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Cyanobacterial-Lichen Soil Crusts of San Nicolas Island

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Abstract. Cyanobacterial-lichen soil crusts are a dominant feature on the soils of San Nicolas Island. These crusts can play many important roles in ecosystems in which they occur. These roles can include contribution of nitrogen to soil nitrogen pools, enhancement of element uptake in vascular plants, increase in vascular plant seedling establishment and survival, and stabilization of soil surfaces. Species composition of crusts on San Nicolas Island are discussed, along with the roles the crusts play in the different habitat types found on the island, and the effects of disturbance on the crusts, including successional sequences, nitrogenase activity, and recovery rates.

Keywords: Nitrogen cycles; *Microcoleus vaginatus*; Collema; soil stabilization; revegetation; arid lands; semi-arid lands.

Introduction

Cryptobiotic soil crusts, consisting of cyanobacteria, mosses, and lichens, are an important component of semiarid and arid ecosystems. These crusts represent up to 70% of the living ground cover in many of these areas. Many roles have been ascribed to these crusts, including stabilizing soils (Harper and Marble 1988; Belnap and Gardner 1993); increasing water infiltration and nutrient status of soils; contributing to nitrogen fixation (West and Skujins 1977; Skujins and Klubek 1978; Belnap 1991; Belnap et al. 1993; Evans and Ehlringer 1993; Harper and Pendleton 1993); and enhancing seedling establishment (Belnap 1993a). Data suggest that these crusts are slow to recover from severe disturbance, requiring 40 yr or more to recover on even small areas (Belnap 1993a). This paper discusses the role of cryptobiotic soil crusts in the functioning of desert ecosystems in general, and 2 Channel Islands (Santa Barbara and San Nicolas) more specifically. Data are drawn from several different studies conducted over the past 5 yr by Belnap (1991, 1993a, 1993b), Belnap and Gardner (1993), Belnap and Harper (1993), Belnap et al. (1993), Harper and Pendleton (1993), and recent work by Belnap on the Channel Islands.

Methods

Crust surveys were done on 2 of the Channel Islands, Santa Barbara Island and San Nicolas Island. The survey of Santa Barbara Island was brief, and only general conclusions of that survey are discussed in this paper. Crust surveys on San Nicolas Island were extensive. All soil map units as defined by the Soil Conservation Service were sampled. In addition, sites with varying disturbance histories were sampled. Lichen and moss species were identified, and unusual specimens collected. Collections were made to identify cyanobacterial and green algal components of the major crustal types encountered. These samples were cultured on agar in media with and without nitrogen to separate cyanobacteria and green algae. Cultures were then examined microscopically, and species identified.

Nitrogenase activity of crustal organisms on San Nicolas Island was measured. Samples were collected dry from heavily crusted areas and flown to a portable laboratory located at Point Mugu, arriving within an hour of collection. Samples were wetted equally with distilled water and injected with sufficient acetylene to create a 10% acetylene atmosphere. After injection, samples were incubated for 4 hr at 26° C in 2.5-cm diameter, clear, gas-tight tubes. Incubation occurred in a chamber lighted with Chromo50 (5,000 K) and cool white fluorescent bulbs. Subsamples (0.25 ml) of the head space within the tubes were then analyzed for acetylene and ethylene content on a Carle FID gas chromatograph equipped with an 8-ft column (8% NaCl on alumina), using helium as carrier gas (30 ml/min). Units reported are gas chromatographic units and are not convertible to kg/ha of N without calibration by N^{15}, which was not done. Measurements obtained were used to determine relative rates of fixation between sample sites, sample dates, and geographic locations. There were 20 replicates per site. Statistical analyses were done using analysis of variance and a multiple range test.

Results and Discussion

Results of survey

Minimal crustal development was seen on Santa Barbara Island. This is probably attributable to the high shrink-swell potential of most soils found on this island. Areas with these types of soils supported a minimal cyanobacterial flora. Sandy, rocky soils on the north and east portions of the island supported lichenaceous crusts; however, these areas represented only a small portion of the island. In contrast, minimally developed crusts represented only 17% of San Nicolas Island (beaches, 2%; dune areas, 8%; and clays with high shrink-swell potential, 7%), while extraordinarily well-developed crusts were found on 83% of the island. Maximal crustal development was found on steep slopes, where presumably impacts from pre-1940 sheep grazing would have been less.

All crusts examined on both San Nicolas and Santa Barbara islands were dominated by the cyanobacterium *Microcoleus vaginatus*. In the weakly developed crusts, this was generally the only species found in any significant number. Species composition of these crusts were found to be remarkably similar to those found in cold-desert regions, especially in the early phases of crustal development. On both the Colorado Plateau and San Nicolas Island, disturbances are first colonized by *M. vaginatus*. The same lichens, *Collema tenax* and *Catypyrenium lachneum*, are also the first to appear on the soil surfaces on both the Colorado Plateau and San Nicolas Island. At the intermediate stages of cyanobacterial and lichen development, similar genera are found, including the cyanobacteria *Scytonema*, *Lyngbya*, and *Oscillatoria*, and the lichen genera *Fulgensia*, *Diploschistes*, and *Toninia*, though often these were represented by different species. Fully developed crusts in the 2 areas are quite similar in their cyanobacterial and green algal genera and species, but different in their lichen flora. The only moss found in the survey, *Barbula zinealis* (Brid.), is also found on crusts of the Colorado Plateau. The plateau, however, has many additional moss species.

Structure and function of crusts

Figures 1 and 2 show *M. vaginatus* and the structure of *M. vaginatus*-dominated crusts. *M. vaginatus* has a large, distinct, sticky extracellular sheath that surrounds groups of living filaments (Fig. 1). When wetted, this sheath material swells, and filaments within are mechanically extruded. As the substrate dries, exposed filaments secrete additional sheath material. Rewetting repeats this cycle, resulting in sheaths that wind among the sand particles much like fibers in fiberglass (Fig. 2). Even when dry or no longer containing living filaments, the sheath material firmly adheres to soil particles, thereby reducing wind and water erosion. It also holds otherwise loose soil material on slopes well beyond the angle of repose. The crust-covered steep slopes of San Nicolas Island are a dramatic demonstration of these crusts' ability to hold slopes in place.

When wetted, the sheath material swells and covers the soil surface even more extensively than when dry. Sheath material can absorb up to 8 times its weight in water, thus absorbing precipitation and increasing the water-holding capacity of soils (Brock 1975; Campbell 1979; Campbell et al. 1989). Even when swollen, scanning electron micrographs demonstrate there is space for rainwater and vascular plant roots to penetrate into the soil (Belnap and Gardner 1993). In addition, the combination of cyanobacteria, lichens and mosses create a roughened surface that slows water velocity, enhances water infiltration and decreases water runoff.

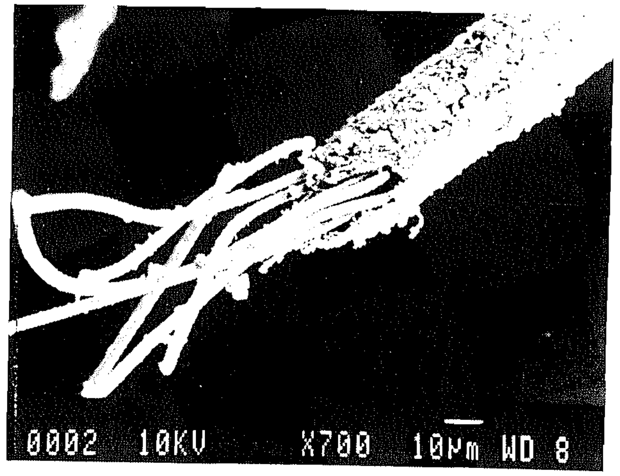

Figure 1. Scanning electron micrograph of *Microcoleus vaginatus*, the dominant cyanobacterium in soil crusts of the Colorado Plateau. Note the living filaments extruded from the sticky extracellular sheath (magnification x 700), as occurs when the organism is wetted.

Figure 2. Scanning electron micrograph of dry cyanobacterial sheaths winding through sandy soils from Moab, Utah. Note firm attachment of sheath material to the individual sand grains, even though sheath material is dry (magnification x 90).

Since living filaments are seldom found below 1 cm (Belnap, unpublished data), sheath material below that depth probably represents remnants of cyanobacterial crusts once found near or at the soil surface. As aeolian and water-borne materials are trapped in the sheaths of *M. vaginatus* and other cyanobacteria growing on the surface of desert soils, these sheaths are gradually buried; consequently their ameliorating influences on soil processes, such as water-holding capacity, cation exchange capacity and soil stability may extend far below the depth to which light can penetrate.

Semi-arid and arid areas, such as San Nicolas Island, generally have extremely low levels of nitrogen available for vascular plants. Cyanobacteria and cyanobacterial components of soil lichens "fix" atmospheric nitrogen, reducing it to a form useable by vascular plants. Studies utilizing radioactive isotopes of nitrogen have demonstrated that nitrogen fixed by cyanobacteria in the crusts is available to neighboring vascular plants (Mayland et al. 1966; Mayland and McIntosh 1966). In some desert systems, these crusts have been demonstrated to be the dominant source of this often-limiting element for associated seed plants (Evans and Ehlringer 1993).

Rates of nitrogenase activity measured under standard conditions for crusts from 3 sites on San Nicolas Island showed that potential fixation levels were approximately the same as crusts from across the Colorado Plateau. However, the annual nitrogen contribution of crusts on San Nicolas Island probably far exceeds that for the crusts from the Colorado Plateau. Maximum fixation and photosynthesis rates for these crusts occur at soil surface temperatures of approximately 26° C, conditions that would be much more common on San Nicolas Island than mainland semi-arid areas. Lack of snow cover and the almost daily dewfall that activates the crustal organisms would provide even longer time periods for nitrogen fixation. In addition, denitrifying bacteria generally perform better at temperatures above 30° C; therefore, they are probably less active on San Nicolas Island than in warmer areas, leaving available nitrogen in the system longer. Approximately 10% of San Nicolas Island is covered with potentially nitrogen-fixing leguminous plants. If these species are capable of nitrogen fixation, crusts would be less critical in areas where those plants occur in substantial numbers. Crusts would be an essential part of the nitrogen cycle in the other ecosystems on the island. Fixation capability of these plants should be verified to establish whether restoration of crusts in these particular areas is a high priority from a nutrient cycling standpoint.

Levels of other elements in vascular plant tissue, such as P, K, Mg, Fe, Ca, and Mg, can be affected by the presence of these crusts. Dry weights of plants growing in crusted soils far exceed those growing in uncrusted areas. Field and laboratory experiments have shown this repeatedly (Belnap and Harper 1993; Harper and Pendleton 1993; Belnap, unpublished data; Harper and Marble, unpublished data). Similar experiments should be conducted on San Nicolas Island to establish the importance of crusts in nutrient cycles of these ecosystems.

Several mechanisms have been postulated to explain this effect. Fletcher and Martin (1948) reported that crusts trapped soil fine particles, which are more nutrient-rich than sand (Black 1968). Lange (1974) demonstrated that compounds in the gelatinous sheath material of half the cyanobacteria species studied were able to chelate elements essential for their growth (e.g., iron, copper, molybdenum, zinc, cobalt, and manganese). Four of the 5 genera shown to possess this ability (*Anabaena*, *Anacystis*, *Lyngbya*, and *Nostoc*) are represented by common species in the cryptobiotic crusts of western North American deserts (Shields and Durrell 1964). Belnap and Gardner (1993) showed that cyanobacterial sheath material was often coated with negatively-charged clay particles, providing a mechanism for holding positively charged macronutrients against leaching from the soil profile. It is also possible that nutrient differences are a result of a thermal effect, as dark crusts would be warmer than lighter uncrusted soils, and uptake of nutrients would occur at a higher rate.

The presence of soil crusts can also affect seedling establishment and survival. Experiments done in sites with both fine and coarsely textured soils demonstrate that seedling establishment was much higher in crusted areas when compared to areas where the crust had been removed for both forbs and grasses (Belnap 1993b). Survival over a 3-yr period was enhanced in the 4 species (grasses and forbs) measured at these sites as well. Other studies have reported similar enhancement of seedling germination and establishment in crusted areas when compared to non-crusted surfaces (St. Clair et al. 1984; Harper and St. Clair 1985). It is not known if crusts are a factor in seedling establishment on San Nicolas Island.

Damaging factors and recovery rates

Compressional and shear forces, such as produced by grazing and recreational use, negatively affect the cohesion of soils and the coverage of cyanobacterial crusts; soil aggregates and cyanobacterial filaments are easily crushed, and connections between soil particles broken under these stresses (Webb and Wilshire 1983). Different soils have different intrinsic soil strengths that vary with moisture content. While arid soils with little tendency to form inorganic aggregates (such as coarse sandy soils) are more susceptible to stresses when dry, soils with inorganic crusting are more susceptible to impacts when soil moisture content is 5% or more. Most soils of San Nicolas Island are in the second category: crusts on San Nicolas Island are fairly resistant to damage when dry, but even low levels of soil moisture make them highly susceptible to impacts.

Any damage to the underlying abandoned sheath material is non-repairable, since living cyanobacteria are no longer present at these depths to regenerate filament and sheath materials. As a consequence, trampling not only can reduce soil stability, but soil fertility and soil moisture retention as well. Impacts do not need to be direct to be devastating to crusts, as water- or wind-borne sediments from nearby destabilized areas can bury living crusts. Since crustal organisms need to photosynthesize, burial often means death.

The presence of crusts on the soils of San Nicolas Island are especially important, where the combination of highly erodible soils, steep slopes, sparse vegetation and inorganic crusting of soils is found. Under such conditions, large amounts of water runoff and soil loss would occur unless soil surfaces are protected. The presence of crusts can mitigate these effects, although ongoing activities that increase and localize runoff, such as construction and asphalt-covered surfaces, or activities that break up the crusts, such as grazing, often overwhelm the stability of the system. Such activities on San Nicolas Island have resulted in high rates of soil loss and deep gully formations over the past 100 yr.

Restoration of these crusts has been studied by several investigators. These studies have examined both natural recovery and the use of inoculants. Recovery rates 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 natural recovery of cryptobiotic crusts from disturbance have varied widely, ranging from a few years to well over 100 yr for full recovery of all components (Anderson et al. 1982; Callison et al. 1985; Jeffries and Klopatek 1987; Cole 1991). Belnap (1993a) reported that visual estimates of crustal recovery are not always accurate, however, calling into question many previous recovery time estimates. These estimates often give the impression that the cyanobacterial and green algal components of the crusts are mostly or fully recovered, when in fact, chlorophyll *a* levels demonstrate that the amount of photosynthetic material present may be far less than nearby undisturbed areas. Other aspects of crust recovery, including the depth of accumulated cyanobacterial sheath material, and lichen and moss species number and cover, are estimated to be much slower than cyanobacterial recovery. Several studies have demonstrated that inoculation can hasten the biological recovery of disturbed crusts (Lewin 1977; Tidemann et al. 1980; St. Clair et al. 1986; Belnap 1993a). In Belnap's 1993a study, inoculated plots had far greater chlorophyll a concentrations than uninoculated plots, indicating a larger biomass of cyanobacteria and green algae in inoculated sites. Inoculated plots also had significantly greater lichen species richness and greater lichen and moss cover than uninoculated plots. However, although lichen and moss cover was significantly greater on inoculated than uninoculated plots, recovery for both lichens and mosses was still extremely slow for both treatments.

Inoculation also hastened some aspects of visual recovery of the cyanobacterial/green algal component. Areas that had been inoculated had greater pedicellation sooner than areas that were not inoculated. Apparent coverage of the soil surface by this crustal component, however, was not hastened by inoculation, since all soil surfaces appeared completely covered within 1 yr. Inoculation somewhat hastened the visual recovery of the lichens and mosses; however, absolute differences were so small, it was difficult to tell treatments apart, even with close examination.

Recovery rates on the Channel Islands are expected to be much faster than on mainland sites. Since crustal organisms are only active when wet, crusts in mainland climates that are drier and/or hotter have less metabolically active time available. Consequently, recovery from impacts would take longer. On San Nicolas and Santa Barbara islands, however, moderate temperatures result in effective precipitation being greater than on mainland areas with comparable rainfall. In addition, morning fog and dew contribute almost daily surface moisture. As a result, crusts are probably active almost daily, and much faster repair and colonization would be possible than in other regions.

Conclusion

Cyanobacterial-lichen ecosystems on soil crusts can contribute in many ways to the ecosystems in which they occur, including the Channel Islands. Such crusts can enhance soil stability, reduce water runoff by producing more microcatchments on soil surfaces and adding absorptive organic matter, improve nutrient (nitrogen and some essential mineral elements) relations for at least some vascular plants, and enhance germination and establishment of some vascular plants. These black crusts may also stimulate vascular plant growth and nutrient uptake by producing warmer soil temperatures during cool seasons when free water is most likely to be available. Crusts on San Nicolas Island have been observed to be capable of all these roles, and should be an important part of any restoration effort. Until we have a greater understanding of the short- and long-term effects of impacts on the ecology and functioning of these crusts, and how to re-establish them, land managers should minimize activities that may disturb them.

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