chap. 25).

27.3 What Ecosystem Characteristics Confer Resistance to Soil-Surface Disturbance?

Biological soil crusts occur in many different habitats, ranging from subhumid areas that evolved with large herds of hooved animals (e.g., the Great Plains of the US, the Serengeti Plain in Africa, and the central Asian steppes) to arid and semiarid areas where limited food and water prehistorically supported few grazing animals. In habitats that evolved with high numbers of grazers, crusts are highly resistant to trampling, and grasses have characteristics that increase their tolerance of grazing (e.g., tillering, secondary compounds, and high tissue silica content). In contrast, most arid and semiarid desert areas have grasses with very low tolerance of grazing, and crusts intolerant of trampling, as even limited disturbance results in severe damage or extirpation of most crust species present (Martin 1975; Stebbins 1981; Mack and Thompson 1982; Belnap 1995, 1996).

   Comparing regions with different evolutionary histories can aid in identifying ecosystem characteristics that support trampling-resistant crusts. For this purpose, crusts in four regions were compared: two regions that evolved with large hooved herds (central Asian steppes, Serengeti Plains); one region with herds of nonhooved animals (southeastern Australia) and one region without any large herds (Colorado Plateau). Crusts along rainfall gradients (200–400 mm) in these ecosystems were compared (J. Belnap, unpubl.). The cyanobacterium *Microcoleus* sp. was present on all soils, regardless of grazing pressure or precipitation. More-developed soil crusts showed increases in the biomass of *Microcoleus*, cover of the lichens *Collema* sp. and *Catapyrenium* sp. and biomass of surface-dwelling colonies of *Nostoc*

commune. Several factors were present when more-developed soil crusts were observed in areas of heavy grazing pressure: (1) soils were highly weathered, fine-textured to loamy (<50% sand), moderately to highly calcareous, had high water-holding capacity, high bulk density (and thus did not churn easily), and some physical crusting. If sandy, soils were highly calcareous and very shallow; (2) sites had high effective rainfall, due to (a) greater total amount of rainfall, (b) cool-season rainfall, and/or (c) soils where water ponding occurred; (3) crust species present were those known to be resistant to trampling; (4) live and dead grass clumps were closely spaced (10 cm) or soils were very rocky, which protected much of the soil from direct hoof contact; and (5) animals did not stay in one area for more than a day, but kept moving through the landscape. Two important features were noted. First, high lichen diversity (>three species) was found only where grazing pressure was absent or minimal, or grazing pressure was due to animals without hooves (kangaroos). Secondly, where hooved animals were continually present, only cyanobacterial soil crusts were found.

27.4 Recovery of Biological Soil Crusts

27.4.1 Natural Recovery Rates

Recovery rates are dependent on many factors, including the type, severity, and extent of disturbance; structure of the vascular plant community; condition of adjoining substrates; availability of inoculation material; and climate during and after disturbance (Fig. 27.1). As discussed in the Introduction (Sect. 27.1), comparing reported recovery rates is problematic, as studies include a wide range of climatic zones, soil types, and levels of disturbance, and these factors are seldom quantified. Thus, most studies can only be used to define the general range of recovery rates.

All published estimates of crust recovery time are based on linear extrapolations of observed recovery rates (e.g., Anderson et al. 1982; Callison et al. 1985; Jeffries and Klopatek 1987; Cole 1990; Belnap 1995; Eldridge 1996). It is not known under what conditions this method is valid. On the Colorado Plateau, scalped plots were reassessed 2–5 and 10–14 years after disturbance. After 2–5 years, cyanobacterial cover was predicted to recover in 45–110 years, whereas it recovered within 14–34 years; thus, extrapolations based on 2–5 years greatly overestimated recovery time. Estimate of moss recovery after the first sample time was 400 years; after the second sampling time, it was 42 years. As with cyanobacteria, extrapolations based on early assessments overestimated recovery time. In contrast, *Collema* recovery after

3 years was estimated at 85 years; after 14 years, estimates for full recovery were 50 years, a fairly close match. *Collema* recovery at another site was highly variable: after 2 years, recovery time was estimated at 487 years; after 11 years, estimates at plots within the site ranged from 40 to 766 years. Thus, original estimates were both under- and over-optimistic, depending on individual plot characteristics. Sites with more shade and less sandy soils were faster to recover than the original estimates predicted, while sunnier sites with sandier soils were slower to recover than the original estimates (J. Belnap, unpubl.).

Sequence of Species Appearance. Large filamentous cyanobacteria such as *Microcoleus* spp. are generally the first photosynthetic organisms to appear (Fig. 27.3), especially on unstable sandy soils (Ashley and Rushforth 1984; Belnap 1995). This is probably due to their mobility across soil surfaces and their ability to easily disperse via the air (Schlichting 1969). These large cyanobacteria are then followed by smaller cyanobacteria and green algae. Rarely, desert soils are slightly acidic, and here green algae can be the first to appear (Johansen 1993).

Lichens and mosses require stable soil surfaces for growth. This can be provided by a physical crust or by colonization of large, filamentous cyano-bacteria. Once soils are stabilized, gelatinous N-fixing lichens (e.g., *Collema* spp.) are generally the first lichens to appear in disturbed areas, followed by early successional phycolichens and mosses (Johansen et al. 1984; Belnap 1993). Early-colonizing lichen species often disperse photobiont-containing tissue (e.g., isidia, soredia, thallus fragments, or algal-covered spores), as opposed to bare spores, thus precluding the need to find photobionts on site. In addition, cyanolichens may be the first to colonize alkine desert soils, as the cyanobiont *Nostoc* is much more numerous than any of the phycobionts required by phycolichens.

Colonization times vary widely for mid- and late-successional crust species, depending on site characteristics. Little is known about growth rates once colonization occurs. *Psora crenata* requires 55–100 years to regain full size in Australia (240 mm annual rain; Eldridge and Ferris 2000). Similar recovery times have been observed for *Diploschistes* in southern Idaho (R. Rosentreter, unpubl.).

Soil Texture. Soil texture influences recovery rates. In general, when climate and disturbance characteristics are similiar, recovery of all crust components is faster in fine-textured soils that form physical crusts compared to coarse-textured soils that do not form physical crusts when climate and disturbance characteristics are similar (Fig. 27.2; Table 27.2; reviewed in Harper and Marble 1988; Johansen 1993; Ladyman and Muldavin 1996). This is true both for disturbances severe enough to remove crusts and those crushed in place. Recovery of wind resistance is also more rapid in fine-textured soils, due to
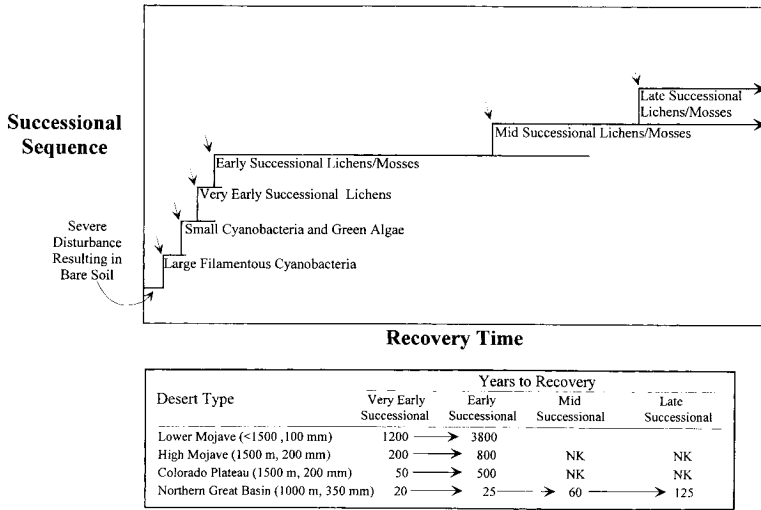
Fig. 27.3. Colonization sequence and estimated recovery times for crustal species in the western US. *Top panel* Arrows indicate colonization events; *length of line* indicates relative time for recovery of each successional group. Species indicative of successional groups include: large filamentous Cyanobacteria: *Microcoleus* spp.; small Cyanobacteria: *Nostoc* spp.; very early-successional: *Collema* spp.; early-successional: *Catapyrenium* 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. Elevation and annual precipitation of characteristic regions are *in parentheses*. Reported estimates are averages, as sites show considerable variation in recovery times. Recovery rates of mid- and late-successional species are not known (*NK*) in drier deserts, where slow recovery times have precluded estimates. Estimates are based on published rates from studies cited in text

formation of chemical crusts after rainfall. While silty and sandy soils show a similar reduction in wind resistance to vehicle disturbance (83 and 74%, respectively), silty soils show a 50% recovery of wind resistance after a single large rain event. Sandy soils can take up to 10 years for a similar recovery (Belnap and Gillette 1997; J.E. Herrick et al., unpubl. data).

Climate Regimes. Crustal organisms are metabolically only active when wet; thus, recovery is faster in regions with greater effective precipitation (Figs. 27.1, 27.3; Table 27.2; Harper and Marble 1988; Johansen et al. 1993). Table 27.2 shows that cool-desert sites at higher latitudes (and thus lower annual temperatures) have quicker recovery for all crustal components than hot-desert sites with the same precipitation but higher annual temperatures, when disturbed similarly. Sites with lower annual precipitation and higher annual temperatures are the slowest to recover.

Table 27.2. Estimated recovery times of dated disturbances of known severity in the Mojave, Sonoran, Chihuahuan and Colorado Plateau deserts of the western US (J. Belnap et al., unpubl.)

Desert type	Disturbance severity	Soil texture	Annual rainfall range (mm)	Elevation range (m)	Years since disturbance	Estimated recovery times (years)				No. of lichen species	
						Cyanobacteria	Collema	Other lichens	Moss	Disturbed	Control
Coastal	Removed	Fine	179	100	5		>20–200	>200		1	5
Cool	Removed	Coarse	220–230	1500–1800	10–14	14–34	50–400	>200–875	82–>766	1	4–5
		Fine	230	1600	14	9	>20–240	>200	>140	1	3–5
	Crushed	Coarse	220–230	1500–1800	6–13	7–14	10–71		26–39	1	1–4
		Fine	215	1550	2	2	6	3	4	1	2
Hot	Removed	Coarse	119–230	271–1730	50–80	<81–100	217–1250	580–3700	<81	2	2–7
	Crushed	Coarse	74–248	500–950	2–20	3	10–90	>9		1	1–2
		Fine	248–256	500–1300	2	2–3	4–15	>4		1	2

The "<" indicates that the component was fully recovered when the site was sampled. If a crust component was observed in the control plots but not found in the disturbed plots, a value of 0.01 % relative cover was used to calculate a minimum recovery time; these calculated values are preceded by a ">". The last two columns indicate the number of lichen species present in the disturbed areas relative to the number of species in the control areas.

Type, Frequency, Severity, and Size of Disturbance. We found no work that addressed recovery rates of soil-crust lichens or cyanobacteria from air pollution. Recovery from fire is specifically covered in Chapter 28. In general, crusts are highly susceptible to damage by hot fires; thus, recovery will depend on the size and intensity of fires. As noted previously in Section 27.2 above, most compressional disturbances have similar types of impacts. However, severity of mechanical disturbance can vary widely with disturbance type. Thus, on similar soils, vehicle tracks generally have longer recovery times than disturbances that do not churn the soil or make continuous tracks (Wilshire 1983; Belnap 1996). Repeated disturbance will generally keep crusts at an early-successional stage (e.g., cyanobacteria-dominated) by preventing colonization of lichens or mosses (Fig. 27.3; Belnap 1996).

Severity of disturbance can control recovery rates. In the western US, recovery of adjacent sites within a given soil and climate type is generally faster when disturbance is not severe enough to remove crustal material (Table 27.2). In addition, because recolonization of disturbances occurs mostly by material washing or blowing in from adjacent, less-disturbed areas, the rate of lichen recovery is much slower in areas with higher internal surface areas relative to perimeter area (Eldridge and Ferris 2000; J. Belnap, unpubl. data).

Condition of Adjoining Substrate. In general, recovery is slower if soils adjacent to disturbed areas are destabilized. Detached sediment can both bury adjacent crusts and/or provide material for sandblasting nearby surfaces, thus increasing wind erosion rates and reducing recovery rates (Belnap 1995; McKenna-Neuman et al. 1996; Leys and Eldridge 1998).

Vascular Plant Structure. Crusts recover more quickly under shrub canopies than adjacent plant interspaces. This is probably due to greater soil moisture and fertility under shrub canopies. In the Mojave Desert, lichen recovery 50 years after total removal was 36 % complete under shrub canopies and only 4 % complete in the shrub interspaces (Belnap and Warren 1998). A similar pattern was seen in plots on the Colorado Plateau, where lichen recovery was two to three times faster under shrubs than in adjacent interspaces (J. Belnap, unpubl. data).

The growth of biological soil crusts and vascular plants can be an interactive process (Danin et al. 1989). Eldridge and Greene (1994) present a conceptual model in which crust development at sites is strongly linked to the restoration of vital soil processes. As primary colonizers of recovering sites, biological soil crusts enhance microsite fertility and provide safe sites for seeds (see Chap. 21). In turn, established vascular plants help stabilize soils, provide shade, and reduce wind speeds at the soil surface, providing conditions conducive to further diversification of the biological soil crusts (Wood et al. 1982; Danin et al. 1989).

Nitrogen and Carbon Fixation. Recovery of N and C fixation rates after disturbance is dependent on the species composition, biomass, and physical structure of the crust. Thus, recovery of N fixation is dependent on recovery rates of cyanobacteria and cyanolichens (see Sect. 27.3.1). Nitrogen fixation in crusts can require anaerobic microzones in the soils, which may be dependent on the buildup of cyanobacterial biomass (Belnap 1996). Recovery of C fixation is mainly dependent on moss and lichen cover. As recovery is faster with higher available moisture, N and C fixation rates are expected to recover faster in cool deserts than in hot deserts, other factors being equal.

Lichen cover may not fully recover after disturbance, as conditions which allowed its initial establishment may no longer be present. For example, 30 years after cessation of grazing, soil space previously occupied by lichens was occupied by mosses in SE Utah, and thus lichens are not necessarily expected to return (Evans and Belnap 1999). Consequently, soil N, plant N, and N fixation are still lower in the previously grazed areas when compared to an ungrazed area. Reduced N inputs are expected as long as lichen recovery does not occur.

Surface Albedo. Restoration of normal surface albedos and temperatures will depend on the restoration of predisturbance cover of cyanobacteria, lichens, and mosses. While cyanobacteria form a darkish matrix in which other components are embedded, most mosses and lichens are much darker (Belnap 1993). Consequently, recovery of surface albedos will be limited by factors that control recovery of lichens and mosses.

27.4.2 Enhancing Recovery with Inoculation

Inoculants can be used to speed soil-crust recovery (Lewin 1977; Tiedemann et al. 1980; Ashley and Rushforth 1984; St. Clair et al. 1986; Belnap 1993; Buttars et al. 1998). Applied inoculants have ranged from commercially available preparations (Lewin 1977) to laboratory-prepared material (Buttars et al. 1998) to material transported from nearby areas (Belnap 1993). In all cases, inoculation enhanced recovery rates of cyanobacterial and lichen biomass and species diversity. For example, 3 years after scalping and inoculating plots with nearby crumbled crusts (10:1 removed to inoculated material), cyanobacterial biomass in inoculated plots was almost twice that of uninoculated plots (0.14 vs. 0.077), lichen cover was 43.3 versus 3.6% (respectively) and lichen species were 4.3 versus 1.8 species (respectively). The entire surface area of the inoculated plots appeared covered by cyanobacteria, and pedicellation had begun (Belnap 1993). In a laboratory study, Buttars et al. (1998) isolated, cultured, and then made alginate pellets of *Microcoleus vaginatus*. These pellets were then placed on petri dishes. After 3 months, inoculated dishes had higher filament density and N fixation rates.

27.5 Conclusions

Disturbance can directly and indirectly affect many aspects of the structure and function of biological crust communities. Moderate to severe disturbance generally results in the simplification of the crust community from one containing multiple species of cyanobacteria, lichens, and mosses to a community consisting of only a few species of cyanobacteria. This alteration of species composition reduces C and N inputs from the crusts. Disturbance is also generally accompanied by loss of surface roughness, which affects local hydrologic regimes and vascular plant seed entrapment. Compressional disturbances break the cyanobacterial connections to soil particles, thus increasing vulnerability of the underlying soils to wind and water erosion. As fine soil particles are preferentially lost, increased erosion reduces site fertility. Disturbance also increases soil albedo and reduces soil temperatures. This, in turn, affects the soil microbial and vascular plant communities.

Some generalizations can be made regarding recovery rates for crusts. Recovery rates are faster for infrequent or minor disturbances where crustal material is crushed in place compared to severe or repeated disturbances that result in complete removal of crustal material. Recovery is faster on fine-textured compared to sandy soils. Recovery is also faster in regions with greater effective precipitation. Recovery is different among crust functional groups, with rates increasing in the following order: cyanobacteria > gelatinous cyanolichens > annual mosses, perennial phycolichens with dispersal mechanisms that avoid early growth stages > perennial phycolichens and mosses without specialized dispersal mechanisms. Recovery of physiological functioning is dependent on the recovery of specific species, e.g., N inputs are dependent on recovery rates for cyanobacteria and cyanolichens. Complete recovery to predisturbance states may not be possible, due to altered edaphic or climate regimes, or lack of source material for colonization.

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