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A break in the nitrogen cycle in aridlands? Evidence from $\delta^{15}N$ of soils

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Abstract. We examined the content and isotopic composition of nitrogen within soils of a juniper woodland and found that a cryptobiotic crust composed of cyanobacteria, lichens, and mosses was the predominant source of nitrogen for this ecosystem. Disturbance of the crust has resulted in considerable spatial variability in soil nitrogen content and isotopic composition; inter-canopy soils were significantly depleted in nitrogen and had greater abundance of ^{15}N compared to intra-canopy soils. Variations in the $^{15}N/^{14}N$ ratio for inter- and intra-canopy locations followed similar Rayleigh distillation curves, indicating that the greater $^{15}N/^{14}N$ ratios for inter-canopy soils were due to relatively greater net nitrogen loss. Coverage of cryptobiotic crusts has been reduced by anthropogenic activities during the past century, and our results suggest that destruction of the cryptobiotic crust may ultimately result in ecosystem degradation through elimination of the predominant source of nitrogen input.

Key words: $\delta^{15}N$ – Cryptobiotic crusts – Deserts – Nitrogen cycling – Rayleigh distillation

Identifying sources of nitrogen input and processes affecting nitrogen export from an ecosystem are critical in determining the extent of nutrient cycling within ecosystems and for global nitrogen cycles. Nitrogen input can occur either through atmospheric deposition or *in situ* biological nitrogen fixation (Fig. 1), and a knowledge of the relative importance of these processes is needed to predict the long-term stability of an ecosystem and its susceptibility to anthropogenic change (Boring et al. 1988). Despite their low productivity, arid regions may be important components of the global nitrogen cycle contributing as much as 30% of the total gaseous nitrogen emissions (N_2, N_2O, NO_X, NH_3) from undisturbed lands (Bowden 1986). Yet despite their importance, the relative contributions of biological nitrogen fixation and atmospheric deposition to many arid regions have not been clarified.

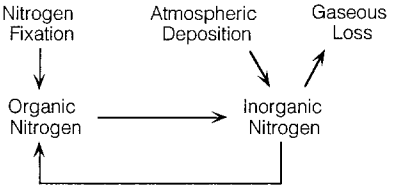

Fig. 1. Sources of input and loss for nitrogen within the soil. Organic nitrogen can originate from *fixation* of atmospheric nitrogen by organisms, or by assimilation of inorganic nitrogen from wet and dry *atmospheric deposition. Organic nitrogen* is converted to *inorganic nitrogen* by mineralization and nitrification. *Inorganic nitrogen* is either lost from the soil by volatilization or denitrification, or returned to the organic nitrogen pool through assimilation by plants or microorganisms. More than 98% of the organic nitrogen pool in aridlands is found in soils, while the remainder is in litter and higher plants (Peterjohn and Schlesinger 1990; West and Skujins 1977)

In the arid Intermountain West of North America, undisturbed soils are covered by a cryptobiotic crust composed of cyanobacteria, lichens, and mosses (Harper and Marble 1988; West 1990). The cryptobiotic crust can be as much as 10 cm thick and is held together by cyanobacteria that exude a gelatinous sheath binding both organisms and soil particles together (Campbell et al. 1989; Belnap and Gardner 1993). Cryptobiotic crusts often form a continuous cover in undisturbed communities (Harper and Marble 1988), extending both under canopies and into the inter-canopy spaces such that spatial coverage is often greater than that of higher plants (Kleiner and Harper 1972; Harper and Marble 1988). Much of the uncertainty surrounding ecosystem nitrogen inputs in these arid regions concerns the potential contribution of nitrogen-fixing organisms within the cryptobiotic crust to the total ecosystem nitrogen inputs (Peterjohn and Schlesinger 1990; West 1990). Both the dominant cyanobacteria in the cryptobiotic crust, *Microcoleus vaginatus* and *Scytonema myochrous*, and the com-

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mon lichen *Collema tenax*, are capable of nitrogen fixation (Harper and Marble 1988). West and Skujins (1977) estimated that over 80% of the nitrogen in these ecosystems originated from nitrogen fixation by cryptobiotic crusts. West (1990) however, recently concluded that for methodological reasons rates of nitrogen fixation have been over-estimated. The lack of reliable estimates has led researchers to ignore nitrogen inputs from cryptobiotic crusts in models of the nitrogen cycle in aridlands (Peterjohn and Schlesinger 1990).

Simultaneous analyses of both soil nitrogen content and nitrogen isotopic composition can provide information on nitrogen sources for an ecosystem. Soil nitrogen content decreases during decomposition because of net mineralization of soil organic matter and subsequent gaseous loss by volatilization and denitrification (Fig. 1). These decreases in soil nitrogen content are accompanied by a corresponding increase in the ratio of ^{15}N to ^{14}N (Nadelhoffer and Fry 1988). The increase in $^{15}N/^{14}N$ is due solely to fractionation during net mineralization, and not differential preservation of components of litter with greater $^{15}N/^{14}N$ (Nadelhoffer and Fry 1988). As soil organic matter decomposes it moves through the soil profile, causing an overall increase in $^{15}N/^{14}N$ and decrease in nitrogen concentration with depth (Nadelhoffer and Fry 1988). The absolute differences in $^{15}N/^{14}N$ among soils are small, and so isotopic compositions are expressed in delta notation ($\delta^{15}N$) relative to an atmospheric-air standard (Mariotti 1984) as

$$\delta^{15}N = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000‰ \quad (1)$$

where R_{sample} and R_{standard} are the molar ratios of $^{15}N/^{14}N$ of the sample and standard, respectively. The decrease in nitrogen content and corresponding increase in $\delta^{15}N$ of soil nitrogen during decomposition follows Rayleigh distillation kinetics (Mariotti et al. 1981; Nadelhoffer and Fry 1988) and can be described by

$$\delta^{15}N_{s,t} = \delta^{15}N_{s,0} + \varepsilon \ln\left(\frac{C_t}{C_0}\right) \quad (2)$$

where $\delta^{15}N_{s,t}$ is the isotopic composition of the substrate at time t, $\delta^{15}N_{s,0}$ the isotopic composition of the substrate at the start of the reaction, ε the isotopic enrichment factor associated with the reaction, and C_t/C_0 the fraction of substrate remaining at time t. When $\delta^{15}N_{s,t}$ is plotted against C_t/C_0, the slope of the linear relationship (ε) is equal to the fractionation associated with decomposition (Mariotti et al. 1981). Extrapolation back to $C_t/C_0 = 1$ yields the expected isotopic composition of the original nitrogen source. If values of ε are similar among soils, then differences in the y-intercept between soils would indicate sources of different isotopic composition. The isotopic composition and concentration of the original substrate are seldom known and so Eq. 2 is rewritten as

$$\delta^{15}N_{s,t} = k + \varepsilon \ln([N]) \quad (3)$$

where $\delta^{15}N_{s,0}$ and C_t/C_0 in Eq. 2 are replaced by a constant (k) and soil nitrogen concentration ([N]), respectively (Fustec et al. 1991).

We applied the Rayleigh distillation model to soils from a relatively simple, aridland ecosystem: a juniper woodland at the Coral Pink State Park (37° 03′ N, 112 45′ E, 1750 m elevation) in southern Utah. This ecosystem consists primarily of Utah juniper *(Juniperus osteosperma)*, interspersed with big sagebrush *(Artemisia tridentata)* and occasionally rabbitbrush *(Chrysothamnus nauseosus)*. Together these species comprised more than 95% of the vegetation; nitrogen-fixing higher plant species were nonexistent at this site. Soils were nutrient-poor aeolian deposits that are typical of this region. The soils lacked any visible development of horizons, and roots were uncommon below 5 cm. Our objective was to determine if disturbed and undisturbed soils shared a common nitrogen input source and to determine the extent to which cryptobiotic crust disruption influenced soil nitrogen levels.

Materials and methods

Soil samples were collected at four depths (0–10, 15–25, 45–55, and 95–105 cm) under the canopies of the dominant tree *(Juniperus osteosperma)* and shrub *(Artemisia tridentata)* species and in the inter-canopy spaces. Cryptobiotic crust samples were collected at Coral Pink and at a second site in Canyonlands National Park (300 km to the northeast). Nitrogen within the soil and cryptobiotic crust samples was converted to N_2 by combustion at 850° C for at least 6 h in evacuated Vycor tubes with CuO and Cu (Fiedler and Proksch 1975; Minagawa et al. 1984). The isotopic composition of the cryogenically purified sample was determined on a Finnigan MAT model delta S mass spectrometer. Nitrogen content was determined on a Technicon autoanalyzer following Kjeldahl digestion.

Results and discussion

The content and $\delta^{15}N$ of soil nitrogen differed significantly between locations only at the 0–10 cm depth (nitrogen content, $P = 0.011$; $\delta^{15}N$, $P < 0.001$). Soil nitrogen

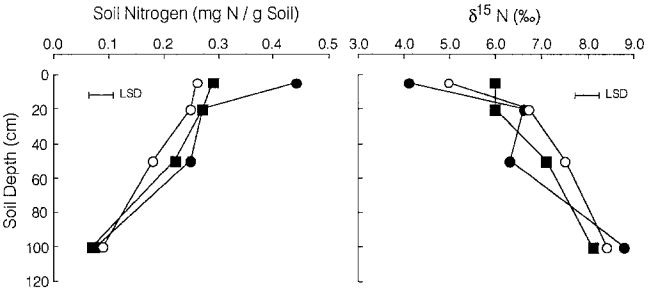

Fig. 2. Nitrogen content (mg N/g soil) and isotopic composition ($\delta^{15}N$ in ‰) of soils collected in a juniper woodland. Soils were collected under the canopies of the dominant tree *(Juniperus osteosperma) (solid circles)* and shrub *(Artemisia tridentata) (open circles)* species, and in the inter-canopy spaces *(solid squares)*. Each *value* is the mean of three observations. The minimum difference between means that is statistically significant is indicated by *LSD*. Differences in nitrogen content and isotopic composition between sampling locations are significant only at the 5 cm depth. Values for all three locations change significantly with depth

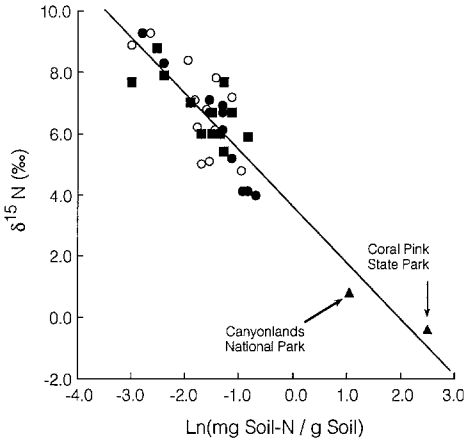

Fig. 3. The relationship between nitrogen isotope ratio ($\delta^{15}N$) and ln(nitrogen content) for soils located in a juniper community. Soils were collected under the canopies of the dominant tree *(Juniperus osteosperma) (solid circles)* and shrub *(Artemisia tridentata) (open circles)* species, and in the inter-canopy spaces *(solid squares)*. Each value for the cryptobiotic crusts *(solid triangles)* is the mean of two observations. The regression equations for the three locations were statistically equal and the relationship between $\delta^{15}N$ and ln(soil nitrogen content) was significant for the pooled data ($\delta^{15}N = 3.63 - 1.85 \times \ln$(soil nitrogen content), $P < 0.0001$, $r = 0.79$). Values for cryptobiotic crusts were not included in regression calculations

content at 0–10 cm was greatest under *Juniperus* canopies (Fig. 2), and did not differ significantly between soils under *Artemisia* canopies and the inter-canopy spaces. Soils in the inter-canopy spaces showed the greatest enrichment of ^{15}N at 0–10 cm, while soils under the *Juniperus* canopy had the lowest $\delta^{15}N$ values. The content and isotopic composition of soil nitrogen changed with depth for all locations (Fig. 2). The mean ($\pm$ SE) soil nitrogen content for the three locations decreased to 0.081 ± 0.013 mg N/g soil at 100 cm, while $\delta^{15}N$ increased to 8.4 ± 0.3‰. Neither the slopes ($P = 0.079$) nor the intercepts ($P = 0.087$) for the relationships between $\delta^{15}N$ and ln(soil nitrogen content) were different for the three locations, indicating similar input sources of soil nitrogen for all three locations (Fig. 3). The isotopic enrichment factor for the combined data was -1.8, well within the range of ε values (-1.5 to -4.8) reported for soils in other ecosystems (Nadelhoffer and Fry 1988).

On the basis of the data in Fig. 3, it is unlikely that atmospheric deposition is an important source of nitrogen for the soils examined in this study. Our study site is located well away from any sources of anthropogenic nitrogen input (> 100 km). The $\delta^{15}N$ of nitrogen originating from dry deposition in undisturbed areas is generally in excess of 5‰ (Heaton 1986), whereas the $\delta^{15}N$ of the original nitrogen source for these soils must be less than 4‰ (Fig. 3). Furthermore, the modal value for $\delta^{15}N$ of nitrogen in precipitation in undisturbed areas is approximately -7.5‰ (Heaton 1986), which would require an unreasonably large nitrogen source concentration of 410 mg N/g which was clearly not observed (Fig. 2). However, the observed soil $\delta^{15}N$ values and nitrogen contents are consistent with nitrogen fixation as the source of ecosystem nitrogen input. The $\delta^{15}N$ values of nitrogen originating from nitrogen fixation vary between -2 and $+2$‰ (Shearer and Kohl 1986), with a mode near 0‰. By extrapolation in Fig. 3, this would require the source nitrogen concentration to be in the range 0.2–2.1% which is well within the range reported for nitrogen-fixing organisms. Symbiotic and heterotrophic nitrogen fixing organisms are not common in the arid regions of the Intermountain West (West and Skujins 1977), leaving the cryptobiotic crusts as the most likely source of nitrogen input into these ecosystems.

The $\delta^{15}N$ values and nitrogen contents for cryptobiotic crusts from both locations agreed with expected values if the cryptobiotic crusts were the source of nitrogen for the ecosystem (Fig. 3). Previously reported rates of nitrogen fixation by cryptobiotic crusts can be as high as 41 kg N ha^{-1} $year^{-1}$ (West 1990), whereas atmospheric deposition input is less than 10% of this value (Junge 1958; Young et al. 1988; Peterjohn and Schlesinger 1990). Reported rates of nitrogen fixation by the cryptobiotic crusts are at the lower end of the range reported for other nitrogen fixing organisms (10–160 kg N ha^{-1} $year^{-1}$) (Boring et al. 1988), but annual uptake of nitrogen by plants in this ecosystem is also low (12 kg N ha^{-1} $year^{-1}$) (West and Skujins 1977). Given the lack of other nitrogen input sources, the cryptobiotic crusts play a key role as the primary source of nitrogen to this ecosystem. It is thus not surprising that spatial coverage of cryptobiotic crusts is positively correlated with soil nutrient concentration (Harper and Marble 1988), floristic diversity (Kleiner and Harper 1972; Beymer and Klopatek 1992), and seedling survivorship of higher plants (Harper and Marble 1988).

What is surprising, though, is the significant decrease in soil nitrogen levels associated with disruption of the cryptobiotic crust, as is clearly seen when comparing soil nitrogen contents and $\delta^{15}N$ values in the intra- versus inter-canopy spaces. Disturbance at our study site disrupted the cryptobiotic crusts, which are now only visible as remnants underneath tree and shrub canopies. The relationship between soil nitrogen content and $\delta^{15}N$ predicted by the Rayleigh distillation curve provides a valuable mechanism to better understand nutrient dynamics in this aridland ecosystem and to assess degradation of that ecosystem. One consequence of anthropogenic disturbance is an increase in spatial variation of soil nitrogen content (Schlesinger et al. 1990), a direct result of increased nitrogen loss from the inter-canopy spaces and localized zones of litter deposition beneath plant canopies (Schlesinger et al. 1990; Virginia and Jarell 1983). Based on the relationship in Fig. 3, soils from the inter- and intra-canopy locations at Coral Pink have similar nitrogen sources, and so the increase in $\delta^{15}N$ and decrease in nitrogen content for soils in the inter-canopy spaces indicates greater net nitrogen loss relative to intra-canopy locations.

The contribution of cryptobiotic crusts to nitrogen input in aridlands and its disruption by anthropogenic activities have important implications for the nitrogen cycle in arid regions. Next to water, low availability of nitrogen is the abiotic variable that most limits plant growth. The destruction of cryptobiotic crusts through

cattle and livestock trampling, vehicle traffic, and current land-management practices can eliminate the predominant source of nitrogen input into these communities. In the long term, removal of this input nitrogen source, coupled with continued gaseous losses of nitrogen from the ecosystem, will ultimately decrease the amount of nitrogen available for plant growth and reproduction. Recovery of the crust is exceptionally slow (Belnap 1993), and so, in effect, the nitrogen cycle is broken, with significantly reduced nitrogen inputs but continued and possibly accelerated rates of nitrogen loss from the ecosystem. This ecosystem degradation leads to decreased soil fertility and will ultimately result in degradation of community structure and shifts in community composition towards species that are either capable of nitrogen fixation or are tolerant of low nitrogen availability (Schlesinger et al. 1990). Comparative studies of grazed and nearby pristine sites in the Intermountain West already provide evidence for these changes in species composition (Kleiner and Harper 1972).

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