

Potential Nitrogen Contribution of Soil Cryptogams to Post-Disturbance Forest Ecosystems in Bandelier National Monument, NM.

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Abstract.--The nitrogen-fixation (N_2 -fixation) potential and annual N contribution of soil cryptogamic crusts were estimated in three previously burned ponderosa pine (*Pinus ponderosa*) and one previously grazed pinyon/juniper (*Pinus edulis/Juniperus monosperma*) forest ecosystems in Bandelier National Monument, NM. The ponderosa pine forest sites were burned in the 1977 La Mesa Fire and burro grazing on the pinyon/juniper site ended in approximately (1983). The objective of this research was to determine whether estimated post-disturbance cryptogamic N inputs could offset N losses from the disturbance. Surface cover in each habitat was divided into litter cover, herbaceous cover, bare soil, and obvious cryptogams, in an attempt to quantify the spatial heterogeneity of soil properties. Line intercept transects were used to estimate percent surface cover of each cover type. Soil samples from each cover type were analyzed for total N, C, P, $\delta^{15}N$, and N_2 -fixation potential. At this stage in the recovery process, the potential for cryptogamic N_2 -fixation was determined to occur in all sampled habitats and cover types. Correlations between N_2 -fixation potential and other soil variables indicated that none are suitable as indirect estimators of N_2 -fixation potential. Estimates of ecosystem N input as a result of cryptogamic N_2 -fixation range from 3.6 - 27.0 kg ha⁻¹ yr⁻¹. Evidence from soil analyses indicated that soil loss was greatest at the pinyon/juniper site.

INTRODUCTION

In a stable forest ecosystem, inputs and losses of mass and energy are considered to be in equilibrium over broad spatial and temporal scales. Decomposition, the process by which nutrients stored in organic detritus are returned to their mineral forms, is slow in ponderosa pine (PP), which leads to an accumulation of organic matter in the absence of fire (C. White, This Volume). Fire causes near immediate mineralization of nutrients. Carbon (C) is released as CO₂, nitrogen (N) as NH₄, and other mineral nutrients as their oxides in the ash. However, mineralization by fire is a radical process and results in a net loss of N by volatilization and loss of fine particulates in smoke and ash carried to the atmosphere (Vitousek and Howarth 1991).

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The significance of this problem is better understood when viewed in a broad temporal context. Ponderosa pine forests, some pinyon/juniper (P/J) associations, chaparral, and some grasslands are dependent upon frequent fires to maintain a stable species composition (Figure 1). If fire-dependent ecosystems are stable, total ecosystem N will be relatively stable over long time periods. However, if the loss of N following fire is not returned through inputs, the plant community will ultimately be unstable and unable to maintain itself.

Nitrogen losses from disturbed ecosystems can also occur as a result of soil erosion. The potential for soil erosion is influenced by the type and magnitude of the disturbance. Because grazing animals can disturb the structural integrity of surface soils, overgrazing can result in an increased susceptibility to soil erosion.

Cryptogamic crusts, also called microbiotic or microphytic crusts, can contain cyanobacteria, fungi, algae, lichens and mosses. Some species of cyanobacteria (free-living or as lichen symbionts) have the ability to "fix" or convert biologically unavailable atmospheric N₂ to biologically available forms. Observations of several post-disturbance habitats within Bandelier National Monument have indicated that colonization of bare mineral soils by cryptogamic crusts may be both rapid and extensive. The importance of soil lichens and cyanobacteria to the overall N budget is relatively unknown, but cryptogamic crusts may act to retain N by reducing erosion through soil stabilization (Eldridge 1993; W. White, chapter XX, this volume) and contribute N through atmospheric N₂-fixation (Rychert and Skujins 1974; Jeffries et al 1992). Harper and Marble (1988) and West (1990) are excellent reviews of the ecological role of soil cryptogamic crusts in arid and semiarid regions.

This research addresses the following questions related to the role of soil cryptogamic crusts in post-fire ponderosa pine forests, and previously grazed P/J woodlands.

1. Does the potential for cryptogamic N₂-fixation exist?
2. Can the spatial heterogeneity of potential N₂-fixation be assessed by field observation?
3. Do other soil properties correlate with N₂-fixation potential?
4. What is the potential N contribution of cryptogamic crusts to these ecosystems?

Question 1 is fundamental to this research, for if N₂-fixation does not occur the remaining questions are meaningless. Question 2 is based on *a priori* assumptions that were made in the field before any soil analyses were conducted. We assumed that the soil surface cover would affect N₂-fixation potentials and that soil covered by obvious cryptogams would have the highest potentials. Question 3 states an attempt to identify easily quantifiable soil properties that could be used to estimate N₂-fixation potential because the acetylene reduction method for estimation of N₂-fixation potential is labor-intensive. Question 4 addresses the overall importance of cryptogams to the N budget of these recovering ecosystems.

Research Approach

Because of the absence of pre-disturbance data, this research utilized several indirect approaches to address the questions listed above. Relative cryptogamic N₂-fixation potential was estimated by acetylene reduction assay. Biological N₂-fixation occurs when the enzyme nitrogenase breaks the N₂ triple bond and reduces atmospheric N to ammonium (NH₄⁺). Nitrogenase also preferentially converts acetylene to ethylene in an atmosphere of approximately 10% acetylene. The acetylene reduction assay estimates nitrogenase activity by quantifying the amount of ethylene produced through time. Although the accuracy of potential N₂-fixation estimates by the acetylene reduction assay has been questioned (Weaver 1986), this analysis should be useful to compare the relative N₂-fixation potential between sites.

Cryptogamic N contribution can be estimated by means other than N₂-fixation potentials. Two separate and independent estimates of total cryptogamic N contribution (TCNC) were made based upon total soil N (TN) and stable nitrogen isotope (δ¹⁵N) values. The first estimate is based on differences in TN between soils of each of four surface cover types (litter, herbaceous, bare soil, and obvious cryptogams). We assumed that the nitrogen content of the bare soil represented the nitrogen content of the soil after fire and subsequent soil erosion. The bare soil is used as a standard for comparison because any subsequent inputs of N through wet and dry deposition is assumed to have occurred equally in all soil types. Thus the increase in N in the other soils should be a result of N₂-fixation by nodulated plants and cryptogams. This method yields a potentially conservative estimate of TCNC because any N contribution by non-crustal or free living N₂-fixing organisms occurring in the bare soil is not accounted for in the final estimate.

Stable isotope analysis of soil N can also be used to estimate N inputs. Nitrogen exists as two stable isotopes ¹⁵N and ¹⁴N. The relationship between the isotopes is expressed as a δ¹⁵N value. The δ¹⁵N value of a sample is calculated using the following equation (1):

$$\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where R_{sample} is the ratio of ¹⁵N:¹⁴N in the sample, and R_{standard} is the ratio of ¹⁵N:¹⁴N in an atmospheric N standard. Sources of N input tend to have a δ¹⁵N near 0 because N₂-fixation does not discriminate between isotopes (Figure 2). The δ¹⁵N of soil N increases through time because biological processes such as N mineralization, nitrification, and denitrification discriminate against ¹⁵N and selectively remove a greater proportion of ¹⁴N (Evans and Ehleringer 1993). As the quantity of residual N decreases, its δ¹⁵N increases. Stated differently, as N losses increase, soil δ¹⁵N increases because processes that lead to N loss will discriminate against the heavier isotope. As N inputs increase, the soil δ¹⁵N will decrease through time because N inputs do not discriminate against ¹⁵N and "recent N" dominates the soil N pool.

A hypothetical soil profile distribution of δ¹⁵N and TN (Figure 3) is based on profiles reported for a juniper/sagebrush ecosystem in southern Utah (Evans and

Ehleringer 1993). This profile distribution is based on assumptions that surface N inputs have low $\delta^{15}\text{N}$ values, the $\delta^{15}\text{N}$ of soil N will increase the longer it remains in the soil, and the age of soil N generally increases with depth.

Surface soil TN and $\delta^{15}\text{N}$ values may indicate the recent occurrence of soil erosion (Figure 3). Erosion removes surface soil and its associated N resulting in altered profile N distributions. Eroded surface soils should have higher $\delta^{15}\text{N}$ and lower TN than undisturbed soils. Comparison of $\delta^{15}\text{N}$ of surface soils within or between sites may indicate relative degree of soil loss.

METHODS

Four previously disturbed forest sites in Bandelier National Monument (Figure 4) were chosen as study sites. Sites A, B, and C were located in ponderosa pine forests which burned in the 1977 La Mesa Fire and provide estimates of post-fire cryptogam establishment and potential N inputs. Site A (elev. 8230') was located on Apache Mesa, less than 1 km southwest of the Apache Springs Trailhead. Site B (elev. 7450') was located adjacent to one of Terry Foxx's permanent plots on Escobas Mesa. Sites A and B both have understory vegetation dominated by New Mexico locust (*Robinia neomexicana*), Gambel's oak (*Quercus gambelii*), and sheep fescue (*Festuca ovina*). Site C (elev. 6600') was within the P/J - ponderosa pine ecotone, south of Frijoles canyon and west of the trail that continues to Alamo Canyon. Site C has understory vegetation dominated by mountain muhly (*Muhlenbergia montana*), and junegrass (*Koeleria cristata*). Site D, a P/J woodland (elevation 6390') is east of the Burro trail in the southeastern portion of the Monument. Due to a past history of overgrazing and disturbance by livestock and feral burros (Koehler 1974; Allen 1989), this P/J woodland has very little interspace vegetation and most of the litter is under the canopy of the trees.

Line intercept transects were used to estimate the cover of four surface types: litter, characterized as having greater than 50% dead plant material on the surface; herbaceous vegetation; bare soil; and cryptogamic crust, which was characterized as having greater than 50% recognizable lichen or algal surface crust. Transect data for sites A, B, and C are from previously burned areas only, whereas transect data for site D includes mature pinyon and juniper trees and their associated litter mats. Three, 50 m transects were established within each of the four sites and cover was recorded by centimeter increments along the transects. Within each site, soil surface samples (approx. 3 cm dia. by 3 cm deep) were collected from within areas dominated by each of the four cover types. Soil samples (approximately seven/cover type/site) from all cover type/site combinations were analyzed for total soil N, C, P, and $\delta^{15}\text{N}$. Soil C was estimated by combustion and total P was estimated by **Kjeldahl digest**. Soil $\delta^{15}\text{N}$ and TN values were provided by Isotope Services, Inc., White Rock, NM. Ratios of elements (C:N, N:P) were calculated from respective analyses. Soils and vegetation transects for sites A, B, C, and D were sampled on 6/18/93, 5/27/93, 5/28/93, and 6/17/93, respectively.

Potential N₂-fixation in all soil samples was estimated using the acetylene reduction assay. Soil surface samples were incubated under optimal moisture conditions in closed chambers in an atmosphere of approximately 10% acetylene for 48 hrs in the Department of Biology greenhouse on the campus of the University of New Mexico. All soil samples from one habitat type were incubated simultaneously. However, it was not possible to standardize incubation conditions between sites because of the lack of environmental control in the greenhouse. Consequently, comparisons of N₂-fixation potential between sites are not valid.

The potential N contribution to these forest ecosystems was indirectly estimated using differences in soil TN and $\delta^{15}\text{N}$. These estimates of annual TCNC were calculated using the following equation (2):

$$(\text{TCNC})/\text{cover type} = (\text{TN}_{\text{sample}} - \text{TN}_{\text{bare}}) * (\text{BD}) * (\% \text{ cover}_{\text{sample}}) / 16 \text{ yr}$$

where $\text{TN}_{\text{sample}}$ is the mean TN for the sample soil type (litter, herbaceous, or cryptogamic crust), TN_{bare} is the mean TN for the bare soil type, BD is a constant (3,000) that converts the value to kg ha^{-1} (assuming a bulk density of 1.0 g cm^{-3}), $\% \text{ cover}_{\text{sample}}$ is the % cover of that cover type, and 16 yr is the approximate amount of time since the La Mesa Fire. The sum of the TCNC for each cover type is an estimate of TCNC for a particular site.

The second estimate of cryptogamic crust N contribution is based on differences in $\delta^{15}\text{N}$ between soils of each cover type. The $\delta^{15}\text{N}$ value of a soil is a result of the effects of the fire and erosion, atmospheric and cryptogamic crust N inputs, and subsequent soil processing. Atmospheric inputs and soil processing are assumed to be equal in all soil types. The proportion of soil N (% contribution) for each cover type (X) is determined by the following equation (3):

$$[\delta^{15}\text{N}_{\text{bare}}(1-X)] + [\delta^{15}\text{N}_{\text{cryp}}(X)] = \delta^{15}\text{N}_{\text{sample}}$$

where $\delta^{15}\text{N}_{\text{bare}}$ is the $\delta^{15}\text{N}$ of the bare soil, $\delta^{15}\text{N}_{\text{cryp}}$ is the $\delta^{15}\text{N}$ of N derived from N₂-fixation by cryptogamic crusts and $\delta^{15}\text{N}_{\text{sample}}$ is the $\delta^{15}\text{N}$ of the sample cover type soil. The TCNC for individual cover types is then determined by the following equation (4):

$$X * (\text{TN}_{\text{sample}}) * (\text{BD}) * (\% \text{ cover}) / 15 \text{ yr}$$

where X is the % contribution of cryptogams to the $\delta^{15}\text{N}$ of the cover type soil and the other components are the same as in equation 2. The $\delta^{15}\text{N}$ values of the bare and sample soils are known and the N contributed by cryptogamic N₂-fixation is assumed to have a $\delta^{15}\text{N}$ of 0. Again, an estimate of site TCNC is generated by summing the TCNC for each cover type.

Within site correlations (Lotus 123 regression routine) were conducted between N₂-fixation potential and all other measured soil variables.

RESULTS

Above-ground cover estimates of cover categories in each site are shown in Figure 5. Herbaceous cover was greatest in sites A and B. The cover of bare soil and obvious cryptogams was greatest in sites C and D.

In general, soil N, C, P, and N:P (Figures 6, 7, 8, and 9 respectively) were highest in site A and lowest in site D. Soil $\delta^{15}\text{N}$ (Figure 10) was relatively constant in sites A, B, and C but higher and less uniform in site D. C:N ratios (Figure 11) were relatively constant across all sites.

Relative N_2 -fixation potentials for all sites and cover types are shown in Figure 12. For most sites the obvious cryptogam cover had the highest potentials, while the bare soil had the lowest potentials.

Within site correlations between N_2 -fixation potential and all other measured soil variables (Table 1) indicated that none of the variables were good indirect estimators of N_2 -fixation potential.

Estimates of annual TCNC for method 1 (TN) and method 2 ($\delta^{15}\text{N}$) are shown in Table 2. Values of annual TCNC range from 3.4 - 25.4 $\text{kg ha}^{-1} \text{yr}^{-1}$.

DISCUSSION

Cryptogamic N Contribution

Two important findings were made with respect to potential N_2 -fixation: 1) N_2 -fixation potential exists in all cover types; and 2) total cryptogam cover may be a poor indicator of the overall importance of cryptogams at these sites. Current cover of cryptogamic crusts may be more sensitive to, or a function of, the amount of bare soil still available for cryptogam establishment following 16 years of ecosystem succession. For example, the relatively high cover of litter and herbaceous vegetation and low cover of cryptogams and bare soil in sites A and B (Figure 5) is probably a result of rapid post-fire recovery because of more mesic conditions at the upper elevations. Although the estimated cover by cryptogams is now low at the upper elevation sites, little is known about cryptogam cover changes in these habitats following the La Mesa Fire (but see W. White, This Volume).

Although no between-site comparisons of N_2 -fixation potential estimates were made, it is possible to compare the relative N_2 -fixation potential of each cover type within the sites (Figure 12). At site A, soils covered by herbaceous vegetation and litter both had higher N_2 -fixation potentials than obvious cryptogamic crusts, which is the cover type with the highest relative potential at all other sites. Bare soil had the lowest N_2 -fixation potentials except for site B. At this point we do not understand the ecology of cryptogamic organisms well enough to offer an explanation for these results. Undoubtedly, our visual estimates of potential cryptogam activity do not correlate well with what is occurring in the real world. Although necessary information on cryptogam

activity is lacking that would permit quantification of current cryptogamic N contributions under field conditions using N₂-fixation potentials, it is clear that N₂-fixation is occurring at all sites and in all cover types.

Estimates of total N contribution by soil cryptogamic crusts are remarkably similar between methods and sites (Table 2). However, the total N contribution of cryptogams at the high elevation sites may be greater than at the low elevation sites, despite the discrepancy in cryptogam cover. Because of the more mesic environment, cryptogamic crusts of the upper elevation sites may have longer periods of active N₂-fixation, which could offset the differences in % cover. The litter and herbaceous cover types, which have highest % cover in sites A and B, are more mesic than the bare soil or obvious cryptogam cover types and may promote even greater cryptogam activity. The total annual N input to comparable sites from wet and dry deposition is approximately 2 - 4 kg ha⁻¹ yr⁻¹ (Evans and Ehleringer 1993). Rychert and Skujins (1974) estimated cryptogamic N₂-fixation inputs to Great Basin Desert ecosystems to range from 10 - 100 kg N ha⁻¹ yr⁻¹. The calculated estimates of annual cryptogamic N-contribution at our study sites are within the range reported by other researchers and well above the estimates for atmospheric N input. Consequently, this is evidence that cryptogamic N₂-fixation is a very important source of N for these Bandelier sites.

Interestingly, both the lowest and highest estimates of N contribution are from site B. The relatively divergent and extreme estimates at this site may be the result of high N inputs from elk that use this area extensively (Allen, This Volume). The resultant high TN inputs from elk would increase the estimated cryptogam N contribution from method 1, and the high $\delta^{15}\text{N}$ values of the elk-added N would lower the N contribution estimate from method 2, based on differences in $\delta^{15}\text{N}$ values.

Disturbance and Soil Erosion

Soil erosion is a process that removes soil and nutrients from ecosystems and leads to desertification. Lower elevation mesas at Bandelier National Monument were most susceptible to erosion following the La Mesa Fire, probably as a result of lower plant recovery rates (White 1981). Two lines of evidence from this study suggest that greater rates of soil erosion have occurred at the lower elevation P/J woodland site (D), probably because of its relative aridity and disturbance history. First, bare soil comprises 25 - 35% of the surface in sites C and D (Figure 5). Second, soil TN (Figure 6) and $\delta^{15}\text{N}$ (Figure 9) are lowest and highest, respectively, in site D. This pattern is consistent with removal of N rich, low $\delta^{15}\text{N}$ surface soil and exposure of low N, high $\delta^{15}\text{N}$ subsurface soil (Figure 3). The interspace soils (herbaceous, bare soil and cryptogam cover types) are particularly susceptible to erosion because they are not protected by the tree canopies and their associated litter mats. Stabilization and recovery of these soils could take many years. Evidence from crust removal and reinoculation experiments in Utah suggest that it may take 40 - 85 years for full recovery of disturbed cryptogamic crusts (Belnap 1993).

CONCLUSIONS

Acetylene reduction assays of surface soils show that the potential for N₂-fixation occurs in all soils at all sites. The actual N contribution of cryptogamic crusts depends on the abundance and activity of the crust organisms. Actual contributions of N by crusts in the higher elevation sites may be greater than at lower elevations because of more favorable climatic conditions. Although soils with obvious cryptogamic crusts generally had the highest N₂-fixation potential, this was not always the case. Visual observations of cryptogamic crusts are not reliable estimates of N₂-fixation potential. None of the soil analyses (TN, TC, C:N, TP, N:P, and $\delta^{15}\text{N}$) were good estimators of N₂-fixation potential. Estimates of total N contribution by crusts show annual inputs ranging from 3.6 - 27 kg ha⁻¹ yr⁻¹. These estimates indicate that cryptogamic N₂-fixation is an important source of N to these post-disturbance ecosystems. However, without broad scale spatial estimates of all N inputs through time, as well as estimates of disturbance-induced N loss, it is impossible to determine whether or not these forested ecosystems maintain a stable N level. Undoubtedly, recovery from catastrophic disturbances such as the La Mesa Fire or severe overgrazing will require a much greater period of time than recovery from low intensity fires and grazing that were characteristic of ponderosa pine forests and P/J savanna before the arrival of European man.

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Table 1. Within site correlation coefficients (all cover types) of N₂-fixation potential against all other measured soil variables.

Variable	Site			
	. A	. B	. C	. D
N	0.37	<0.01	.. 0.08	<0.01
C	0.38	. 0.04	.. 0.08	<0.01
C:N	0.02	. 0.03	<0.01	. 0.03
P	0.38	<0.01	.. 0.06	. 0.01
N:P	0.06	. 0.01	.. 0.09	. 0.03
δ ¹⁵ N	0.02	<0.01	.. 0.01	. 0.08

Table 2. Estimates of annual total cryptogam N contribution in kg ha⁻¹ yr⁻¹. Calculations based on TN and δ¹⁵N methods.

. Site	Method 1 (TN)	Method 2 (δ ¹⁵ N)
A	24.6	20.2
B	25.4	3.4
C	8.3	11.4
D	14.3	12.6

FIGURES

Figure 1. A conceptual outline of changes in ecosystem N as a function of time. The solid line represents succession to a climatic climax in the absence of any disturbances. The dotted and dashed lines represent the N dynamics of stable and unstable ecosystems, respectively, when subject to recurrent fire events.

Figure 2. Conceptual model of ecosystem N and $\delta^{15}\text{N}$ dynamics. The values are means or ranges of $\delta^{15}\text{N}$. Nitrogen inputs from N_2 -fixation and wet and dry precipitation have a mean $\delta^{15}\text{N}$ of zero. Through time the $\delta^{15}\text{N}$ of soil organic and inorganic N increases because of processes such as denitrification that discriminate against (leave behind) ^{15}N .

Figure 3. Hypothetical soil profile distribution of TN and $\delta^{15}\text{N}$ based on Evans and Ehleringer (1993). Dashed lines represent potential soil surfaces that would result from soil erosion.

Figure 4. Location of study sites within Bandelier National Monument, NM.

Figure 5. Mean surface cover of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

Figure 6. Mean soil N of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

Figure 7. Mean soil C of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

Figure 8. Mean soil P of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

Figure 9. Mean soil N:P ratios of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

Figure 10. Mean soil $\delta^{15}\text{N}$ of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

Figure 11. Mean soil C:N ratios of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

Figure 12. Total N_2 -fixation (μmol) for cover types within sites. Due to uncontrollable environmental conditions during sample incubation, comparisons should not be made across sites.