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ORIGINAL PAPER

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Nitrogen fixation in biological soil crusts from southeast Utah, USA

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Abstract Biological soil crusts can be the dominant source of N for arid land ecosystems. We measured potential N fixation rates biweekly for 2 years, using three types of soil crusts: (1) crusts whose directly counted cells were >98% *Microcoleus vaginatus* (light crusts); (2) crusts dominated by *M. vaginatus*, but with 20% or more of the directly counted cells represented by *Nostoc commune* and *Scytonema myochrous* (dark crusts); and (3) the soil lichen *Collema* sp. At all observation times, *Collema* had higher nitrogenase activity (NA) than dark crusts, which had higher NA than light crusts, indicating that species composition is critical when estimating N inputs. In addition, all three types of crusts generally responded in a similar fashion to climate conditions. Without precipitation within a week of collection, no NA was recorded, regardless of other conditions being favorable. Low (<1°C) and high (>26°C) temperatures precluded NA, even if soils were moist. If rain or snow melt had occurred 3 or less days before collection, NA levels were highly correlated with daily average temperatures of the previous 3 days (r^2=0.93 for *Collema* crusts; r^2=0.86 for dark crusts and r^2=0.83 for light crusts) for temperatures between 1°C and 26°C. If a precipitation event followed a long dry period, NA levels were lower than if collection followed a time when soils were wet for extended periods (e.g., winter). Using a combination of data from a recording weather datalogger, time-domain reflectometry, manual dry-down curves, and N fixation rates at different temperatures, annual N input from the different crust types was estimated. Annual N input from dark crusts found at relatively undisturbed sites was estimated at 9 kg ha^{-1} year^{-1}. With 20% cover of the N-fixing soil lichen *Collema*, inputs are estimated at 13 kg ha^{-1} year^{-1}. N input from light crusts, generally indicating soil surface disturbance, was estimated at 1.4 kg ha^{-1} year^{-1}. The rates in light crusts are expected to be highly variable, as disturbance history will determine cyanobacterial biomass and therefore N fixation rates.

Keywords Cryptobiotic crusts · Microbiotic crusts · Microphytic crusts · Nitrogen budgets · Semi-arid lands

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Introduction

In desert ecosystems, N fixed by the cyanobacteria and cyanolichens found in the biological soil crusts (also known as microbiotic, cryptobiotic, or microphytic crusts) can be the dominant source of N (Evans and Ehleringer 1993). This is especially true for regions where rainfall and anthropogenic inputs of N are low. Most cyanobacterial fixation takes place in heterocysts, which are thick-walled cells that lack the oxygen-producing photosystem II (Paerl 1990). Heterocystic genera that commonly occur in soil crusts include *Anabaena*, *Calothrix*, *Cylindrospermum*, *Dicothrix*, *Hapalosiphon*, *Nodularia*, *Nostoc*, *Plectonema*, *Schizothrix*, and *Scytonema* (Harper and Marble 1988). N fixation has also been measured in non-heterocystous soil genera such as *Lyngbya*, *Microcoleus*, *Oscillatoria*, *Phoridium*, and *Tolypothrix* (Rogers and Gallon 1988; Belnap 1996), although this may be a result of bacteria associated with the cyanobacteria (Steppe et al. 1996). Soil lichens with cyanobacterial photobionts also fix N. Common N-fixing soil lichens include *Collema* spp. and *Peltula* spp., which contain the cyanobacterium *Nostoc*, and *Heppia* spp., which contains the cyanobacterium *Scytonema*. Cyanobacteria can also live epiphytically on soil mosses and lichens that have green algae as phycobionts; thus this consortium of organisms can also show N fixation activity (Peters et al. 1986).

Laboratory studies have demonstrated that N fixation rates in individual species of soil crust lichens and cyanobacteria are controlled by species composition, moisture, temperature, and light (Nash 1996; Kershaw 1985,

1998). Only a few studies have assessed N fixation rates throughout the year in a given locality, and few have used a "crust community" approach. In this study, potential N fixation was monitored biweekly for 2 years in three types of soil crust communities.

Materials and methods

Site description

Samples were collected just outside the Island-in-the-Sky District of Canyonlands National Park, located in southeastern Utah in the Colorado Plateau biogeographic province. Based on a 50-year record for nearby Moab, Utah, precipitation averages 215 mm yearly. Total rainfall has a bimodal pattern, with high amounts in winter-early spring and during summer monsoons (late July–October). Monsoons provide 35% of yearly rainfall. Evaporation exceeds precipitation during most of the year (Fig. 1). This area is a cold desert at an elevation of 1,370 m. Annual high temperatures average 28°C, while annual low temperatures average –2°C. The growing season is generally March–October. At the study site, soils are shallow Begay fine sandy loams, with clay and silt averaging about 15–20% and a pH of approximately 8.1. The vegetation is dominated by *Coleogyne ramosissima* (blackbrush).

Soil crust types

Three types of soil crusts were collected biweekly from 1 January 1996 to 24 September 1997: (1) crusts whose directly-counted cells were >98% *Microcoleus vaginatus* (called "light" crusts, due to the lack of soil surface coloration); (2) crusts dominated by *M. vaginatus*, but with 20% or more of the directly-counted cells represented by *Nostoc commune* and *Scytonema myochrous* (called "dark" crust, due to the blackish color they give the soil surface); and (3) the soil lichen *Collema* sp. (>90% of surface area covered by the lichen).

Analysis

Samples were transported back to the laboratory, where they were analyzed immediately for nitrogenase activity (NA). Air and soil temperatures were recorded at the time of collection. Potential NA was determined using the acetylene-reduction assay (ARA) (Belnap 1996) under previously-determined optimal temperature and moisture regimes (Belnap, unpublished data). Samples were placed in clear, gas-tight tubes and the entire crust surface was equally and completely wetted with distilled water. Tubes were injected with enough C_2H_2 to create a 10% C_2H_2 atmosphere. After injection, samples were incubated for 4 h at 26°C 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 analyzed for C_2H_2 and ethylene (C_2H_4) content on a Shimadzu GC-14 A gas chromatograph, using helium as the carrier gas (30 ml min^{-1}). Calibrations with ethylene standards were done at the time of observations. Results of the observed NA are reported in nmol C_2H_4 m^{-2} h^{-1}.

Estimates of annual N input

To determine soil dry-down curves, precipitation events were recorded by a Campbell Scientific datalogger (with a tipping rain-bucket) between 15 June 1998 and 15 November 2000 (CLIMMET 2001). Data were grouped into six temperature categories (–4 to 4°C, 5–8°C, 9–17°C, 18–23°C, 24–27°C, and 28–35°C). A combination of manual dry-down curves and time-domain reflectometry (that measured soil moisture in the top 1 cm of soil) was used to estimate how long precipitation at different air temperatures lasted in the study soils. Multiplying the amount of precipitation in each category by the time soils took to dry at that temperature gave an estimate of the number of hours soils were wet for each season. Average laboratory and field-obtained N fixation values for each temperature category were then multiplied by the number of hours the soil was wet. Because crusts are able to fix for 4–6 h in the dark (see below), 50% of the nighttime hours that were wet were considered available for N fixation.

Converting C_2H_4 values to N_2 is controversial, as the ratio used varies widely depending on the organism and habitat conditions (reviewed in Belnap 2001). For Arctic soil crusts, Liengen (1999) used simultaneous measures of ARA and incorporation of ^{15}N to obtain a maximum conversion ratio of 0.062 for cyanobacteria free-living in soils and 0.38 for sheets of *N. commune* lying on the surface. S. Phillips and J. Belnap (in preparation) measured *N. commune* sheets lying on the surface in southern New Mexico and obtained a ratio of 0.32, extremely close to the Liengen value. Because the result obtained for *N. commune* from these two environments was so similar, the calculations of N input presented here assume that the ratio for free-living cyanobacteria is also similar (0.062).

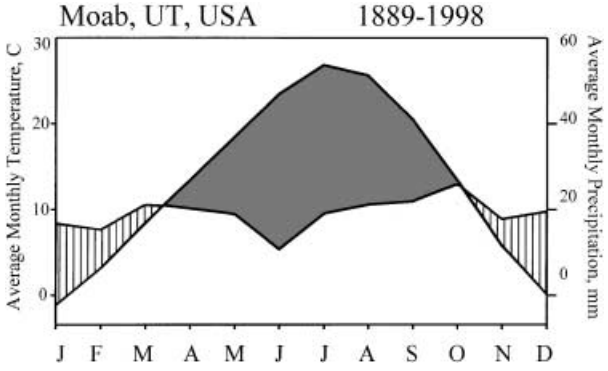

Fig. 1 Walter-type diagram for Moab, Utah. *Shaded area* shows months with precipitation >evaporation. *Black area* shows months with precipitation <evaporation. *J* January, *F* February, *M* March, *A* April, *M* May, *J* June, *J* July, *A* August, *S* September, *O* October, *N* November, *D* December

Results and discussion

The results of the biweekly measurements relative to air temperature and precipitation are presented in Fig. 2. As can be seen in this figure, *Collema* crusts had higher NA than dark crusts, which had higher NA than light crusts, at all observation points. In addition, all three types of crusts generally responded in a similar fashion to climate conditions. If rain had not fallen within a week previous to the collection time, no NA was recorded, regardless of other conditions being favorable. Low (<1°C) and high (>26°C) temperatures precluded NA, even if soils were moist. If rain or snow melt had occurred 3 or less days before collection, NA levels were highly correlated with daily average temperatures of the previous 3 days (r^2=0.93 for *Collema* crusts; r^2=0.86 for dark crusts and r^2=0.83 for light crusts) for temperatures between 1°C and 26°C. If a precipitation event followed a long dry period, NA levels were lower than if collection followed a time when soils were wet for extended periods (e.g., winter).

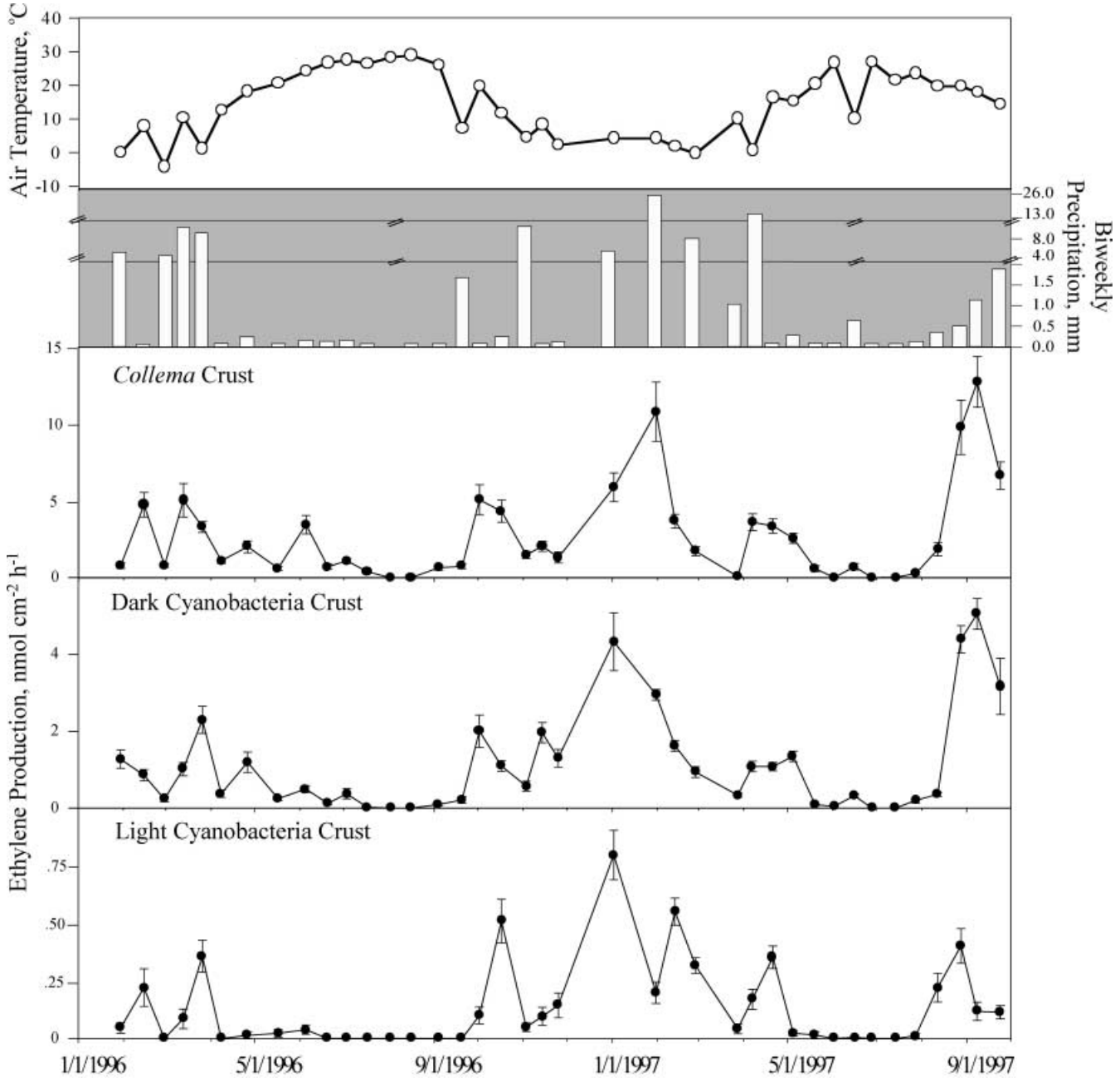

Fig. 2 Biweekly measurement of acetylene reduction assay for 2 consecutive years in field-collected *Collema*, dark cyanobacterial crusts (*Microcoleus-Scytonema-Nostoc-Collema* crusts), and light cyanobacterial crusts (*Microcoleus*) from southeastern Utah, measured under standard laboratory conditions (see Materials and methods). *Top panel* Daily average air temperatures on the sampling date. *Second panel* Precipitation (mm) estimates, measured 10 miles from the sample site. *Note* break in scale. *Bottom three panels* Nitrogenase activity in *Collema*, dark cyanobacterial, and light cyanobacterial crusts, respectively

Acetylene-reduction assay

N fixation activity is generally measured as $^{15}N_2$ incorporation or by ARA. As $^{15}N_2$ uptake is a direct measure of N fixation, it is the most reliable method. However, it is costly and requires highly controlled conditions; thus, most studies (including this one) use ARA. In the presence of C_2H_2, the nitrogenase enzyme produces C_2H_4 (ethylene), so the measurement of C_2H_4 production is a measure of NA. There are problems associated with ARA, however. C_2H_2 can affect physiological functioning of the organism, especially when exposure lasts longer than 6 h (David and Fay 1977). The biggest issue with ARA is that conversion of ARA data to absolute amounts of N_2 fixed requires calibration by $^{15}N_2$, which is seldom done (see discussion in Materials and methods).

Hierarchical controls on N fixation

This study showed that controls on N fixation are hierarchical. As with photosynthesis, the ultimate control on the duration and rate of N fixation is the moisture content of the organism (Belnap 2001; Lange 2001), as cyanobacteria and cyanolichens are only physiologically active when wet (Kershaw 1985; Nash 1996). Liquid water is necessary for cyanobacterial C fixation and can come from rainfall, snow melt, dew, or fog (Lange 2001). Moisture for N fixation varies widely with species and habitat. Cyanobacteria show NA at water contents ranging from 6% dry weight to total water immersion (Jones 1977c; Kershaw 1985; Belnap et al. 1999). Most soil cyanolichens, including *Collema* sp., require at least 80% dry weight water content to initiate C fixation activity (Lange et al. 1998); this ultimately affects N fix rates. NA in *Microcoleus-Collema* soil crusts drops rapidly below soil water potentials of –0.33 kPa, with a 50% reduction by –1 kPa (Rychert et al. 1978). At a given moisture content, NA rates can vary within and between species, due partially to pre-experimental conditions (DuBois and Kapustka 1983; Kershaw 1985). In subtropical soils, *N. commune* had maximal NA rates at 22–126% water content (by weight) (Jones 1977c), while *N. commune* from a northern temperate grassland showed maximal NA rates at 500% water content (Coxson and Kershaw 1983b). *N. commune* from Mongolian soils had the highest NA rates when totally saturated (Belnap et al. 1999). Long periods of desiccation can increase the time required to reach maximal N fixation rates after rewetting (Jeffries et al. 1992; Dodds et al. 1995; Nash 1996). Conversely, constant hydration over long periods of time can also reduce N fixation rates in *N. commune* (Jones 1989), as it may result in a massive efflux of glucose from the organism (Kershaw 1985). Thus, where soils are wet for long periods of time (e.g., subtropical or arctic regions), continuously high soil moisture may reduce overall N fixation, while alternation between wet and dry soils, as occurs in most deserts, may lead to greater N fixation rates per unit "moist soil time" than wetter regions.

Given sufficient hydration, the amount and accessibility of photosynthetic products act as the next determinant of N fixation rates. Photosynthesis provides the ATP for energy and C compounds for electron donors in support of the N fixation process (Paul and Clark 1996). Consequently, the duration and rate of N fixation depends on past and present conditions such as moisture, temperature, light intensity, and supply of assimilates, that influence the C balance of the fixing organism. Thus, rains that are infrequent, occur at night (when light is not available for photosynthesis), or are too small to keep soils wet long enough for a net C gain, can result in a depletion of C stores and N fixation rates will be lower and/or time of fixation will be shorter (Fig. 2; Jones 1977b). Microprobes show incorporation of ^{15}N is correlated with gross photosynthetic rates in *Nostoc* (Dodds 1989). Consequently, it is clear that past environmental conditions affecting C fixation rates must be taken into account when estimating current N fixation activity or annual inputs. Adequate C stores also enable crusts to fix N in the dark for 4–6 h (Jones 1977a, 1977b, 1977c; Coxson and Kershaw 1983a, 1983b; Davey and Marchant 1983; Scherer et al. 1984; Potts et al. 1987).

With sufficient hydration and access to C stores, temperature controls fixation rates until C stores are exhausted. Minimum air temperatures for NA varies by species and habitat as well, and is also dependent on pre-experimental conditions. NA was present, but very low, in free-living and lichenized *Nostoc* (in *Leptogium*) at –7.6 and 0°C, respectively (Horne 1972; Davey and Marchant 1983). *Stigonema* and *Scytonema* crusts from the tropics showed no NA at 0°C (Isichei 1980). Freezing can damage nitrogenase in *Nostoc* (DuBois and Kapustka 1983; Scherer et al. 1984). Low temperatures can reduce photosynthetic rates and thus reduce available ATP and reductant pools, creating a lag time after freezing before N fixation is initiated (Kershaw 1985).

Between minimum and maximum temperatures, N fixation rates show a strong and positive response to increasing air temperature (Coxson and Kershaw 1983c; Nash 1996). In this study, NA in all three types of crusts was strongly related to average air temperatures of the previous 3 days, as long as crusts had received moisture within 3 days prior to collection, and were between 1°C and 26°C. As seen in this study, the maximum (and thus also optimal) temperatures for NA are 20–30°C for crusts throughout the world, including the Arctic, Antarctica, Scotland, Canada, South Africa, and subalpine regions (Jones 1977b; Stewart et al. 1977; Coxson and Kershaw 1983a; Davey and Marchant 1983; DuBois and Kapustka 1983; Fritz-Sheridan 1988; Lennihan et al. 1994). *Nostoc-Microcoleus-Schizothrix* crust showed higher NA at 20°C than at 39°C (Englund 1978). *Stigonema* from Brazil and *Scytonema* from Nigeria showed maximum NA at 25–30°C, and a sharp decline above 30°C (Isichei 1980). *N. commune-Cylindrospermum* crust from Scotland reached maximum NA at 15–25°C. Subalpine *Tolypothrix* crusts showed maximum NA at 20–30°C (Fritz-Sheridan 1988; Stewart et al. 1977). This restriction of NA at high temperatures is expected to limit N fixation in desert crusts during summer. Conversely, low temperatures in the polar regions restrict N fixation in soil crusts to the summer season (Horne 1972; Davey and Marchant 1983).

It is also important to keep in mind that the reported temperature optimum must be interpreted carefully. In the laboratory, hydration levels are difficult to maintain at higher temperatures (Kershaw 1985). In field studies, air temperatures are generally reported, despite the fact thalli can be 15–25°C warmer than air temperatures on cold sunny days, while being a similar temperature on cloudy days (Belnap 1995). In addition, Coxson and Kershaw (1983b) show that while *N. commune* has a short-term optimal N fixation at 35°C (air temperature) for several hours, the long-term optimum is 28°C.

Table 1 Total rainfall recorded from 15 June 1998 to 15 September 2000, within temperature categories by season. As outlined in the Materials and methods section, these values were combined with manual dry-dry curves and time-domain reflectometry to estimate time of soil wetness during a given season. Resultant values were then multiplied by average N fixation at these temperatures to derive seasonal estimates of N input. Annual highs and lows were estimated by totaling the highest and lowest values for each season across years

	No. of precipitation events	Precipitation (mm)			Hours available for N fixation			N fixation (kg ha^{-1} year^{-1})	
		Daytime	Nighttime	Total	Daytime	Nighttime	Total	Light crust	Dark crust
Spring 1	12	22	36	57	96	155	251	0.5	3.2
Spring 2	7	25	2	28	121	10	131	0.2	1.4
Summer 1	14	24	32	56	34	43	77	0.4	2.3
Summer 2	27	49	57	106	90	64	154	0.7	4.4
Summer 3	16	8	13	21	8	11	19	0.1	0.8
Fall 1	18	50	30	80	241	159	400	0.6	3.7
Fall 2	5	15	8	22	91	51	142	0.2	1.1
Winter 1	8	20	6	27	134	42	176	0.2	1.3
Winter 2	16	23	16	39	162	100	262	0.3	2.0
Annual high								0.7	5.0
Annual low								2.0	13.0

The same hierarchical controls found in this study were also reported by Coxson and Kershaw (1983c). Their field study simultaneously recorded field temperatures, rainfall, thallus moisture, and NA in arctic soil crusts. Their results were very similar to those reported here: NA dropped as moisture dropped, in spite of favorable temperatures and light. If the crusts were sufficiently hydrated, rising temperatures increased NA, while temperature declines resulted in a NA decline. Above air temperatures of 26–30°C, little NA was observed; however, as soon as air temperatures dropped below this maximum, NA resumed. Although the overall patterns are clear and similar in both data sets, there are still some anomalous data points that resist explanation, indicating that refinement of these relationships is still needed.

Seasonality

Seasonality in NA has been repeatedly reported in the literature, with lower NA during hot and cold periods (summer and winter), and higher rates in late spring and early fall (Stewart 1967; Huss-Danell 1978; Johnson 1982; Coxson and Kershaw 1983b; DuBois and Kapustka 1983; Kershaw 1985). However, the observed "seasonality" can also be a result of the pre-experimental condition of measured material. The observed low rates in summer could result from many days of low soil moisture and high air temperatures preceding the collection of experimental material, while observed high rates in winter may result from many days of wet soils before collection, and thus high C stores. Soil moisture and moderate temperatures most often occur together during fall and spring; therefore, these seasons would be the time when collected material would most likely have the highest C stores (Coxson and Kershaw 1983b; Kershaw 1985). Cyanobacterial biomass is also often greatest after warm (but not hot), wet periods, such as are found in late spring or fall (Lynn and Cameron 1972; Johansen and Rushforth 1985; Johansen et al. 1993). No endogenous component to N fixation has been discovered, and it appears more likely that pre-experimental conditions, especially C store levels, dictate NA throughout the year (Kershaw 1985).

Estimates of annual N inputs

Rainfall events were surprisingly common between 15 June 1998 and 15 September 2000, with 129 soil-wetting events recorded (intermittent rains during consecutive days were considered one event if the soils did not dry between rain showers). The number of rain events in any given season and the amount of rainfall were highly variable, and within the 2-year measurement period showed no obvious pattern among seasons (Table 1). Combining these results with average N fixation rates at given air temperature, seasonal and annual N inputs were estimated for each of the crust types. For dark crusts, which are common in relatively undisturbed desert areas, annual inputs for 100% crust cover were estimated at 9 kg N ha^{-1} year^{-1}. For light crusts, most often found in areas with frequent soil surface disturbance, annual input rates for 100% crust cover were estimated to be from 0 (for recently or severely disturbed areas) to 1.4 kg N ha^{-1} year^{-1}. This latter rate is expected to be highly variable, as fixation rates will be dependent on the cyanobacterial biomass, which, in turn, is dependent on the frequency and severity of disturbance. Soils where more frequent or severe disturbance has lowered cyanobacterial biomass would have lower N fixation rates than less disturbed soils.

Because *Collema* cover in undisturbed areas is seldom >20%, annual input rates for a 100% *Collema* crust are not presented in Table 1. Thus, wherever *Collema* occurs, annual estimates of input should be increased accordingly. To estimate input for a given landscape, the

vascular plant basal area also needs to be subtracted. For example, if the total dark crust cover in an area is 80%, with a 20% *Collema* cover, annual N inputs would be estimated at 13 kg N ha^{-1} $year^{-1}$. This particular scenario is fairly common in relatively undisturbed areas on the Colorado Plateau.

While these estimated input rates are high relative to recently reported rates of N inputs from biological soil crusts in general (e.g., Coxson and Kershaw 1983a, 1983b, 1983c; Davey and Marchant 1983; DuBois and Kapustka 1983), and from southeast Utah specifically (Belnap 1995, 1996; Jeffries et al. 1992), they are not high compared to the original studies done (e.g., Mayland and MacIntosh 1966; Stewart 1967, 1970). The major difference between these groups of studies is that the early studies used the direct, and more accurate, ^{15}N technique to estimate N inputs, while later studies used the indirect method of ARA. Because the later studies did not do concurrent ^{15}N calibrations, they used the theoretical conversion ratio of 3:1 when converting from ethylene values to absolute amounts of N fixed. This resulted in very low estimates of N fixation, and thus N inputs. However, Liengen's work (1999) has elegantly shown that the 3:1 ratio is only valid for cultured cyanobacteria and vastly underestimates N fixation, and thus N inputs, of soil organisms. Because Liengen's findings were corroborated by the concurrent measure of ARA and ^{15}N for *Nostoc* from southeast Utah (Phillips and Belnap, in preparation), it appears unlikely the 3:1 conversion ratio is appropriate for soil crust studies.

This study also shows that N fixation rates, and N inputs, are dependent on the species composition of the crusts. Crusts consisting almost exclusively of *M. vaginatus* (light crusts) have relatively low NA, while the presence of free-living *N. commune* and *S. myochrous* (dark crusts) significantly increases NA. *Collema* sp. has the highest NA of the three crust types. Thus, any activities that decrease the cover of *Collema* or dark crusts, and increase the cover of light crusts, will also significantly reduce N inputs. Multiple studies have shown that increasing levels of surface disturbance by animals, recreational traffic, and military activities almost always shift crusts from dark or *Collema*-dominated ones to *Microcoleus*-dominated light crusts (Harper and Marble 1988; Belnap et al. 1994; Belnap 1995, 1996; Belnap and Eldridge 2001). As the light crusts fix much less N than the dark or *Collema* crusts, lower N enters the soil. This reduction can continue for many years, and lower N can be observed in both soils and plants up to 30 years post-disturbance (Belnap et al. 1994; Belnap 1995, 1996; Evans and Belnap 1999). This study also corroborates that relatively undisturbed soil crusts are a major source of N for these ecosystems.

What is the fate of the fixed N?

This study demonstrates that biological soil crusts contribute significant amounts of fixed N to the cold desert ecosystems in southeast Utah. What is the fate of this N? First, it appears that much of the N fixed by crusts is released almost immediately to the surrounding soils. Release of 5–70% of N fixed has been reported for soil-crust organisms, including *Scytonema* from Nigeria, *N. commune* from New Mexico (Dodds et al. 1995; Belnap and Garcia-Pichel, unpublished data), *Microcoleus-Nostoc-Scytonema-Collema* crusts from southeast Utah (Garcia-Pichel and Belnap, unpublished data) and from northern Utah (Klubek et al. 1978), *Nostoc* soil crusts (Stewart 1967), *Collema tenax* from Europe (Henriksson 1957) and southern Utah (Belnap and Garcia-Pichel, unpublished data), and *Peltigera canina* (Millbank 1978). N compounds released are mostly NO_3^-, with small amounts of NH_4^+, amides, peptides, and free amino acids. The released N is readily taken up by surrounding organisms, including vascular plants, fungi, actinomycetes, and bacteria (Stewart 1967; Jones and Stewart 1969a, 1969b; Rogers and Burns 1994). N release may be due to N gradients in soils, membrane deformation during rewetting, as a mechanism to attract beneficial organisms, or as elimination of waste products (Stewart and Rogers 1977; Millbank 1982; Potts 1984; Bergman et al. 1992; Dodds et al. 1995; Silvester et al. 1996).

Given the high rates of N input but low levels of soil N in deserts, much of the fixed N must be leached downwards into the soil or lost to the atmosphere as a gas. Little is known about either pathway in these ecosystems. No studies were found on leaching losses in this region. The only published study of gaseous losses in cold desert crusts (Klubek et al. 1978) used dead and decomposing crusts, and no published studies could be found using live crusts. Preliminary field measurement of N gas flux in living soil crusts of southeast Utah showed very little activity during fall and spring, with higher rates during summer (Barger and Belnap, in preparation). As can be seen in Table 1, most of the N fixed by crusts in this region occurs during fall, winter, and spring. Consequently, much N is fixed when losses appear to be very low. This would mean that the N fixed and released by crusts would be readily available to plants and microbes from fall through late spring. This decoupling of N inputs and losses may be the primary explanation of why plants growing in crusted soils have consistently been observed to have higher N than plants growing in uncrusted soils (Belnap and Harper 1995; Pendleton and Warren 1995; Harper and Belnap 2001), yet overall soil N levels are low.

In conclusion, biological soil crusts can be an important source of fixed N in arid and semi-arid soils. The major factors controlling N fixation rates are species composition of crusts, temperature, light, and moisture. Soil surface disturbance is increasing throughout the western United States and arid lands worldwide. Such increases in activity generally mean lichen-dominated or dark crusts are replaced by light *Microcoleus*-dominated crusts. When this occurs, N fixation rates plummet.

As crust organisms are only active when wet, moisture is the ultimate control on N fixation. Given adequate

nutrients and sufficient hydration, access to fixed C is the next limiting factor. This reliance on C stores makes N fixation rates highly dependent on pre-experimental conditions that influence C fixation rates. With sufficient hydration and C stores, N fixation in soil crusts from southeast Utah are linearly related to temperature when temperatures are between 1°C and 26°C. Much of the N fixed by crustal species is released soon after fixation. Released N has been shown to be utilized by surrounding organisms, including vascular plants, fungi, actinomycetes, and bacteria. Little is known about denitrification or volatilization losses from biological soil crusts, but it appears that when N inputs from southeast Utah soil crusts are greatest, gaseous losses are minimal.

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