Distribution and activity of hypolithic soil crusts in a hyperarid desert (Baja California, Mexico)

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Abstract:

Widespread and ecologically important, biological soil crusts include those microbial communities living on the surface of the soil and those which live beneath semi-translucent rocks (a.k.a. hypolithic crusts). We examined the distribution, abundance, physiology, and potential soil N contributions of hypolithic, biological crusts in hyperarid ecosystems of the Baja California peninsula and islands in the midriff region of the Gulf of California, Mexico (Sonoran desert). Crusts were limited in distribution to areas with translucent quartz rocks less than 3 cm thick, were not found on areas of islands with seabird guano deposition, but covered as much as 1% (12,750 m^2) of the surface area of one island. The percent of available rocks colonized by crusts was similar between the mainland (38%) and islands without seabird guano (26%). Carbon fixation rates in the field, which have not been previously reported, ranged between 0 and 1.23 μmol m^{-2} s^{-1}, and in the lab ranged between 0.66 and 0.94 μmol m^{-2} s^{-1}. Evidence of low rates of N fixation was inferred from $\delta^{15}N$ values of crust and soil. Hypolithic crusts were found to have minimal if any influence on soil salinity, pH, and NO_3^-, but may represent up to 14% of the biomass of primary producers on these islands and provide C and N to the belowground and possibly aboveground heterotrophic communities where crusts exist. The results of this study suggest a limited but potentially important contribution of hypolithic soil crusts to hyperarid ecosystems.

Keywords: Cyanobacteria, nitrogen fixation, nitrogen isotopes, photosynthesis, soil communities

INTRODUCTION

Biological crusts, which consist of cyanobacteria, algae, microfungi, and mosses form on soil surfaces and below the surface of semi-translucent rocks such as quartz (a.k.a. hypolithic crusts; Belnap et al. 2001; Büdel 2002; Belnap 2003). Hypolithic crusts, which consist primarily of cyanobacteria, are generally more widespread than surface crusts and their species composition is better investigated than that of surface crusts (Büdel 2002 and refs within). However, in contrast to surface crusts (e.g., Evans and Johansen 1999) available data on hypolithic crusts do not allow estimates of their total coverage on earth, or their contributions to food chains and ecosystem carbon (C) and nitrogen (N) cycling (but see Büdel 2002; Schlesinger et al. 2003).

This study provides the first documentation of the distribution and activity of hypolithic crusts in the mid region of the Baja California peninsula and on Gulf of California islands. We assessed distributions in areas of low and high soil nitrogen availability (associated with seabird guano deposition), the potential contributions of these crusts to C and N budgets, and the soil conditions associated with hypolithic crust growth.

METHODS

Study site

We collected data in May 2001, March 2002, May 2002, and March 2003 on the hypolithic crusts of the Baja California peninsula and a group of fourteen hyperarid islands ($0.1 km^2$- $8.5 km^2$) in the Midriff region of the Gulf of California near Bahia de los Angeles, B.C. (28° 55’ N latitude, 113deg 30’ W longitude). Seven of the islands are heavily influenced by seabird guano, one of the islands is partially influenced, and the other six receive virtually no guano deposition (Wait et al. 2005). Mean annual precipitation of this area is 53mm. A detailed description of the study area can be found in Wait et al. (2005).

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We walked through areas of the peninsular desert, covering approximately 10 km^2, and in more regular transects to cover nearly all areas on islands, searching for areas with semi-translucent quartz rocks, since the crusts were found only under those types of rocks. In areas with quartz we randomly chose two 2 x 100 m transects to record the presence or absence of crust on rocks.

On one island we estimated the total area covered and mass of hypolithic crusts. On Isla La Ventana (1.275 km^2) we surveyed a total of 11.25 m^2, in the form of 45 randomly placed 0.25 m^2 quadrats. The approximate area covered by hypolithic soil crust was determined by tracing the crusted rocks and the crust coverage. The tracings were then scanned into a digital leaf area meter (CID, Inc. CI420) to determine the area of coverage. The dry weights of crust from a subset of rocks (n=100) was determined by the difference in weights of rocks before and after removing crust.

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Three composite crust samples were dried, ground, weighed out to 3.5mg, and sent to the University of Georgia Stable Isotope Lab for %N and $\delta^{15}N$ isotopic analysis using a NC2500 elemental analyzer. They combusted samples in an oxygen stream at 1100°C then passed them through oxidation and reduction tubes to form N_2 gas. UGSIL then separated gases on a chromatography column allowing N isotope composition to be determined. The precision was greater than 0.4‰.

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Distribution and abundance

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Out of the 10 km^2 searched on the mainland, areas with semi-translucent quartz rocks represented less than 2 km^2. Seven out of the fourteen islands surveyed contained quartz rocks, or, 9 km^2 out of a total island area searched of 11 km^2, although the entire area of islands were not covered by quartz (see below for estimates of coverage). We did not find that islands limited colonization of crusts; on the mainland 38% (34 out of 89) of rocks were colonized by crust, while on islands with no seabird guano deposition and quartz rocks 26% (21 out of 82) were colonized by crust. This is in sharp contrast to the 100% (295 out of 295) colonization found in the 1 x 50 m transect sampled in the southern Mojave Desert, California, USA by Schlesinger et al. (2003) which averages 34% more precipitation annually. Of special note, in areas with seabird guano deposition and quartz rocks (4 islands), 0% of the rocks were colonized by crust. For example, one island influenced by seabird guano deposition with over 1% of the surface area covered by quartz rocks did not have a single rock that was colonized. These data indicate that low pH and high nitrate concentrations on islands with seabird guano deposition (Wait et al. 2005) presumably limit crust colonization and that desert regions influenced by N deposition may lose hypolithic crust.

Crusts were found in greatest abundance on Isla La Ventana where they covered approximately 1% of the area sampled. Extrapolating these data to encompass the full island area indicates that approximately 12,750 m^2 of this island could be inhabited by hypolithic crusts. On average the mass of the crust per unit area of rock was 0.011 (± standard deviation, 0.010) g cm^{-2}. Thus, with 1% coverage, average biomass of crust across the island could be as high as 1.1 g m^{-2}. In comparison, average herbaceous plant productivity on this island is approximately 7.6 g m^{-2} yr^{-1} (Wait et al. 2005; Anderson and

Polis 2004); therefore, hypolithic crust biomass potentially contributes up to 14% of total island biomass of primary producers, which is within the wide range of crust contributions found in other studies (Büdel 2002).

Carbon and Nitrogen Fixation

Net photosynthetic rates of hypolithic crust communities measured in the lab and field (Table 1) were lower but within the ranges found by Büdel (1999) and Schlesinger et al. (2003). To our knowledge this is the first *in situ* measure of net carbon dioxide efflux from crust attached to rocks. Surface crusts composed mostly of cyanobacteria do not commonly have maximum rates higher than 1 μmol CO_2 $m^{-2}sec^{-1}$ (Lange et al. 1998; Lange 2001); thus, even the hypolithic crusts in hyperarid regions may reasonably be assumed to follow a similar pattern. Combining our field method with measures of heterotrophic metabolism and environmental response curves would provide the most complete picture of C fixation and potential contributions to the ecosystem.

Evidence of N fixation was inferred from the low range of $\delta^{15}N$ signatures of hypolithic crust samples (Table 1) (Belnap 2001; Evans and Ehleringer 1993; Rao and Burns 1990). However, we did not find any evidence that excess crust-fixed NO_3^- was accumulating in soils (Table 1) in contrast to Büdel's (1999) study in a tropical region.

Soil characteristics associated with crust

Soil electroconductivity indicated that soils under both crusted and uncrusted rocks had higher salinity than bare soils (Table 1). Soils with a high electrical conductivity have been shown to enhance cyanobacterial growth (Anderson et al. 1982); thus, the elevated conductivity of soils under crusted rocks in this study may be a cause rather than an effect of colonization. Although soil nitrate concentrations did not vary among conditions, bare soils and soils under crusted rocks were less enriched in ^{15}N than soils under uncrusted rocks (Table 1). Soil pH, which was basic, did not vary among bare soil, under uncrusted rocks and under crusted rocks on Isla La Ventana (Table 1).

Soil organic matter was significantly greater under crusted rocks than under uncrusted rocks or bare soils (Table 1). This is likely due to the accumulation of both crust biomass and the carcasses and frass from microarthropods that may consume crust biomass. Although no live animals were observed under crusted rocks, burrows, carcasses and frass were found under most crusted rocks. It is likely that hypolithic crusts may provide a significant carbon and nitrogen source for these belowground communities.

In conclusion, hypolithic soil crusts on the Baja California peninsula and the desert islands of the Gulf of California may be widespread in areas with exposed quartz rocks on the surface. Although the environment under quartz rocks is less harsh than the surface environment in such a hyperarid desert (Rosentreter and Belnap 2001; Schlesinger et al 2003), temperature extremes and intense drought likely limit net C and N fixation of the crust communities. Future studies should examine the contribution of hypolithic crusts to soil food webs.

Acknowledgements

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Table 1 Biological activity of hypolithic crusts under quartz rocks and soil characteristics associated with those hypolithic crusts in Baja California, Mexico. Soil in the open is the baseline condition, and soils under uncrusted rocks control for a rock effect. Data are mean ± SE with ranges, when appropriate, in parentheses. Different letters within a row represent significance of $p<0.05$ for one-way ANOVAs followed by Tukey's pairwise comparisons.

Measured Variable	Crust	Soil in the Open	Soil Under Uncrusted Rocks	Soil Under Crusted Rocks
Net Photosynthesis in the Lab ($\mu mol\ CO_2\ m^2/s$)	0.84±0.14 (0.66-0.94)	NA	NA	NA
Net Photosynthesis in the Field ($\mu mol\ CO_2\ m^2/s$)	0.23±0.32 (0-1.23)	NA	NA	NA
$\delta^{15}N$ (‰)	2.07±0.45 [a] (1.6-2.5)	3.71±0.03 (3)[b]	5.67±0.24[c]	4.29±0.36[b]
% Total N (%)	1.01±0.04[a] (0.97-1.05)	0.02±0.01[b]	0.02±0.00[b]	0.03±0.01[b]
NO_3^- (ppm)	NA	176.23±38.96[a]	130.83±35.75[a]	119.96± 32.13[a]
Organic Matter (%)	NA	1.46±0.18[a]	2.43±0.16[b]	2.89±0.16[c]
pH	NA	7.86±0.07[a]	7.82±0.06[a]	7.80±0.06[a]
EC (mmhos/cm)	NA	4.11±1.62[a]	9.18±1.53[b]	14.22±2.98[b]

NA: Not Applicable

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Table 1 Biological activity of hypolithic crusts under quartz rocks and soil characteristics associated with those hypolithic crusts in Baja California, Mexico. Soil in the open is the baseline condition, and soils under uncrusted rocks control for a rock effect. Data are mean ± SE with ranges, when appropriate, in parentheses. Different letters within a row represent significance of $p<0.05$ for one-way ANOVAs followed by Tukey's pairwise comparisons.

Measured Variable	Crust	Soil in the Open	Soil Under Uncrusted Rocks	Soil Under Crusted Rocks
Net Photosynthesis in the Lab (µmol CO_2 m^2/s)	0.84±0.14 (0.66-0.94)	NA	NA	NA
Net Photosynthesis in the Field (µmol CO_2 m^2/s)	0.23±0.32 (0-1.23)	NA	NA	NA
$\delta^{15}N$ (‰)	2.07±0.45 [a] (1.6-2.5)	3.71±0.03 (3)[b]	5.67±0.24[c]	4.29±0.36[b]
% Total N (%)	1.01±0.04[a] (0.97-1.05)	0.02±0.01[b]	0.02±0.00[b]	0.03±0.01[b]
NO_3^- (ppm)	NA	176.23±38.96[a]	130.83±35.75[a]	119.96± 32.13[a]
Organic Matter (%)	NA	1.46±0.18[a]	2.43±0.16[b]	2.89±0.16[c]
pH	NA	7.86±0.07[a]	7.82±0.06[a]	7.80±0.06[a]
EC (mmhos/cm)	NA	4.11±1.62[a]	9.18±1.53[b]	14.22±2.98[b]

NA: Not Applicable