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Variation with slope aspect in effects of temperature on nitrogen mineralization and nitrification in mineral soil of mixed hardwood forests

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Abstract: This study examined the effects of temperature on soil nitrogen (N) dynamics and variation with slope aspect (northeast (NE) versus southwest (SW)) at two forested sites in West Virginia — Beech Fork Lake (BFL) and Fernow Experimental Forest (FEF) — with similar soil and overstory characteristics but with different latitudes and elevations. Previous work on mineral soil from both sites had shown sharp differences in microbial communities between SW slopes and NE slopes. Mineral soil was sampled from three and eight plots per aspect at FEF and BFL, respectively. Inorganic N was extracted from samples, which were then divided into polyethylene bags for 7-day incubations at 4 °C, 15 °C, 25 °C, and 35 °C. Following incubation, soils were extracted and analyzed for inorganic N. Net N mineralization varied significantly between aspects and temperatures but did not vary between sites; net nitrification varied significantly between aspects, temperatures, and sites. Net N mineralization increased with incubation temperature at all aspects and sites. Net nitrification rates increased with incubation temperature for BFL soils; however, maximum net nitrification rates occurred at 20–25 °C for FEF soils. Net nitrification was essentially undetectable for SW soils at either site. Results underline the complexities of the N cycle in temperate forest ecosystems, representing challenges in predicting alterations in soil N dynamics under conditions of global climate change.

Key words: nitrogen mineralization, nitrification, forest ecology, global warming, temperate forests.

Résumé : Cette étude s'intéresse aux effets de la température sur la dynamique de l'azote (N) dans le sol et sa variation selon l'exposition de la pente (nord-est (NE) vs sud-ouest (SO)) dans deux stations forestières en Virginie-Occidentale : lac Beech Fork (LBF) et forêt expérimentale de Fernow (FEF), dont les caractéristiques du sol et de l'étage dominant sont similaires mais dont la latitude et l'altitude sont très différentes. Des travaux antérieurs réalisés à chaque endroit ont montré qu'il y avait de nettes différences dans les communautés microbiennes du sol minéral entre les pentes SO et NE. Le sol minéral a été échantillonné dans respectivement trois et huit placettes échantillons par exposition à la FEF et au LBF. L'azote inorganique a été extrait des échantillons qui ont ensuite été divisés et placés dans des sacs de polyéthylène pour être incubés pendant 7 jours à 4 °C, 15 °C, 25 °C et 35 °C. Les sols ont été extraits après l'incubation et analysés pour la présence de N inorganique. La minéralisation nette de N variait de façon significative selon l'orientation et la température mais pas selon la station; la nitrification nette variait de façon significative selon l'orientation, la température et la station. La minéralisation nette augmentait avec la température d'incubation peu importe l'orientation ou la station. La nitrification nette augmentait avec la température d'incubation dans les sols du LBF, mais les taux maximum ont été observés à 20–25 °C à la FEF. La nitrification nette était significativement reliée à la minéralisation nette de N dans les sols orientés NE dans les deux stations peu importe la température d'incubation, sauf 35 °C. La nitrification nette était pratiquement indétectable dans les sols orientés NO dans les deux stations. Les résultats mettent en évidence la complexité du cycle de N dans les écosystèmes de forêt tempérée, ce qui représente un défi pour prédire les modifications de la dynamique de N dans le sol dans le contexte du changement mondial. [Traduit par la Rédaction]

Mots-clés : minéralisation de l'azote, nitrification, écologie forestière, réchauffement climatique, forêts tempérées.

Introduction

Predicted increases in global temperatures have important implications for future changes in the dynamics of soil nitrogen (N) in many regions, especially those that are dominated by temperate forests (Rustad et al. 2001; Booth et al. 2005). Cycling of soil N is facilitated in large part by microbial communities, including prokaryotes, protists, and fungi, with one prominent process — nitrification — being carried out by bacteria (McArthur 2006). Soil microbes display a high level of sensitivity to variation in temperature, with microbial activity generally increasing with increasing temperatures throughout typical ambient ranges (Schütt et al. 2014). At high temperatures, microbial activity can be greatly inhibited, especially for nitrifying bacteria, which generally display temperature optima (Stark 1996).

Forests of montane regions exhibit topographic complexity relevant to the response of soil N dynamics to temperature because of the widely contrasting microclimates created by complex terrain, including elevation and slope aspect. It is widely recognized that north- versus south-facing slopes experience notable differences in net solar radiation (R_n), which drives a number of other factors important in forest ecosystems such as soil weathering and ambient air and soil temperatures (Bennie et al. 2008; Beaudette and O'Geen 2009).

Forests throughout most of the Appalachia, especially those comprising the mixed mesophytic forest region (MMF) (Braun 1950; Dyer 2006), are well recognized for their high plant species richness in both the woody overstory and the herbaceous layer

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Table 1. Study site characteristics (mean ± 1 standard error) on contrasting slope aspects of Beech Fork Lake (BFL) and Fernow Experimental Forest (FEF).

Site and aspect	Elev. (m)	BA ($m^2 \cdot ha^{-1}$)	OM (%)	pH	*F*:*B*	SI	NH_4^+ (μg N·(g soil)$^{-1}$)	NO_3^- (μg N·(g soil)$^{-1}$)
BFL								
Northeast	213	28.3±2.5	12.5±1.0	5.35±0.22	0.20±0.01	0.51±0.04	2.3±0.2	2.1±0.2
Southwest	221	21.6±2.4	8.3±0.9	4.44±0.22	0.27±0.01	0.88±0.15	2.6±0.2	0.2±0.1
FEF								
Northeast	833	39.3±2.6	13.7±0.6	5.20±0.08	0.12±0.06	0.88±0.04	6.6±1.5	9.1±1.1
Southwest	808	33.3±1.4	14.1±1.1	4.85±0.14	0.24±0.12	1.97±0.44	5.4±1.2	0.7±0.1

Note: Data were summarized from Gilliam et al. (2014) and Gilliam et al. (2011) for BFL and FEF, respectively. Variables included are elevation (Elev.), overstory basal area (BA), soil organic matter (OM), microbial fungi to bacteria ratio (*F*:*B*), and microbial stress index (SI; the ratio of fatty acid methyl esters cy19 to 18:1n7c; see Kaur et al. (2005)); NH_4^+ and NO_3^- represent soil-extractable NH_4 and NO_3, respectively. For BFL, *N* = 8 for each aspect; for FEF, *N* = 3 for each aspect.

communities. Indeed, West Virginia is notable for having the highest relative cover of MMF in the United State (US), with ~75% of the state forested (ranking third in US forest cover) and virtually all of it being MMF (Dyer 2006). Previous work at two MMF sites varying in elevation and latitude in West Virginia found sharp, aspect-related contrasts in several mineral soil parameters, including soil microbial groups and in situ rates of net N mineralization and net nitrification. Working at the Fernow Experimental Forest (FEF; higher elevation and latitude), Gilliam et al. (2011) found the predominance of fungal microbial markers and indicators of higher microbial stress in soils of the southwestern (SW) aspect versus soils of the northeastern (NE) aspect, along with lower extractable NH_4^+ and a virtual absence of extractable NO_3^- in soils of the SW aspect (Table 1). Working at the Beech Fork Lake State Wildlife Area (BFL; lower elevation and latitude), Gilliam et al. (2014) found similar contrasts when comparing forest stands on SW aspects versus NE aspects (Table 1). Further evidence (e.g., soil pH) indicated that for both sites, SW soils were more highly weathered than NE soils and that observed aspect-related differences in soils arose largely from differential weathering of soils, i.e., higher weathering in SW soils that receive higher net R_n, which drives weathering processes.

This study examined the effects of temperature on net N mineralization and net nitrification and how these effects may vary with slope aspect. Further emphasis was placed on comparing these relationships between two forested sites with similar soil and overstory characteristics but different latitudes and elevations. We hypothesized that (*i*) soils from NE aspects will exhibit a more sensitive response of net N mineralization and nitrification rates than soils from SW aspects, and (*ii*) soils from lower elevations and latitudes have higher temperature optima (T_{opt}) for both net N mineralization and net nitrification than soils from higher elevations and latitudes.

Materials and methods

Study sites

Soil samples for this experimental study were taken from two sites in West Virginia, namely BFL and FEF. BFL is in Wayne County, West Virginia (38°18′N, 82°25′W), located on the far western edge of the Appalachian Plateau. FEF is adjacent to the Monongahela National Forest in Tucker County, West Virginia (39°03′N, 79°49′W), and occupies ~1900 ha of the Allegheny Mountain section of the state. Mean precipitation at these sites is approximately 1123 mm·year^{-1} and 1430 mm·year^{-1} at BFL and FEF, respectively. Mean monthly temperatures for BFL and FEF vary from a minimum in January of 0.0 °C and –2.7 °C, respectively, to a maximum in July of 23.7 °C and 20.4 °C, respectively (Fig. 1). Differences between sites in long-term temperatures were most pronounced for the minimum monthly temperatures and least pronounced for the maximum monthly temperatures (Fig. 2). The long-term reference watershed at FEF (i.e., watershed 4 (WS4)) was used in this study.

Fig. 1. Long-term (1981–2010) mean monthly temperatures (°C) for Beech Fork Lake, West Virginia (open squares), and Fernow Experimental Forest, West Virginia (solid squares) (data source, http://www.ncdc.noaa.gov/).

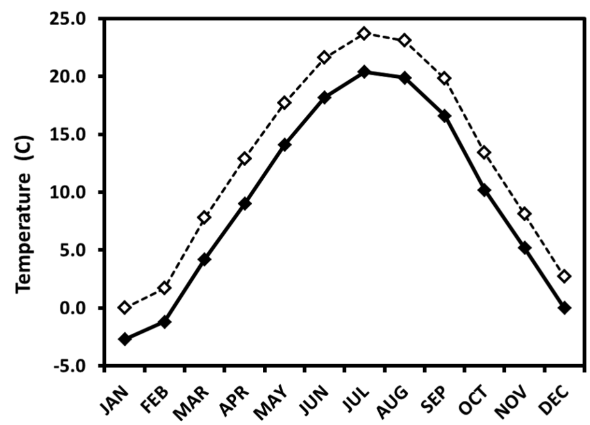
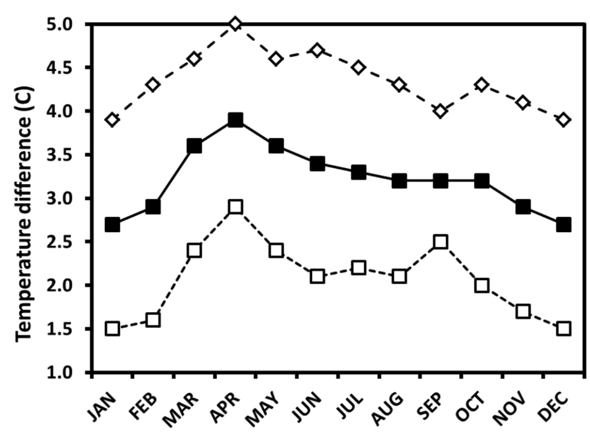


Fig. 2. Differences in mean monthly temperatures (1981–2010) between Beech Fork Lake (BFL) and Fernow Experimental Forest (FEF) sites, West Virginia, calculated as BFL – FEF. Minimum temperatures (open diamonds), mean temperatures (solid squares), and maximum temperatures (open squares) (data source, http://www.ncdc.noaa.gov/).



Soils at BFL are moderately deep, well-drained, and primarily of the Gilpin–Upshur complex. Soils on both NE and SW aspects were formed from the same parent material, i.e., largely weathered acidic bedrock from intermixed shale, siltstone, and sandstone. Gilpin soils are fine–loamy, mixed, and mesic Typic Hapludults, and Upshur soils are primarily fine, mixed, and mesic Typic Hapludalfs, both occurring on ridgetops, benches, and side slopes.

Soils are moderately to slightly acidic, with soil pH ranging from 4.4 to 5.4 (Table 1).

Soils of WS4 at FEF are predominantly from the Calvin and Berks soil series (loamy–skeletal, mixed, active, and mesic Typic Dystrudepts), originating from uniform parent substrates of the Upper Devonian Hampshire formation (Adams et al. 2006). These soil series are acidic, moderately deep, well-drained, and formed in material that is weathered from interbedded shale, siltstone, and sandstone, with soil pH varying from 4.8 to 5.2 (Table 1).

Common tree species at BFL are sugar maple (*Acer saccharum* Marsh.), buckeye (*Aesculus octandra* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and white oak (*Quercus alba* L.). The herb layer at this site comprises moist woodland species such as chickweed (*Stellaria media* (L.) Vill.), harbinger of spring (*Erigenia bulbosa* (Michx.) Nutt.), and narrow-leaved spring beauty (*Claytonia virginica* L.), as well as several ericoid and graminoid species (Gilliam et al. 2014).

Common tree species at WS4 of FEF are sugar maple, black cherry (*Prunus serotina* Ehrh.), and northern red oak (*Quercus rubra* L.). The herb layer of WS4 also comprises species typical of montane eastern deciduous forests. Common herb-layer species include seedlings of striped maple (*Acer pensylvanicum* L.), sugar maple, and black cherry, as well as several species of *Viola* and hillside blueberry (*Vaccinium vacillans* Kalm ex Torr.) (Gilliam et al. 2011).

Both sites support stands that are typical of the MMF (Braun 1950; Dyer 2006). Although tree species are not identical between sites, they both exhibit similar patterns of aspect-related contrasts in dominant species. For example, sugar maple is prominent on NE slopes of both sites, whereas SW slopes are dominated at both sites by beech and oak species.

Field sampling

Field sampling for this study was carried out as components of two separate studies at the FEF and BFL sites (for summaries, see Gilliam et al. (2011) and Gilliam et al. (2014), respectively). Accordingly, the number of plots varied between sites, with eight and three plots established per aspect (NE and SW) at the BFL and FEF sites, respectively. Plots were circular and 400 m^2 in area. Mineral soil was sampled from all plots using identical methods. Although, as associated with separate studies, soils were sampled in different years at each site, they were sampled at the same time of year in May. Organic horizons are also important in understanding N dynamics in forest ecosystems; however, we focused solely on the mineral soil to add to previous work that has quantified microbial functional groups (via phospholipid fatty acid analysis) in the mineral soil of these sites (Gilliam et al. 2011, 2014). After removing humus layers, soil was taken at a 5 cm depth, using a hand trowel, at five random locations throughout each plot, mixed into a single composite sample, and placed in 500 mL sterile polyethylene Whirl-Pac bags; these were stored on ice for transport to the Weeds and Dirt Laboratory, Marshall University, Huntington, West Virginia. As stated, soils were sampled in different years as part of the separate studies at each site, so the interpretation of the results should be made with that in mind. It is our contention, however, that site-related differences between sites are more strongly influenced by sharp contrasts in latitude and elevation between sites.

Experimental treatment and laboratory analyses

On return to the laboratory, each soil sample was extracted with 1 mol·L^{-1} KCl at an extract to soil ratio of 10 to 1 (volume to mass) and analyzed for NH_4^+ and NO_3^- with an AutoAnalyzer 3 system. The remaining soil from each sample was separated into four 100 mL sterile polyethylene Whirl-Pac bags and placed into incubators for 7 days at the following temperature treatments: 4 °C, 15 °C, 25 °C, and 35 °C. Polyethylene is permeable to O_2 but not to water vapor; therefore, soil moisture, which was between 20% and 25% for all samples (i.e., did not vary between aspects and sites), did not change during incubation. The length of the incubation period varies greatly among studies such as this, from as short as 1 day (Ross et al. 2006) to up to 4–12 weeks (Rustad et al. 2001). In lieu of other periods of incubation, we chose an incubation period of 7 days for two main reasons. First, previous work with soils from FEF has shown linear relationships between N rates and temperature up to and beyond 7 days. Second, we wanted to maintain methodology consistent with published work from this laboratory (e.g., Gilliam et al. 2011, 2014). Following incubation, soil was extracted and analyzed for extractable N via the same methods as those used prior to treatment.

Data analyses

Net N mineralization was calculated for each temperature treatment by subtracting the sum of pretreatment NH_4^+ and NO_3^- concentrations from the sum of NH_4^+ and NO_3^- concentrations following incubation, whereas net nitrification was calculated for each treatment by subtracting pretreatment NO_3^- concentrations from post-treatment NO_3^- concentrations. All difference calculations were divided by seven to yield daily rates (i.e., μg N·(g soil)$^{-1}$·day^{-1}). Net N mineralization and nitrification rates were compared between aspects, sites, and incubation temperatures with analyses of variance and least significant difference tests, with a priori levels of acceptance of significant differences at $P < 0.05$ (Zar 2010). Patterns of change in both net N mineralization and net nitrification with temperature were assessed with second-order polynomials. Relationships between net nitrification and net N mineralization were assessed on a plot basis for each site and aspect separately using linear regression (Zar 2010).

To determine the relative contribution of nitrification to the overall N mineralization, relative net nitrification (RNN) was calculated as the following, expressed as %:

$$\mathrm{RNN} = \left(\frac{\text{net nitrification rate}}{\text{net N mineralization rate}}\right) \times 100$$

Given the general absence of net nitrification in SW soils for both sites, this calculation was performed only on NE soils. The relationship between RNN and incubation temperature for the NE soils of each site was determined by linear regression.

Results and discussion

As predicted, rates of mineral N transformation — both net N mineralization and net nitrification — generally responded sensitively to temperature throughout the experimental range from 4 °C to 35 °C (Tables 2 and 3). However, the nature of this relationship varied substantially with aspect and, to a lesser extent, between sites. Net N mineralization was dominated by net nitrification in NE soils but was predominantly in the form of ammonification in SW soils, consistent with previous work at both sites using in situ ("buried bag") incubations that demonstrated negligible net nitrification in SW soils (Gilliam et al. 2011, 2014). In general, the results support our first hypothesis regarding the sensitivity of N dynamics to increases in temperature, i.e., greater for NE aspect soils than for SW aspect soils.

Although several studies have shown N mineralization to increase linearly with temperature, at least in the range used in this study (e.g., Myers 1975; Emmer and Tietema 1990; Guntiñas et al. 2012), it increased in a curvilinear fashion for all site–aspect combinations up to 35 °C. Thus, there was no T_{opt} for N mineralization within this range for soil contrasting in site types and slope aspects. In general, rates of N mineralization differed more between slope aspects than between sites, being higher in soil from NE slopes than in soil from SW slopes. Maximum rates of net N mineralization (at 35 °C) were very similar between sites for soils from NE slopes but were significantly higher for BFL soils from SW slopes than for FEF soils from SW slopes (Fig. 3*a*).

Table 2. Analysis of variance for net N mineralization for northeastern and southwestern aspects from Beech Fork Lake (BFL) and Fernow Experimental Forest (FEF) sites across all incubation temperatures.

Source	df	SS	MS	*F*	*P*
Aspect (A)	1	34.3	34.29	67.7	0.00001
Site (S)	1	0.0	0.00	0.0	0.9446
Temperature (T)	3	146.4	48.80	96.4	0.00001
A×S	1	9.2	9.15	18.1	0.0001
A×T	3	14.6	4.86	9.6	0.0001
S×T	3	11.9	3.98	7.9	0.0001
A×S×T	3	3.2	1.08	2.1	0.1035
Error	72	36.5	0.51		

Note: df, degrees of freedom (total number of df, 87); SS, sum of squares; MS, mean square; *F*, *F* test statistic; *P*, statistical significance.

Table 3. Analysis of variance for net nitrification for northeastern and southwestern aspects from Beech Fork Lake (BFL) and Fernow Experimental Forest (FEF) sites across all incubation temperatures.

Source	df	SS	MS	*F*	*P*
Aspect (A)	1	51.1	51.13	102.6	0.00001
Site (S)	1	2.0	1.96	3.9	0.051
Temperature (T)	3	21.4	7.14	14.3	0.0001
A×S	1	0.0	0.00	0.0	0.9251
A×T	3	20.9	6.96	14.0	0.0001
S×T	3	13.1	4.38	8.8	0.0001
A×S×T	3	8.8	2.95	5.9	0.0012
Error	72	35.9	0.50		

Note: df, degrees of freedom (total number of df, 87); SS, sum of squares; MS, mean square; *F*, *F* test statistic; *P*, statistical significance.

In contrast to net N mineralization, the response of net nitrification to temperature displayed sharp differences between sites; net nitrification response also sharply contrasted between slope aspects (Fig. 3*b*), supporting our second hypothesis. As with net N mineralization, second-order polynomials closely approximated the response of net nitrification to temperature for all site–aspect combinations (r^2 values ranged from 0.696 to 1.0). In contrast to BFL data, wherein rates of net nitrification increased throughout the range of incubation on both slope aspects, with a maximum of ~4 μg N·(g soil)$^{-1}$·day^{-1} for the NE slope, FEF data exhibited T_{opt} for net nitrification, approximately 0.50 μg N·(g soil)$^{-1}$·day^{-1} (at 20 °C) and 3.00 μg N·(g soil)$^{-1}$·day^{-1} (at 25 °C) on SW and NE slopes, respectively, similar to the T_{opt} for net nitrification found by Emmer and Tietema (1990) for forest floor material from an acidic oak–beech forest in the Netherlands. Working in an oak woodland – annual grassland transition in California, Stark (1996) found relatively consistent T_{opt} values at just over 30 °C.

In soils where nitrifying populations and net nitrification rates are high, there is often a positive linear relationship between net N mineralization and net nitrification. This relationship arises when NH_4^+ generated by ammonifying microbes is rapidly converted to NO_3^- by nitrifying bacteria. However, Lavoie and Bradley (2003) summarized findings from 56 published studies and found that high relative nitrification is rare among forest mineral soils. Of the 117 sites represented by these publications, only five sites had a relative nitrification of 90% or more. Furthermore, 43 sites had relative nitrification rates of ≤10%, among which, 10 sites had relative nitrification rates of 0% (Lavoie and Bradley 2003). Thus, notable from our results is that SW soils from both sites were of the latter category, with many samples exhibiting no net nitrification and other samples exhibiting net NO_3^- immobilization (negative net nitrification). It is further notable that, other than at 35 °C, NE soils from both sites had net nitrification rates of >100%, exceeding rates from all of the studies summarized in Lavoie and Bradley (2003) (Fig. 4).

The most consistent pattern of contrast in this study was the stark contrast between SW and NE soils at both sites. Previous work at BFL and FEF have reported similar aspect-related contrasts in soil N dynamics using in situ incubations, and both provided compelling evidence to suggest that soil weathering, being higher on SW aspects than on NE aspects from higher net radiation, drive such patterns in soil N dynamics. They also concluded that such differences were particularly manifested in soil microbial composition. Using phospholipid fatty acid analysis to characterize microbial functional groups, both studies found the predominance of fungal markers (i.e., higher fungi to bacteria ratios; Table 1) and microbial markers that are indicative of environmental stress in soils from SW aspects (i.e., using the stress index of the ratio of fatty acid methyl esters cy19 to 18:1n7c; see Kaur et al. (2005); Table 1). In contrast, they found a prevalence of Gram-negative bacterial markers in soils from NE aspects, sugges-

Fig. 3. Response of (*a*) net N mineralization and (*b*) net nitrification to temperature in soils from southwestern (SW, solid symbols) and northeastern (NE, open symbols) slopes at Beech Fork Lake (BFL, squares) and Fernow Experimental Forest (FEF, circles) sites in West Virginia. Data points represent means for a given aspect–site combination, with superscripts corresponding to the order of points below. Means with the same superscript are not significantly different at $P < 0.05$. Equations for net N mineralization: A (site–aspect, BFL–NE), $y = 0.008x^2 - 0.1546x + 0.7159$, $r^2 = 0.99$; B (BFL–SW), $y = 0.0084x^2 - 0.2171x + 1.0263$, $r^2 = 0.99$; C (FEF–NE), $y = 0.0018x^2 + 0.0867x - 0.093$, $r^2 = 0.98$; D (FEF–SW), $y = 0.0018x^2 - 0.0255x - 0.0102$, $r^2 = 0.99$. Equations for net nitrification: A (BFL–NE), $y = 0.0053x^2 - 0.0858x + 0.4595$, $r^2 = 0.99$; B (BFL–SW), $y = 0.00008x^2 - 0.00006x - 0.1556$, $r^2 = 0.93$; C (FEF–NE), $y = -0.006x^2 + 0.2981x - 0.7961$, $r^2 = 0.70$; D (FEF–SW), $y = -0.0015x^2 + 0.0575x - 0.1256$, $r^2 = 1.00$.

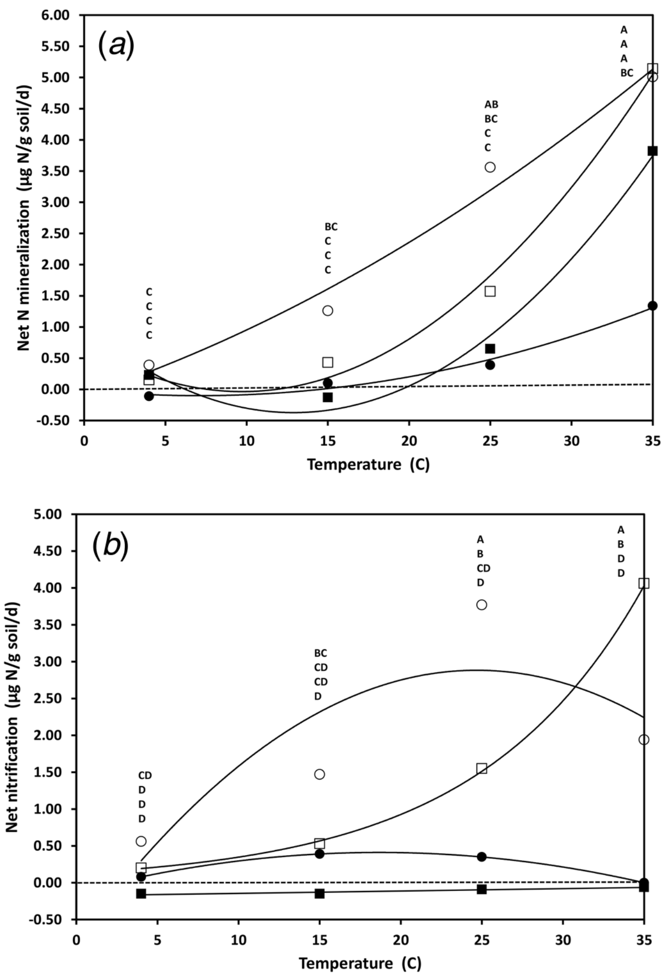
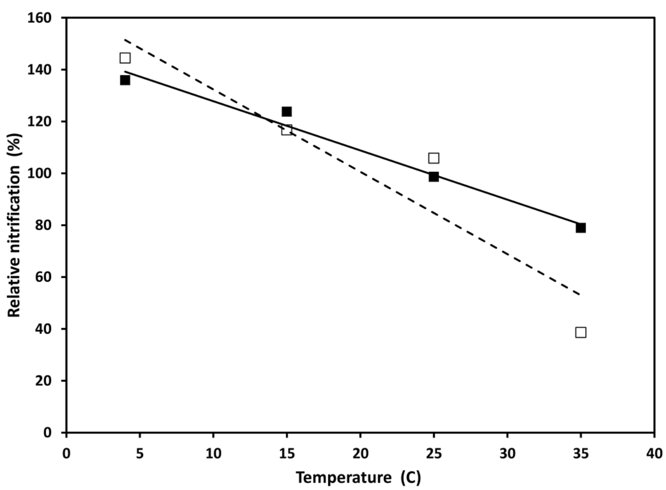


Fig. 4. Response of relative net nitrification (%) to temperature (°C) in northeastern soils of Beech Fork Lake (solid squares; solid line, $y = -1.90x + 146.77$, $r^2 = 0.98$) and Fernow Experimental Forest (open squares; dashed line, $y = -3.18x + 164.10$, $r^2 = 0.88$) sites in West Virginia.



tive of high nitrifying populations (Gilliam et al. 2011, 2014). Thus, a microbial process relevant to the patterns reported here is one often associated with fungi, i.e., N immobilization (Dighton 2003; Näsholm et al. 2013). Fontaine et al. (2011) concluded that soil fungi are essential in mediating long-term sequestration of N via immobilization, emphasizing the ability of fungal hyphae in the soil to extend into pore space, allowing access to reserves of organic matter for energy, and taking up N to meet nutrient demands.

There were also differences in the response of soil N processing between sites, again supporting our second hypothesis. We suggest that this has arisen from microbial adaptation to different temperature regimes. We cannot separate the importance of either latitude or elevation because both vary between sites, with FEF lying almost 1° in latitude to the north of BFL and ranges in elevation of 808–838 m and 180–237 m, respectively. Thus, at both a lower elevation and lower latitude, BFL generally experiences markedly higher temperatures. This occurs on a year-round basis (Fig. 1) but is most pronounced during the growing season (Fig. 2) when soil microbial activity is highest. We also suggest that, regarding contrasts in temperature regimes between sites, minimum temperatures may be of particular importance in driving microbial adaptations (Fig. 2). In short, it is not surprising that net nitrification exhibits T_{opt} values between 20 °C and 25 °C at FEF, considering that the nitrifying microbes of these soils rarely experience ambient conditions above this temperature range, i.e., the highest mean monthly temperature (July) at FEF is ~20 °C (Fig. 1). Although these are ambient air temperatures, soil temperatures are generally always lower, often far lower, than the ambient air temperatures (Jungqvist et al. 2014).

It is clear from this study and others (e.g., Stark 1996; Rustad et al. 2001; Bai et al. 2013) that soil N dynamics are generally quite sensitive to temperature. Site- and aspect-related contrasts, reported herein for this response, underline the complexities in predicting future change in N dynamics of forest soils under global climate change scenarios. Microbial diversity responsible for directing soil N cycling, especially the balance between fungal and bacterial groups, further complicates the predictability of climate-driven change in N dynamics.

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