Patterns of nitrogen mineralization and nitrification in floodplain successional soils along the Tanana River, interior Alaska

K.M. KLINGENSMLTH
Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-0080, U.S.A.

AND

K. VAN CLEVE
Forest Soils Laboratory, University of Alaska Fairbanks, Fairbanks, AK 99775-0080, U.S.A.


Cold climatic conditions govern the productivity of taiga forests, yet within a successional sequence the microclimatic and biogeochemical variations also have a major effect on soil microbial activities, thus affecting plant productivity through nutrient availability. Nitrogen mineralization and nitrification were measured in primary-successional floodplain forests of interior Alaska. Forest floor and mineral soils from an early (open willow), middle (poplar–alder), and late (white spruce) successional stage were used. The effects of temperature, moisture, and NH₄⁺ were tested in the laboratory for each of the successional stages. Potential nitrification was estimated using the chlorate-inhibition technique. Surface mineral soils and white spruce forest floor had low to undetectable rates of nitrogen mineralization and nitrification (<1–3 μg N·g⁻¹·d⁻¹). The poplar–alder forest floor had the most pronounced seasonal patterns and the highest rates of net NH₄⁺ mineralization (<1–7 μg N·g⁻¹·d⁻¹) and net nitrification (<1–21 μg N·g⁻¹·d⁻¹). Temperature was limiting in early and mid-successional stages, and both moisture and temperature were limiting in the later white spruce stage. Ammonium additions increased nitrification only in the poplar–alder forest floor, suggesting the NH₄⁺ is not limiting in the other successional stages. The chlorate inhibition assay indicated that a considerable portion of the nitrification in the poplar–alder forest floor may be due to heterotrophic activity.


Les conditions climatiques froides gouvernent la productivité des forêts de la taïga bien qu’à l’intérieur d’une séquence successionale, les variations microclimatiques et biogéochimiques aient aussi un effet majeur sur les activités microbiologiques du sol, affectant ainsi la productivité des plantes à travers la disponibilité des nutriments. La minéralisation et la nitrification ont été mesurées dans des successions primaires de forêts de plaines de débordement de l’intérieur de l’Alaska. Les couvertures mortes et les sols minéraux d’un stage juvénile (saule ouvert), de mi-succession (peuplier–auprême) et de succession avancée (épinette blanche) ont été utilisés. Les effets de température, d’humidité et de NH₄⁺ ont été testés en laboratoire pour chaque stade successional. Le potentiel de nitrification était estimé avec la technique d’inhibition au chlorate. Les sols minéraux de surface et la couverture morte avaient des taux de minéralisation et de nitrification non détectables (<1–3 μg N·g⁻¹·jour⁻¹). La couverture morte de peuplier–auprême avait les patrons saisonniers les plus prononcés et les plus hauts taux de minéralisation nette de NH₄⁺ (<1–7 μg N·g⁻¹·jour⁻¹) et de nitrification nette (<1–21 μg N·g⁻¹·jour⁻¹). La température était limitante dans les stades juvéniles et de mi-succession tandis que l’humidité et la température étaient limitantes dans le stade avancé de l’épinette blanche. Les ajouts de NH₄⁺ ont augmenté la nitrification seulement dans la couverture morte de peuplier–auprême, suggérant que NH₄⁺ n’est pas limitant pour les autres stades de succession. L’essai d’inhibition au chlorate a indiqué qu’une portion considérable de la nitrification dans la couverture morte peuplier–auprême peut être due à l’activité hétérotrophe.

[Introducción]

**Introduction**

The taiga biome is typically characterized by moderate to low primary productivity due to the overall effects of a cold climate. Yet within the central Alaskan taiga, there are two major landscape patterns that support a diverse range of microclimatic conditions (Slaugh and Vierceck 1986). These are the broad river floodplains and the rolling hills of the uplands. Vegetation development in both landscapes usually leads to a forested white spruce (Picea glauca (Moench) Voss) stand, although the individual pathways of floodplain and upland succession are distinctly different. Temperature and moisture regimes are directly influenced by aspect, slope, and elevation; the more productive south-facing slopes are the warmest and driest sites, while the less productive north-facing slopes and lowlands are the coolest and wettest (Slaugh and Vierceck 1986). Early to mid-successional floodplain soils tend to be warm and well drained and are also identified as the most productive (Vierceck et al. 1993, this issue).

Forest development on the floodplains is recognized as a primary succession, with little or no organic matter present in the recently deposited sediment of the earliest stages (Van Cleve et al. 1993a, this issue). This is in marked contrast with the early stages of the upland secondary successional development; here fire, the major disturbance, releases nutrients bound in trees and forest floor biomass (Van Cleve and Yarie 1986). As the process of plant establishment begins on the bare alluvial bars of the floodplain, microenvironments also develop and in turn regulate soil temperature and moisture conditions. Low soil temperatures are a dominant factor influencing taiga nutrient cycling, although soil moisture can also be an important factor (Van Cleve and Yarie 1986).

In undisturbed forested ecosystems, the mineralization of N-containing organic material is the principal source of available N for plant use. Although generalizations regarding patterns of N mineralization and nitrification within successional chronosequences have been made (Rice and Pancholey 1972; Robertson and Vitousek 1981; Vitousek et al. 1989), no one...
mechanism can explain the variability observed within individual successional seres. The dynamics of a successional stage is dependent on the biogeochemical and physical environment of that particular stage; thus it is important to understand the significance of various controls within stages. The object of the present study was to examine patterns of N mineralization and nitrification within an early, middle, and late successional stage along the Tanana River of interior Alaska and to evaluate the effects of temperature, moisture, and NH₄⁺ availability on these N-cycling processes.

**Study area**

The study area is adjacent to the Bonanza Creek Experimental Forest, approximately 20 km southwest of Fairbanks. Three of the 12 Tanana River floodplain successional stages, described in detail by Vierreck et al. (1993, this issue), were chosen to represent early, middle, and late successions. These are as follows: III-A-C, a 5-year-old open willow (Salix spp.) stand; V-A-C, a 27-year-old poplar–alder stand (open balsam poplar (Populus balsamifera L.) with a dense thinleaf alder (Alnus tenuifolia Nutt.) understory); and VIII-A-C, a 165-year-old white spruce stand. Ages of each of the stands are estimated from date of sandbar formation. Within each of the three stages a 50 × 50 m plot was established.

**Materials and methods**

**Laboratory and field methods**

Forest floors and mineral soils were sampled and tested independently. The open willow stand did not have a forest floor, thus only mineral soil was sampled. At each mineralization sampling, eight soil cores were collected along a randomly chosen transect using a 15 cm diameter soil corer to an approximate depth of 12–15 cm. Net NH₄⁺ mineralization and nitrification were measured using undisturbed soil core sections incubated in polyethylene bags (Eno 1960). Each core was vertically sliced into two sections; one-half were designated T0 and the other half were designated T1. The surface forest floor was left as a distinct layer, while the mineral soil was further divided into three horizontal layers, each approximately 3 cm thick. This was done to evaluate any mineralization gradients. Each core section was then placed, with as little disturbance as possible, into a 0.4-mil (1 mil = 25.4 μm) polyethylene bag and tied with a knot. The samples designated T0 were brought to the laboratory and frozen that same day, until further chemical analyses could be performed. The T1 soil core sections were placed in previously made core holes (the same size as the half cores), at their respective depth of sampling, for the duration of the incubation period.

During the first year of the study (1985) incubation periods were approximately 1 month, whereas second-year incubation periods were 14 days. At the end of each incubation period, T1 samples were collected, brought to the laboratory, and frozen until further analysis could be completed. A new set of soil cores was processed in a similar fashion, at the end of each incubation period. This routine was repeated throughout both field seasons, from May until September, with September’s soil sample incubated from September to the following May.

In the laboratory, individual core sections were mixed, large roots were removed, and a 15-g fresh-weight subsample was extracted with 75 mL of 2 M KCl. Extracts were shaken for 1 h and filtered with glass fiber filters. Filters were analyzed for NH₄⁺, using a phenol hypochlorite assay, and NO₃⁻, using a Griess–Bloysvay method in combination with a Cd reducing column. A modified Technicon AA II system (Technicon Institute 1973) was used for all chemical analyses. Dry weights were determined by oven-drying for 48 h at 65°C for forest floors and at 105°C for mineral soils, Net NH₄⁺ mineralization and net nitrification were calculated as the difference between initial (T0) and final (T1) NH₄⁺ and NO₃⁻ concentrations. Cumulative rates of net N mineralization (net nitrification plus net NH₄⁺ mineralization) were used as an estimate of an average rate of N mineralization. Mineralization and nitrification rates are expressed on a gram dry soil basis for each of the three stands.

Soil for the combined temperature and moisture experiment and the potential nitrification experiment was from composites of soil cores (10 from each site with forest floor and mineral soil collected) collected in early September. Quadruplicate subsamples from each site’s composites were collected and mineral soil were 100 g fresh weight for all mineral soils, 20 g fresh weight for the alder forest floor, and 50 g fresh weight for the white spruce forest floor. Two moisture regimes were used to test for the effects of moisture (the moisture content at the time of sampling, field moisture, and the soil water holding capacity of each soil), and four temperatures (5, 10, 20, and 30°C) were used to test for the effects of temperature. Soil water holding capacity had been previously determined by saturating soils samples with distilled water for 24 h with subsequent drainage for 24 h. It had been determined that all significant drainage occurred within the first 24 h. Field soil moisture and temperatures were measured using a Campbell data logger fitted with soil gypsum blocks and temperature thermists. Soils samples were placed in plastic 250-mL beakers, covered with a sheet of 0.4-mil polyethylene, and incubated for 20 d at each moisture and temperature combination. At the end of the incubation period a 15-g fresh weight subsample was removed from each container and analyzed for NH₄⁺ and NO₃⁻, as described.

Potential nitrification was measured using the chlorate-inhibition assay of Belser and Mays (1980). Quadruplicate subsamples, 15 g fresh weight, were placed in erlenmeyer flasks with the addition of one of four treatments: A, control (50 mL distilled water); B, 15 μg NH₄⁺-N g soil⁻¹; C, 0.5 mL of 1 M NaClO; D, 15 μg NH₄⁺-N g soil⁻¹ and 0.5 mL of 1 M NaClO. All additions were made with 50 mL of distilled water. Samples were incubated for 24 h on a rotary shaker at room temperature. Each sample was then analyzed for NH₄⁺, NO₃⁻, and NO₂⁻ using the above-described methods.

Analyses of variance (Zar 1984) were performed utilizing the Statistical Analysis System (SAS Institute Inc. 1985). Tukey’s multiple comparison test (Zar 1984; SAS Institute Inc. 1985) was used to detect significant differences in estimates of N processes. Ammonium, nitrite, and nitrate were treated separately for each statistical test.

**Results**

Site properties and soil characteristics are described in detail by Vierreck et al. (1993, this issue). Field moisture and temperatures for the 1986 field season are shown in Figs. 1 and 2. A brief flood occurred on the lower terraced, open willow stand in mid-July, causing a gap in the continuous temperature and moisture data collection. Although this flood did not reach the higher elevated poplar–alder stand or the white spruce stand, it did increase the soil moisture at 10 cm depth.

At each of the three sites, among the three 3-cm mineral soil layers there were no significant differences of NH₄⁺ or NO₃⁻ concentrations. The greatest NH₄⁺ concentrations were found in the forest floor layers, with the poplar–alder forest floor exhibiting the highest concentrations of both NH₄⁺ and NO₃⁻. Low to undetectable amounts of NO₃⁻ were observed in the white spruce forest floor and mineral soil samples.

Seasonal patterns of net NH₄⁺ mineralization and net nitrification are shown in Fig. 3. The poplar–alder forest floor had the most seasonality and the highest rates of N mineralization, both NH₄⁺ mineralization and nitrification. Greatest net NH₄⁺ mineralization and in situ NH₄⁺ concentrations were observed in early and midsummer, whereas plant growth N concentrations and in situ NO₃⁻ concentrations were observed in late summer. Net nitrification was low to undetectable in the white spruce forest floor and all mineral soils. All forest floors and mineral soils had negative N min-
Fig. 1. Soil temperatures of the soil surface and at depths of 5 and 10 cm in the open willow, poplar–alder, and white spruce stands. Data for the open willow stand are discontinuous because of a flood.

Fig. 2. Soil moisture at depths of 5 and 10 cm from the exposed surface of the open willow, poplar–alder, and white spruce stands. Data for the open willow stand are discontinuous because of a flood.

eralization rates, possibly resulting from immobilization of \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) and (or) denitrification. Seasonal variation of net \( \text{NH}_4^+ \) mineralization was not pronounced in the white spruce forest floor or in any of the mineral soils. Analysis of variance tests indicated that within the mineral soil layers of the open willow, poplar–alder, and white spruce there was no significant depth variation of the mineralization rates from the three 3-cm horizontal layers sampled. Therefore, mineral soil net \( \text{NH}_4^+ \) mineralization and net nitrification estimates at each site are the pooled means of the three mineral soil layers of each core. Although the lowest N mineralization rates were observed in the early and late successional stage mineral soils, when calculated on an area basis, rates of net N mineralization were similar for both the poplar–alder forest floor and the poplar–alder mineral soil. On an area basis, nitrification was greatest in the poplar–alder mineral soil, due in part to the high bulk density of the mineral soil relative to the forest floor.

In controlled temperature and moisture experiments, among forest floors and mineral soils, mineralization rates were similar at the two moisture regimes; the only exception was in the white spruce forest floor and mineral soil samples at the higher temperatures (Fig. 4). The soil water holding capacity and field moisture content were significantly different (Table 1) for each of the forest floors and mineral soils. Although differences in the two moisture regimes were not consistent for all the soils tested, there was at least a 30% increase from field moisture to soil water holding capacity. Mineralization rates of the poplar–alder and white spruce forest floors were significantly different from each other and all mineral soils. The mineral soils had similarly low N mineralization at 5, 10, and 20°C, increasing only at 30°C. Only the white spruce forest floor at water holding capacity showed higher net nitrification rates at 23 than at 30°C. There were no significant moisture effects in the poplar–alder stand or in the open willow stand.
Nitrification potential was low to undetectable in the white spruce forest floor and in all mineral soils, even with the addition of ammonium. The poplar-alder forest floor had the greatest nitrification potential (Fig. 5). Ammonium additions in the poplar-alder forest floor samples increased nitrate and nitrite concentrations, both in the presence and absence of chloride. In NH₄⁺-amended samples, there was a greater increase in nitrite production with the chloride addition than without.

Discussion

Nitrogen mineralization rates in mineral soils and forest floors of the early and late successional stages were low, relative to the midstage, poplar-alder stand. When averaged, mineralization rates in the three successional stages of this study (<1 to 3 μg N g⁻¹ d⁻¹) are similar to those from other studies that measured N mineralization using incubation periods of 1 month or longer, i.e., <1-4 μg N g⁻¹ d⁻¹ in temperate forests (Christensen and MacAller 1985; Nadelhoffer et al. 1985; Raison et al. 1987) and 4 μg N g⁻¹ d⁻¹ in a tropical forest (Robertson 1984) but are not as high as those measured in agricultural soils, i.e., 1-34 μg N g⁻¹ d⁻¹ (Myrold and Tiedje 1986). On a biweekly scale, the poplar-alder forest floor had a greater net N mineralization range (<1-21 μg N g⁻¹ d⁻¹). The mid-August sampling of the poplar-alder forest floor had the greatest N mineralization rate, the net portion attributed solely to nitrification. Also similar is the range of rates that Van Cleve et al. (1993b, this issue) measured (<1-16 μg N g⁻¹ d⁻¹) over a 3-year period (the first 2 years being the same time period as the present study) at the same sites, but using month-long incubations and disturbed soil samples. Both studies estimated the highest rates of N mineralization in the poplar-alder forest floor and relatively lower rates and little nitrification in the mineral soils. Although both studies come to the same overall conclusions, comparison of the individual years indicates large differences in rates and seasonal fluctuations. These variations are most likely due to the use of different techniques. The use of undisturbed soil samples and shorter incubations can provide increased sensitivity by allowing samples to follow more closely the physical and chemical regimes of the site, while also decreasing the “greenhouse effect” of bag incubations.

High negative rates of net nitrification and net NH₄⁺ mineralization were also observed in the poplar-alder forest floor. While negative rates may be a byproduct of the methods used to measure mineralization, it could also suggest increases in microbial N immobilization and (or) denitrification activity.

Observations of the controlled laboratory experiments indicate the limitations of cold temperatures on N mineralization throughout the successional sequence. When temperatures were higher than those usually occurring in the field (e.g., 20 and 30°C for the poplar-alder and white spruce stands, and 30°C for the open willow stand), N mineralization did increase. Nitrogen mineralization increased dramatically at 30°C in the alder forest floor, whereas increases within mineral soils were relatively small. The combined effects of temperature and moisture increased N mineralization only in the white spruce stand, a later floodplain successional stage that has low soil temperatures and low moisture contents for most of the field season. The inability to detect net nitrification at 30°C within white spruce forest floor samples may have resulted from increased denitrification and (or) immobilization activity. The large increase in white spruce forest floor nitrification at 20°C cannot be fully explained by processes controlling its occurrence at 30°C, but more likely by the heterogeneous characteristic of soil organic matter clumps in the forest floor. Field soil temperatures and moisture fluctuations are greatest in the surface soil of the early, open willow stand. Because of the low temperature elevation of early successional stage alluvial bars, river flooding occurs more often, as did occur in mid-July 1986. Even though the flood did not reach the middle and later stage terraces, the

---

**Table 1. September 1986 field moisture content and soil water holding capacity**

<table>
<thead>
<tr>
<th>Site</th>
<th>Field moisture content (%)</th>
<th>Soil water holding capacity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open willow mineral soil</td>
<td>26±5</td>
<td>34±6</td>
</tr>
<tr>
<td>Poplar-alder mineral soil</td>
<td>33±5</td>
<td>58±8</td>
</tr>
<tr>
<td>Poplar-alder forest floor</td>
<td>148±34</td>
<td>339±57</td>
</tr>
<tr>
<td>White spruce mineral soil</td>
<td>5±2</td>
<td>40±4</td>
</tr>
<tr>
<td>White spruce forest floor</td>
<td>54±7</td>
<td>243±42</td>
</tr>
</tbody>
</table>

Note: Data are presented as means ± SE.
increase in the water table did affect the soil moisture in the poplar–alder and white spruce mineral soil. There was no measurable nitrification activity in the mineral soils of the three successional stages or in the white spruce forest floor with either the ammonium additions or the chlorate-inhibition assay. This suggests a low nitrification potential that is not limited by NH$_4^+$ availability alone. Although the poplar–alder forest floor did have increases of both nitrate and nitrite with these assays, interpretation of the results is difficult. The chlorate-inhibition assay has been reported to be highly sensitive (Groppman 1987), yet complex when attempting to explain the results. Incomplete blockage of NO$_2^-$ oxidation by chlorate (Belser and Mays 1980; Adams 1986), the inhibition of ammonium oxidation by microbial chlorate reduction to chloric (Hynes and Knowles 1983), and (or) the occurrence of heterotrophic nitrification (Schimel et al. 1984) are thought to be some of the difficulties associated with the assay. Inhibition of NH$_4^+$ oxidation was not evident in the poplar–alder forest floor, as both nitrate and nitrite concentrations increased in the presence and absence of chlorate. Incomplete blockage may have been responsible for nitrate accumulation, as significant increases in nitrate did occur in both treatments that included chlorate. Fungal nitrification has been acknowledged since 1986, yet the extent and importance of heterotrophic nitrification in the environment has not been adequately addressed. Heterotrophic nitrification has been reported as a source of NO$_3^-$ in strongly acidic soils, i.e., pH 4.5 (Van de Dijk and Troelstra 1980; Adams 1986), and in a mature conifer forest (Schimel et al. 1984). If one assumes that nitrate production by heterotrophic nitrifiers is not affected by chlorate and nitrate production in the presence of chlorate is not due to incomplete blockage, then the results of this assay indicate that a significant portion of the nitrification potential in the alder forest floor is due to heterotrophic nitrification. These observations point out a need to further clarify the possible role of heterotrophic nitrification in the poplar–alder stand.

Our ability to understand controls over ecosystem functions has become increasingly important because of the complexities of global change. Of the predicted changes, temperature is receiving the most attention, with a considerable amount of debate on expected degrees change per unit time. Regardless of the actual outcome, climatic changes in temperature, moisture, wind, and atmospheric chemistry will have a profound effect on biotic systems, which includes increasing decomposition of the large pools of soil organic matter in northern forests (Anderson 1991). The results presented in this study suggest that N mineralization will be affected by temperature increases of 10–20°C, increases that are not expected to occur for decades, yet slight changes in moisture regimes could have an immediate effect on mineralization rates in later successional, white spruce forests.

Acknowledgments
We thank L. Oliver, R. Erikson, J. Levison, and J. Roth for field and technical assistance. This research was supported by the following National Science Foundation grants to the University of Alaska Fairbanks: BSR-8405269 dealing with salt-affected soils and BSR-8702629 supporting the taiga Long-Term Ecological Research Program. The research was also supported by the USDA Forest Service Pacific Northwest Research Station, the McIntire–Stennis Forestry Research Program, the State of Alaska, the University of Alaska Fairbanks Agriculture and Forestry Experiment Station, and by a University of Alaska Graduate Resource Fellowship.
Technicon Institute. 1973. Industrial method 100-70W and 325-74W. Technicon Institute, Tarrytown, N.Y.