NITROGEN MINERALIZATION IN THE ASPEN ECOSYSTEM[1]

M.C. Amacher*[2], A.D. Johnson[2], T. Christopherson[2],
D.E. Kutterer[2], D.L. Bartos[2], and J. Kotuby-Amacher[3]

[2]USDA Forest Service Rocky Mountain Research Station, Logan, UT 84321 and
[3]Department of Plants, Soils, and Biometeorology, Utah State Univ., Logan, UT 84322

ABSTRACT

Aspen (*Populus tremuloides*) are in decline throughout the interior western U.S. because of conifer invasion, fire suppression, and overbrowsing by domestic livestock and native ungulates. Aspen restoration requires disturbances such as fire or cutting and exclosures to protect against overbrowsing. We measured the effects of the 1996 Pole Creek fire, Fishlake NF, UT on soil N mineralization/immobilization during the summer of 1997 using an ion exchange membrane (IEM) soil core incubation method. Two incubation periods were used: 6/25 to 7/22/97 (27 d) and 7/22 to 9/23/97 (63 d). Net soil N mineralization/immobilization rates in unburned aspen and unburned mixed aspen/conifer areas were very low. Amounts of NH_4 and NO_3 accumulated by IEM's and in soil cores were significantly higher in the burned aspen/conifer area than in unburned areas. More NH_4 was accumulated in the IEM's and soil cores during the first incubation, whereas more NO_3 was accumulated in the IEM's and soil cores during the second incubation indicating an increase in nitrification as summer progressed. Even though more soil cores in the burn area had higher rates of mineralization or immobilization than those in unburned areas, net mineralization/immobilization rates in the burn area one year after the fire were not significantly different from unburned areas because of the balance of the two overall processes. The increased amounts of soil NH_4 and NO_3 as a result of fire provide a source of N for aspen regrowth until N mineralization/immobilization in leaf litter can again become the dominant process of N cycling in the aspen ecosystem.

Aspen provides many benefits including watershed protection, more water yield than conifers, wood fiber, biological diversity, wildlife habitat, forage for domestic livestock and native ungulates, recreational sites, and esthetic considerations (e.g., fall leaf colors) (Bartos and Campbell, 1998a). Unfortunately, aspen are in decline throughout the interior western U.S. (Bartos and Campbell, 1998a). About 60 % of the

---

[1]This paper was written and prepared by U.S. Government employees on official time, and therefore is in the public domain and not subject to copyright. The use of tradenames is for informational purposes only and does not constitute endorsement by the USDA-FS.

aspen stands across the interior western U.S. have been lost since the mid-19th century (Bartos and Campbell, 1998b). Decline of aspen stands is attributed to natural succession (e.g., invasion of conifers)(Harniss 1981), fire suppression (Jones and Debyle, 1985b), and overbrowsing by domestic livestock and native ungulates (Kay, 1990).

Western aspen reproduce primarily by suckering from lateral roots and need disturbances to stimulate the suckering response (Schier 1981). In the past these disturbances included natural fires that killed mature aspen and insects and diseases that weakened old decadent stands prior to toppling by wind events. With the emphasis on suppression of nearly all human-caused and most natural fires throughout the twentieth century, one of the main forces of aspen regeneration has been largely removed from the landscape. Even when a disturbance such as fire or a wind event does stimulate aspen regeneration, overbrowsing of newly emerged aspen suckers by domestic livestock and native ungulates may quickly suppress regeneration. That coupled with conifer and sagebrush invasion of declining aspen stands has led to the precarious state of aspen in the interior western U.S.

Cryer and Murray (1992) proposed an ecological model of aspen to conifer succession that indicates that aspen regeneration may be inhibited in landscapes now dominated by conifers. This is because conifers may alter soil properties to suppress aspen regeneration. Western U.S. soils that developed under stable aspen are Mollisols. The rapid breakdown of aspen leaves added to the soil each year during leaf fall contributes to formation of the organic matter enriched mollic horizon (Jones and DeByle, 1985a; Cryer and Murray, 1992). Aspen stands usually have a significant grass-forb understory. The rapid breakdown of organic matter from this understory also contributes to the formation and maintenance of the mollic horizon.

In declining aspen stands, decreasing leaf fall can lead to a decrease in organic matter accumulation and eventually a decrease in mollic horizon thickness (Cryer and Murray, 1992). This may result in increased water percolation through the soil profile and formation of an albic horizon. Conifer invasion can accelerate this process. In the theory of ecological succession proposed by Cryer and Murray (1992), as conifers invade declining aspen stands, the mollic horizon thins and albic and argillic horizons form. As the mollic horizon decreases and the albic horizon increases, soil pH, organic matter, exchangeable bases, cation-exchange capacity (CEC), nutrient levels, and soil temperature all decrease. The lower pH and nutrient levels are believed to suppress aspen regeneration. Soils under mixed aspen/conifer stands are most often transition type soils with properties intermediate between Mollisols and Alfisols. In such cases, soil properties are mostly influenced by the vegetation that occupied the site for the longest period of time (Jones and DeByle, 1985a).

In a preliminary study of soil properties under aspen and mixed aspen/conifer stands in the Burnt Flat Analysis Area of the Fishlake NF, UT, Bartos and Amacher (1998) found that conifer invasion had not appreciably altered the nutrient status of these soils, although a slight reduction in soil pH was found under mixed aspen/conifer stands compared to pure aspen stands. These findings cast some doubt on whether conifer invasion of declining aspen stands has altered soil properties as much as feared. The findings also indicate that these soils should support aspen regeneration following treatment. Despite these findings, there remains considerable uncertainty about whether fire is needed to return nutrients to the soil to support aspen regrowth in areas where conifers have invaded. Where nutrient return is not needed, cutting alone may be sufficient to stimulate regeneration. In either case exclosures are needed to protect regenerating aspen from overbrowsing.

During June and July, 1996, an 8000-acre natural fire (the Pole Creek fire) occurred in the area of Betenson and Grindstone Flats on the Beaver Ranger District of the Fishlake National Forest, Utah. This moderate-intensity fire burned in mixed stands of older decadent aspen and invading conifers, primarily sub-alpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea englemannii*). After the fire, some cutting of fire-killed aspen and conifers was done to thin the stands and four exclosures were constructed by Utah Division of Wildlife Resources and Fishlake NF personnel to protect aspen suckers from browsing by domestic livestock and native ungulates. Two exclosures were built in the Grindstone Flat area and two in the nearby Betenson Flat area. This paper will present results of the effects of natural fire on soil N availability and mineralization during the first summer after the fire year.

OBJECTIVES

The objectives were to determine the effects of aspen to conifer succession and natural fire on soil N availability and mineralization/immobilization.

METHODS

We measured soil nitrogen mineralization/immobilization during the first summer (1997) following the Pole Creek fire using an ion exchange membrane (IEM) soil core incubation technique. The method was similar to that developed by DiStefano and Gholz (1986) except that we used ion exchange membranes (Ionics Inc., Watertown, MA) in place of ion exchange resin bags. The IEM's have identical ion exchange properties to the more familiar resin beads and have shown considerable promise for assessing soil nutrient availability (Cooperband and Logan, 1994).

The assembly for incubating the soil cores and IEM's is shown in Fig. 1. The soil core is enclosed in a 2-in diameter x 4-in long plastic liner (Forestry Suppliers, Jacskon, MS). End caps were used to hold the IEM's against each end of the soil core. Circular holes (1.5-in diameter) were cut in the center of the 2-in diameter end caps. Cation (CEM) and anion (AEM) exchange membranes were prepared by cutting 2-in diameter circles from the original membrane sheets and drilling nine evenly-spaced 1/8" holes in each circle to allow passage of water and air through the soil cores. The CEM's and AEM's were soaked five times in 1 M HCl and 1 M $NaHCO_3$, respectively, rinsed with deionized water, and sealed in zip-lock plastic bags for transport to the field. To protect the IEM's from abrasion and excessive desiccation, porous screens were prepared by cutting 2-in diameter circles from 114-um Spectra/Mesh polyethylene filter screens.

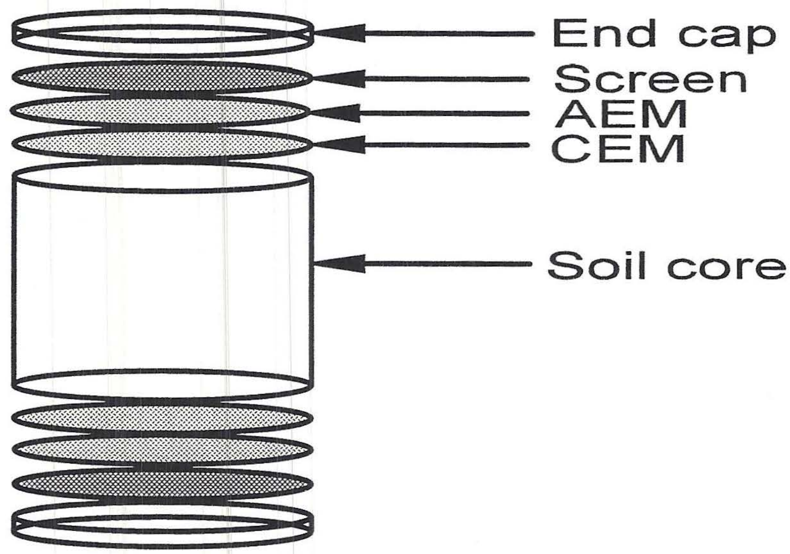

Fig. 1. Ion exchange membrane soil core configuration

We installed the IEM soil cores in the following manner. Leaf litter (unburned areas) or ash layer (buned areas) was first removed from the soil surface and set aside. The soil coring head with a plastic liner was driven into the soil using a slide hammer attachment (Forestry Suppliers, Jackson, MS) until flush with the top of the soil. The intact soil core was removed from the coring head, the ends of the core were trimmed, and the excess soil was returned to the soil hole. The end caps, plastic screens, and IEM's were assembled as shown in Fig. 1, the IEM soil core was placed in the hole with the top end up, and the core was covered with leaf litter or ash. Core locations were marked with flagged rebar stakes. An additional soil core was taken adjacent to the installed IEM soil core to determine initial soil exchangeable NH_4 and NO_3 levels. The initial cores were removed from the coring tool and placed in labeled zip-lock plastic bags. The cores were transported to the laboratory in a cooler and stored at < 4°C until extraction.

IEM soil cores were installed in three areas on Grindstone and Betenson Flats: four cores were installed in each of the four exclosures in the burned mixed aspen/conifer stands, four cores were installed in each of three unburned mixed aspen/conifer stands near the burned areas, and four cores were installed in each of two unburned aspen stands that regenerated as a result of a fire in 1958. Thus, there were 16 replicate cores in the burned areas, 12 in the unburned mixed aspen/conifer, and 8 in unburned pure aspen. Soil temperature in each area was monitored at a 4-in depth using Optic StowAway temperature loggers (Onset Computer Corp., Bourne, MA).

Two incubation periods were used: 6/25 to 7/22/97 (27 d) and 7/22 to 9/23/97 (63 d). At the end of each incubation period, the leaf litter or ash layer was removed from the tops of the cores and the cores were removed from the ground and placed in labeled zip-lock plastic bags. The cores were transported to the laboratory in a cooler and stored at < 4°C until extraction. New initial cores for the second incubation period were collected when the IEM soil cores from the first period were removed and the new IEM soil cores were installed.

The IEM soil cores were disassembled and top and bottom CEM-AEM pairs were rinsed with deionized water to removed soil particles and placed in separate labeled petri dishes. The soil cores were removed from the plastic liners, returned to the zip-lock bags, and mixed by kneading the bags. Each CEM-AEM pair was extracted with 100 mL of 2 M KCl in 250-mL wide-mouth plastic jars by shaking for 1 h on an orbital shaker at 150 rpm. The extracts were frozen until analysis.

Water content of a representative subsample of each soil core was determined gravimetrically at 105 °C. A representative field-moist subsample of each soil core equivalent to 10-g of oven-dry soil was extracted with 100 mL of 2 M KCl in a 250-mL wide-mouth plastic jars by shaking for 1 h on an orbital shaker at 150 rpm. The extracts were filtered through Whatman 40 filter paper and frozen until analysis. The 2 M KCl extract of IEM's and soil cores were analyzed for NH_4-N and NO_3-N by the automated phenate and Cd reduction methods, respectively using a LACHAT flow injection analysis system (Zellweger Analytics, Milwaukee, WI).

The remaining soil from each soil core was air-dried at room temperature and weighed. The total weight of each soil core was calculated by summing the oven-dry weight of the subsample used for determining water content, the oven-dry weight of the subsample used for determining extractable NH_4 and NO_3, and the air-dry weight of the remaining soil in each core. The air-dried soils were sieved through a 2-mm stainless steel sieve to remove coarse fragments. Organic matter content of the < 2-mm fraction was determined by loss on ignition (LOI) for 16 h at 450 °C of an oven-dried (105 °C) subsample. Total C and N contents of the < 2-mm fraction were determined by a LECO CHN analyzer. These soils do not contain free carbonates so total C is a measure of total organic C.

Amounts of NH_4-N and NO_3-N accumulated by the IEM's (ug/cm^2) were calculated by multiplying the NH_4 and NO_3 concentrations in the KCl extracts by the extract volume and dividing by the surface area of the IEM (20.27 cm^2). Rates of NH_4 or NO_3 accumulation by the cores (ug/cm^2/d) were calculated by dividing the accumulated amounts by the incubation time in days. The IEM's at the top of the soil core remove NH_4 and NO_3 in precipitation or leachate passing through the leaf litter or ash layers. The IEM's at the bottom of the soil core remove NH_4 and NO_3 leached from the soil core. Concentrations of NH_4 and NO_3 in the bottom IEM's on a soil weight basis for the entire soil core (mg/kg) were calculated by multiplying the amounts on the IEM's by the IEM surface area and dividing by the dry weight of the soil core.

Total NH_4 and NO_3 concentrations in the IEM soil cores were obtained by summing the concentrations of NH_4 or NO_3 in the soil core plus the amounts extracted from the bottom IEM's. Net ammonification is equal to total NH_4 in the IEM soil core - NH_4 in the initial soil core. Net nitrification is equal to total NO_3 in the IEM soil core - NO_3 in the initial soil core. Net mineralization (or immobilization) is equal to net ammonification + net nitrification. Net ammonification, nitrification, and mineralization rates were calculated by dividing the net amounts by the incubation time. An example of these calculations for one of the soil cores from the burn area is shown in Table 1.

Table 1. Net ammonification, nitrification, and mineralization/immobilization for an IEM soil core from the Betenson 1 exclosure (7/22-9/23/97).

Initial soil core NH_4-N, mg/kg	39.0
Final IEM soil core NH_4-N, mg/kg	107.7
Bottom CEM NH_4-N, mg/kg	0.3
Final total (bottom CEM + IEM soil core) NH_4-N, mg/kg	108.0
Net (final total - initial) NH_4-N, mg/kg	69.1
Net ammonification rate (net NH_4-N / incubation time), mg/kg/mo	32.9
Initial soil core NO_3-N, mg/kg	11.6
Final IEM soil core NO_3-N, mg/kg	2.0
Bottom AEM NO_3-N, mg/kg	10.0
Final total (bottom AEM + IEM soil core) NO_3-N, mg/kg	12.0
Net (final total - initial) NO_3-N, mg/kg	0.4
Net nitrification rate (net NO_3-N / incubation time), mg/kg/mo	0.2
Net mineralization/immobilization rate (net ammonification + net nitrification), mg/kg/mo	33.1

Because the data were non-normally distributed, a Kruskal-Wallis analysis of variance on ranks was run on each measured or derived N variable for each incubation with stand type as the factor and unburned aspen, unburned mixed aspen/conifer, and burned mixed aspen/conifer as levels within stand type (SigmaStat, ver. 2.0, SPSS Science, Chicago, IL). If a statistically significant difference among stand types was found ($p < 0.05$), a pairwise multiple comparisons test was conducted using Dunn's method to isolate which stand type was different from the others ($p < 0.05$).

RESULTS

The Pole Creek fire had an effect on the post-fire rates of accumulation of soil NH_4 and NO_3 by the top and bottom IEM's in the incubated soil cores (Fig. 2). Although there were significant differences in the rates of NH_4 and NO_3 accumulation by the IEM's between burned and unburned areas, there were no significant differences in accumulation rates between aspen and mixed aspen/conifer areas.

During the first incubation period (6-7/97), rates of NH_4 accumulation by top and bottom CEM's in burn area soil cores were significantly greater than those by soil core CEM's in unburned aspen and mixed aspen/conifer areas. However, differences among rates of NH_4 accumulation by both top and bottom CEM's in burned and unburned areas were not significant for the second incubation period (7-9/97). Furthermore, there was a higher rate of NH_4 accumulation by the CEM's during the shorter (27 d) first incubation than during the longer (63 d) second incubation.

During the first incubation period, NO_3 accumulation rates by the top AEM's in the burn area were not significantly different from those in the unburned areas. However, NO_3 accumulation rates by bottom AEM's were significantly greater in the burn area than in unburned areas during the first incubation period. During the second incubation period, NO_3 accumulation rates by both top and bottom AEM's were significantly greater in the burn area than in the unburned areas. Rates of NO_3 accumulation by the AEM's during the second incubation were much greater than those during the first incubation.

There was a shift in the relative distribution of inorganic N species in the burn area from the first to the second incubation period. More NH_4 was adsorbed by the CEM's during the first incubation, but more NO_3 was adsorbed by the AEM's during the second incubation. This shift in the relative distribution of inorganic N species from the first to the second incubation period is an indication of an increase in soil nitrification in the burn area as the summer progressed.

The distribution of NH_4 and NO_3 among the top and bottom IEM's tended to follow the relative mobility of the ions. Nitrate is more mobile than NH_4 so more NO_3 was found in the bottom than top AEM's in the burn area. On the other hand, more NH_4 was found in the top than bottom CEM's.

During the first incubation, significantly more NH_4 and NO_3 were extracted from initial and IEM soil cores and bottom IEM's from burned areas than those from unburned areas (Fig. 3). Net amounts of NH_4 and NO_3 in burned and unburned areas were not significantly different, however, because of higher levels of NH_4 and NO_3 in the initial soil cores from the burn area than from unburned areas. However, more of the IEM soil cores from the burn area tended to show a net decrease in NH_4 and a net increase in NO_3 than those from unburned areas even though the median values were not significantly different. Within unburned areas, no significant differences were found between aspen and mixed aspen/conifer stands for any of these variables.

During the second incubation, only the initial soil cores had a significant difference in extractable NH_4 between burned and unburned areas (Fig. 4). Extractable

NH_4 in IEM soil cores and bottom CEM's and net changes in extractable NH_4 amounts were not significantly different between burned and unburned areas during the second incubation. In contrast, significantly more NO_3 was extracted from initial and IEM soil cores and bottom AEM's in the burned area than those from unburned areas (Fig. 4). However, even though more IEM soil cores in the burn area had a larger net increase than decrease in NO_3, median net NO_3 levels were not significantly different between burned and unburned areas. No significant differences were found between aspen and mixed aspen/conifer stands for extractable soil or IEM NH_4 or NO_3.

There was a shift in the distribution of NO_3 between the soil and AEM's from the first to the second incubation. In the first incubation, most of the measured NO_3 was extracted from the soil cores. The bottom AEM's accounted for only small percentage of NO_3 in the IEM soil cores. In the second incubation, most of the measured NO_3 was extracted from the bottom AEM's indicating that NO_3 was being leached from the soil cores and was being accumulated by the bottom AEM's.

Net ammonification, nitrification, and mineralization/immobilizarion rates were not significantly different between burned and unburned areas or between aspen and mixed aspen/conifer stands (Fig. 5). Even though median rates were not significantly different, there tended to be a greater net loss of NH_4 from soil in the burn area during the early part of summer (first incubation) than later in the summer (second incubation). Net gains in soil NO_3 in the burn area tended to be greater during the latter part of summer than in the early part. The loss in NH_4 was largely balanced by the gain in NO_3 (nitrification), although some loss of NH_4 may have been from direct microbial utilization of this form of N

DISCUSSION

In undisturbed (unburned) aspen and mixed aspen/conifer soils, the various microbial mineralization and immobilization reactions tend to be at steady state. There is little free NH_4 and NO_3 in the soils (Figs. 2, 3, 4) because it is quickly utilized by microorganisms or taken up by plant roots. Thus, net mineralization/immobilization rates tend to be very low (Fig. 5) even though there is active ammonification, nitrification, and immobilization occurring in the soil.

Depending on duration and intensity, fire alters many soil properties including exerting a strong influence on soil microbial mineralization/immobilization processes (Schlesinger, 1997). Losses of gaseous and particulate N occur during combustion of leaf litter and soil organic matter, microbial populations and enzyme activity may decrease, but available nutrients are also returned to the soil by the residual ash (Schlesinger, 1997). Even though total soil N may be lower because of combustion, residual N in the ash is subjected to rapid mineralization and nitrification provided the fire is not too intense and microbial and enzyme populations can recover (Schlesinger, 1997).

Amacher and Bartos (1998) found that although total C and total N in 0-6-inch soil cores from the Last Chance and Betenson/Grindstone Flats burn areas were lower than those from unburned areas, the differences were not significant. In contrast, organic matter (LOI), total C, and total N in the 0-4-inch soil cores (this study) were higher in the Betenson/Grindstone Flats burn area than those from unburned areas (data not shown). Thus, combustion losses seem to be low. Although tree mortality from the fire was high, the Pole Creek fire left a dark colored ash, also an indication of incomplete combustion. Thus, the Pole Creek fire was probably of moderate intensity overall in terms of its impact to the soil.

The source of the high amounts of NH_4 accumulated by the CEM's and in the soil cores in the burn area the first summer after the fire may include NH_4 as a combustion product in the ash layer, release from mineral sources of NH_4, and rapid ammonification of combustion products. Much of this available NH_4 was probably carried over in the soil from the summer in which the fire occurred (6-7/96). Nitrification (microbial oxidation of NH_4 to NO_3) on the other hand occurred mostly in the first summer after the fire (6-9/97) because of the observed decrease in NH_4 and increase in NO_3 accumulated by the IEM's and soil cores from the first to the second incubation period. The IEM soil core incubation method provides a snapshot of soil N mineralization/immobilization for the incubation periods studied, but since we did not have soil cores in place immediately after the fire, we could not quantify soil N transformations in late summer and fall of the fire year (7-9/96).

Nitrification is influenced by many factors including temperature, moisture, and the substrates NH_4, O_2, and CO_2 (Stevenson, 1986). The high amounts of available NH_4 found in burn area soils provide a ready substrate for surviving or post-fire invading populations of nitrifying microorganisms. Summertime soil temperature ranges and means in the burn area were higher than in unburned areas because the relatively open canopy and dark colored ash served to trap heat (data not shown), thus helping to accelerate nitrification. There was a net decrease in mean soil core water content for all areas in the first incubation (25.1 % to 16.4 %), but a net increase in the second (16.4 % to 37.5 %). Although mean soil core water contents for both incubations from unburned mixed aspen/conifer areas (31.3 %) were higher than those from unburned aspen (23.5 %) or the burned mixed aspen/conifer areas (24.1 %), adequate soil moisture was available in the burn areas for nitrification to occur throughout the summer.

Although denitrification and more especially leaching can potentially remove much of the NO_3 produced by post-fire nitrification, the large amounts of soil NH_4 and NO_3 that were available during the growing season provide a ready source of mineral N for uptake by aspen suckers. A strong aspen suckering response was observed on Betenson and Grindstone Flats and in other burned areas on the Fishlake NF the first summer after the fires (Amacher and Bartos, 1998). We do not know how much NO_3 remaining in the burn area soils in the fall will be available for aspen uptake during subsequent summers so this study will continue for two more summers. A longer residence time of post-fire soil NO_3 provides more opportunity for regenerating aspen clones to exploit this source of N. Thus, available N from ash may be an important source of N to young aspen until N mineralization/immobilization in leaf litter can again be the dominant N cycling process in the aspen ecosystem.

ACKNOWLEDGMENTS

This work was supported by a USDA-CSREES Rangelands Special Grant. We thank Scott Walker of the Utah Division of Wildlife Resources and Bob Campbell, Dandy Pollack, and Doug Sorenson of the Fishlake NF for their assistance throughout the project.

REFERENCES

Amacher, M.C., and D.L. Bartos. 1998. Soil properties associated with aspen to conifer succession and aspen restoration treatments. p. 55. In: Abstracts, 51st Annual Meeting, Society for Range Management. 8-12 Feb., 1998. Guadalajara, Jalisco, Mexico.

Bartos, D.L., and M.C. Amacher. 1998. Soil properties associated with aspen to conifer succession. Rangelands 20:25-28.

Bartos, D.L., and R.B. Campbell, Jr. 1998a. Decline of quaking aspen in the interior west - examples from Utah. Rangelands 20:17-24.

Bartos, D.L., and R.B. Campbell, Jr. 1998b. Water depletion and other ecosystem values forfeited when conifer forests displace aspen communities. p. 427-434. In: D.F. Potts (ed.) Rangeland management and water resources. 27-29 May, 1998. Reno, NV. American Water Resources Assoc., Herndon, VA.

Cooperband, L.R., and T.J. Logan. 1994. Measuring in situ changes in labile soil phosphorus with anion-exchange membranes. Soil Sci. Soc. Am. J. 58:105-114.

Cryer, D.H., and J.E. Murray. 1992. Aspen regeneration and soils. Rangelands 14:223-226.

DiStefano, J.F., and H.L. Gholz. 1986. A proposed use of ion exchange resins to measure nitrogen mineralization and nitrification in intact soil cores. Commun. Soil Sci. Plant Anal. 17:989-998.

Harniss, R.O. 1981. Ecological succession in aspen and its consequences. p. 31-39. In: N.V. Debyle (ed.) Situation management of two intermountain species: aspen and coyotes. Vol. 1. Aspen. 23-24 April, 1981. Utah State Univ., Logan, UT.

Jones, J.R., and N.V. Debyle. 1985a. Soils. p. 65-70. In: N.V. Debyle and R.P. Winokur (eds.) Aspen: ecology and management in the western United States. GTR RM-119. Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.

Jones, J.R., and N.V. Debyle. 1985b. Fire. p. 77-81. In: N.V. Debyle and R.P. Winokur (eds.) Aspen: ecology and management in the western United States. GTR RM-119. Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.

Kay, C.E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. PhD Dissertation. Utah State Univ., Logan, UT.

Schier, G.A. 1981. Aspen regeneration. p. 15-21. In: N.V. Debyle (ed.) Situation management of two management species: aspen and coyotes. Vol. 1. Aspen. 23-24 April, 1981. Utah State Univ., Logan, UT.

Schlesinger, W.H. 1997. Biogeochemistry. An analysis of global change. 2nd ed. Academic Press, San Diego.

Stevenson, F.J. 1986. Cycles of soil. John Wiley & Sons, NY.

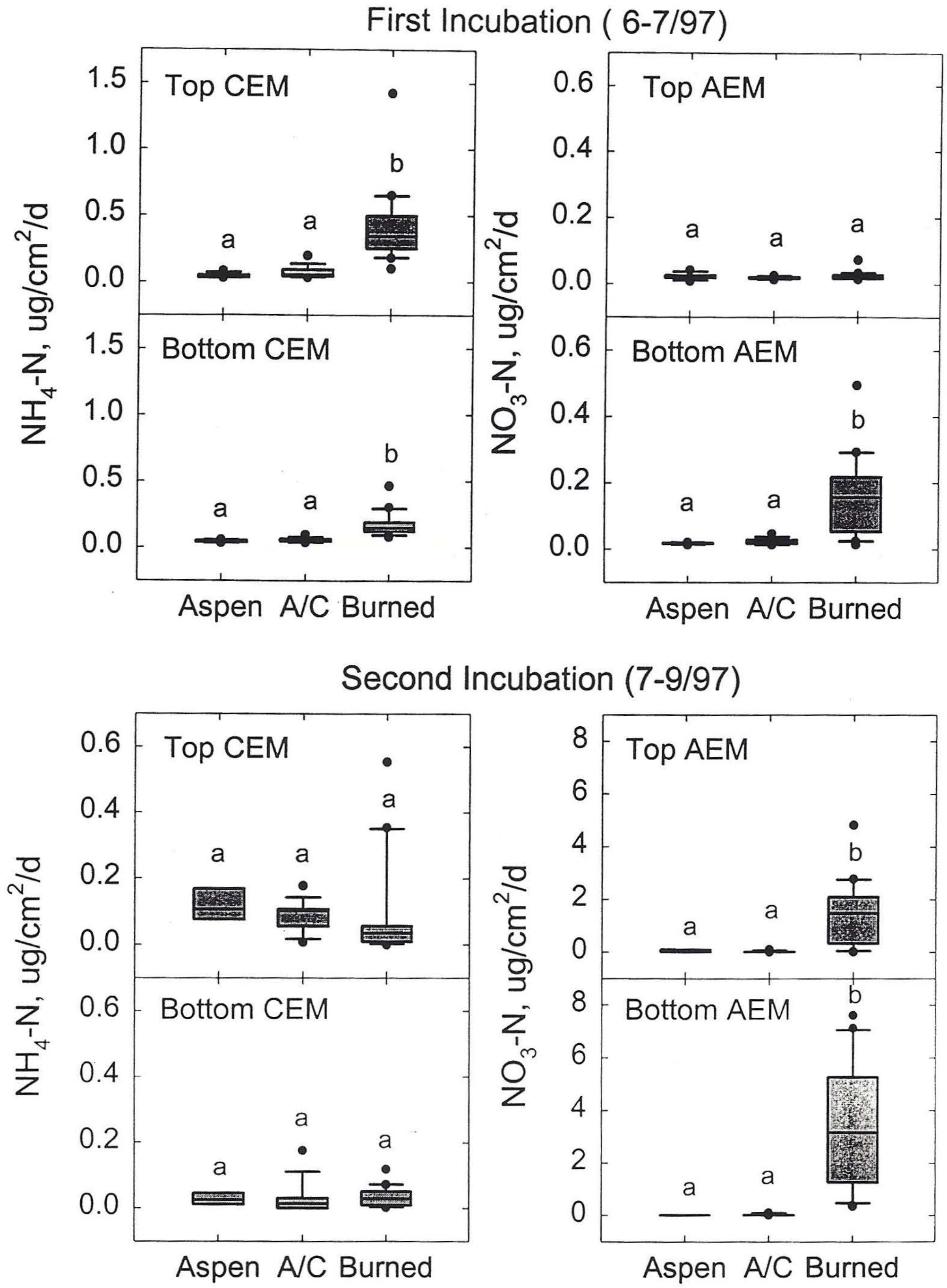

Fig. 2. Box plots of rates of NH_4 and NO_3 accumulation by cation (CEM) and anion (AEM) exchange membranes at the top and bottom of IEM soil cores for two incubation periods in unburned aspen, unburned mixed aspen/conifer (A/C), and burned mixed aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points. Different letters above the box plots indicate that the medians are significantly different ($p < 0.05$).

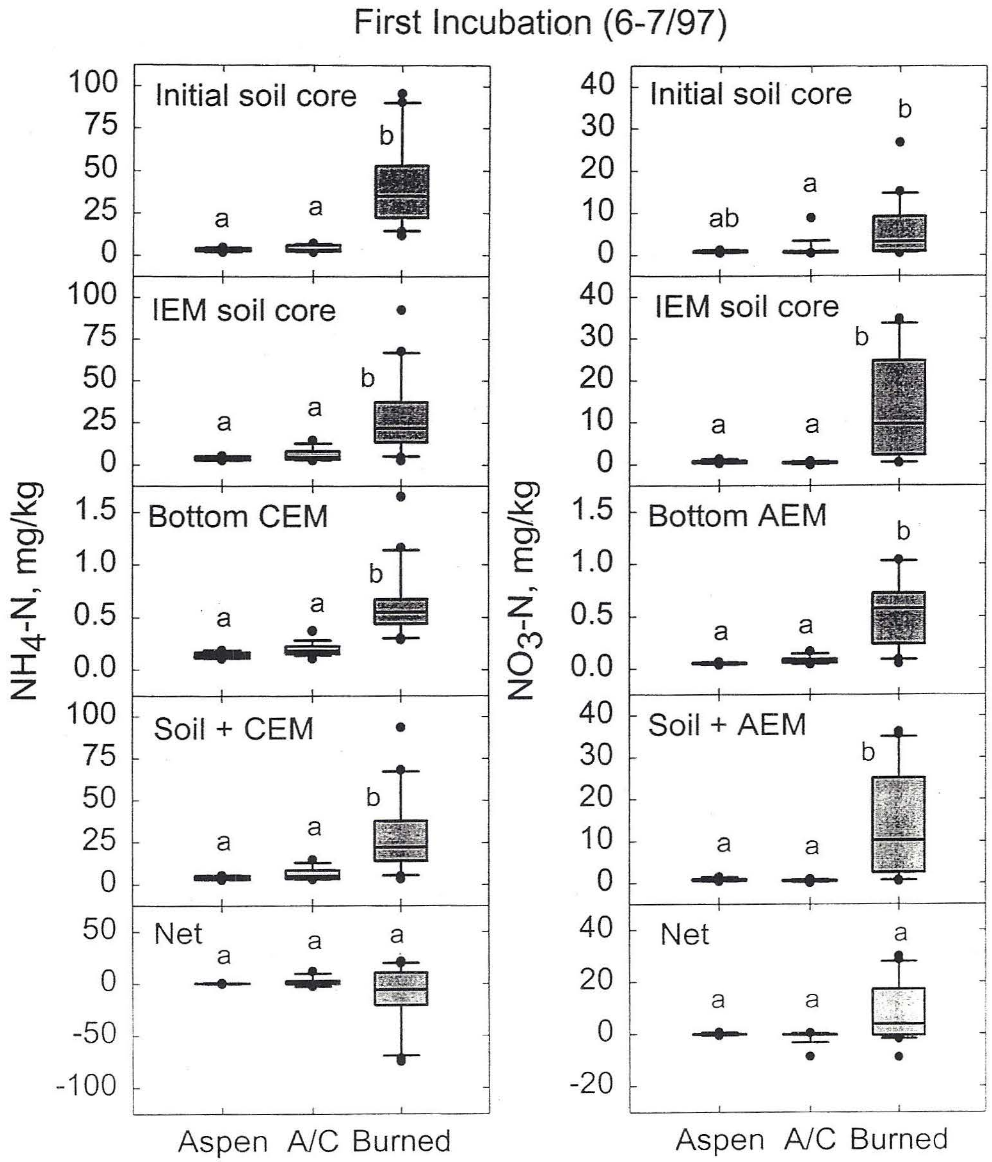

Fig. 3. Box plots of initial and final IEM soil core NH_4 and NO_3, bottom IEM NH_4 and NO_3, final total soil + IEM NH_4 and NO_3, and net NH_4 and NO_3 in IEM soil cores from the first incubation (6/25 - 7/22/97) in unburned aspen, unburned mixed aspen/conifer (A/C), and burned mixed aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points. Different letters above the box plots indicate that the medians are significantly different ($p < 0.05$).

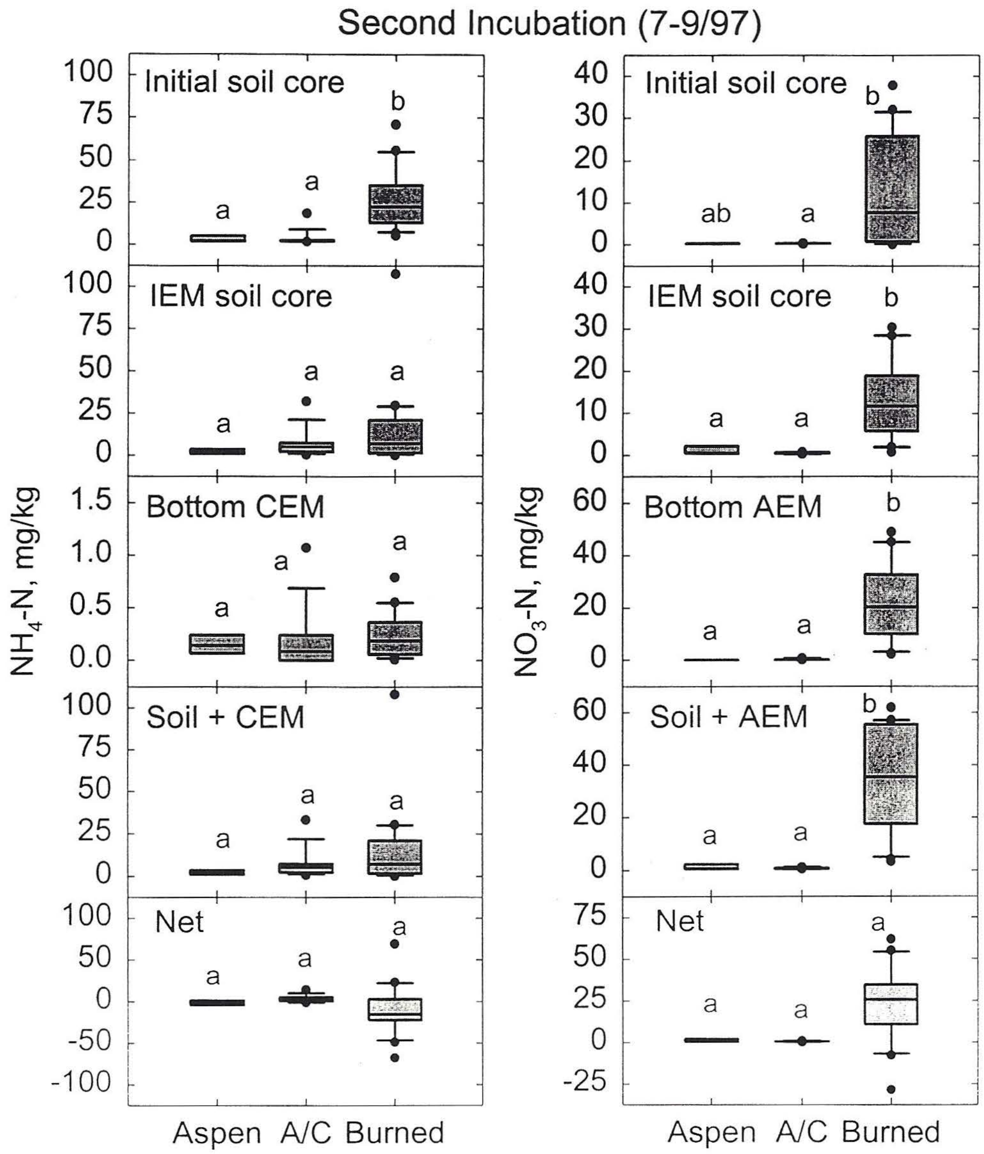

Fig. 4. Box plots of initial and final IEM soil core NH_4 and NO_3, bottom IEM NH_4 and NO_3, final total soil + IEM NH_4 and NO_3, and net NH_4 and NO_3 in IEM soil cores from the second incubation (7/22 - 9/23/97) in unburned aspen, unburned mixed aspen/conifer (A/C), and burned mixed aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points. Different letters above the box plots indicate that the medians are significantly different ($p < 0.05$).

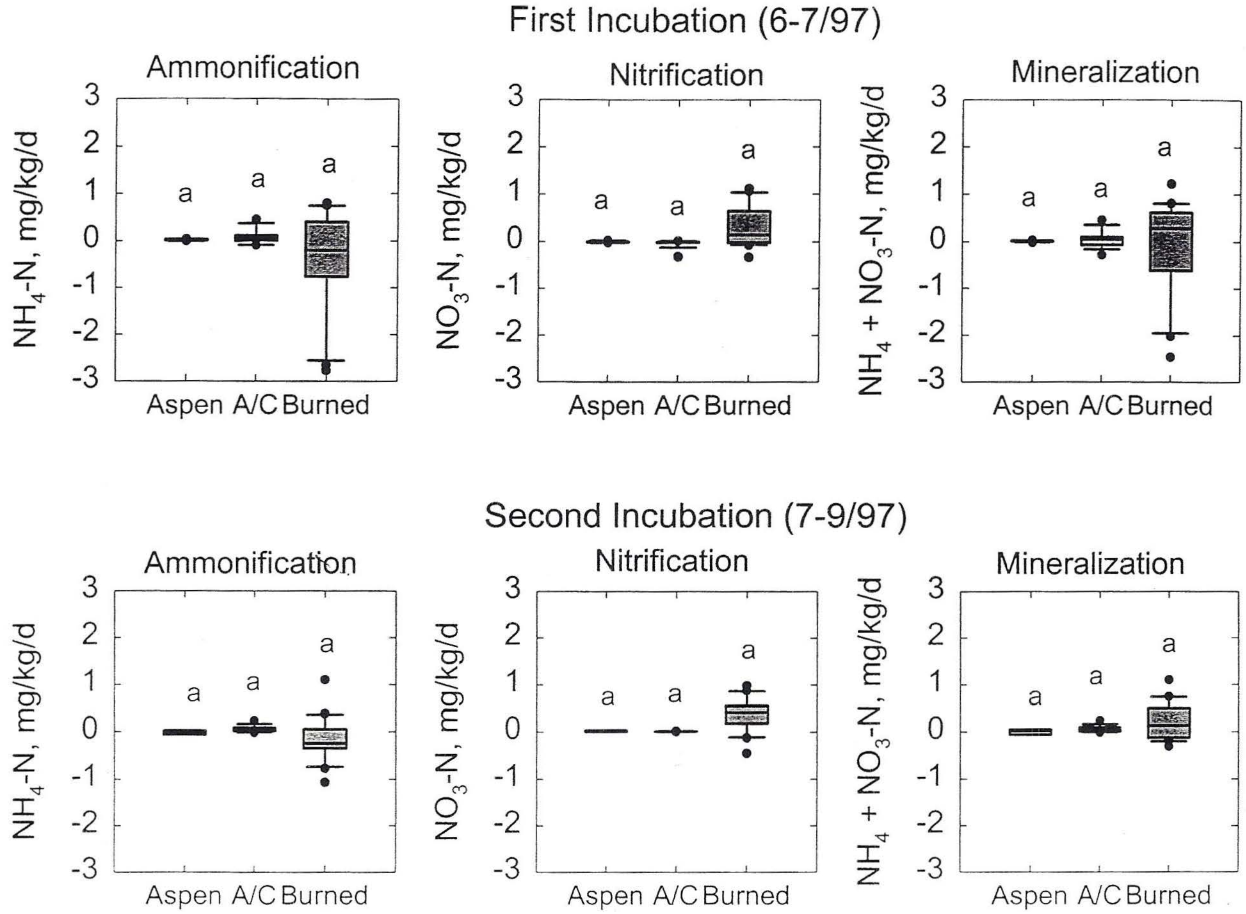

Fig. 5. Box plots of net ammonification, nitrification, and mineralization/immobilization rates in IEM soil cores for two incubation periods in unburned aspen, unburned mixed aspen/conifer (A/C), and burned mixed aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points. Different letters above the box plots indicate that the medians are significantly different ($p < 0.05$).