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Spatio-temporal analysis of nitrogen cycling in a mixed coniferous forest of the northern United States

I. Howard[1] **and K. K. McLauchlan**[2]

[1]Department of Geosciences, University of Arkansas, 216 Ozark Hall, Fayetteville, AR, 72701, USA
[2]Department of Geography, Kansas State University, 118 Seaton Hall, Manhattan, KS 66506, USA

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Correspondence to: I. Howard (ihowardksu@gmail.com)

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Abstract

Nitrogen (N) is the limiting nutrient to primary productivity in a variety of temperate forests, and N cycling is undergoing a variety of anthropogenic changes, notably a doubling of Nr on a global scale. Yet, the local scale impacts of 20th century changes to N cycling have been difficult to document in terrestrial ecosystems, especially old-growth forests. To determine the spatial and temporal variability of anthropogenic effects on old-growth forest N dynamics, we measured the composition of stable nitrogen isotopes (δ^{15}N) in wood from living red pine trees (*Pinus resinosa*) at a single site in northern Minnesota, USA. A synchronous decline in wood δ^{15}N values began approximately in the 1920s C.E. in 18 individual trees at different topographic positions, indicating a common driver. The decline in wood δ^{15}N values corresponded with declines in sedimentary δ^{15}N recorded in lacustrine sediments of the same catchment. Disturbance regime and species composition began to change at the turn of the 20th century with park establishment, providing a likely mechanism of decline in δ^{15}N values toward present. While other mechanisms are possible, we conclude that the consequences of global-scale alterations to N cycling are not being expressed at a local level in this temperate forest ecosystem.

1 Introduction

Global biogeochemical cycles have been altered by human activities, such as elevated levels of atmospheric CO_2, global increases in temperatures, and increased deposition of reactive nitrogen (Nr) through anthropogenic sources (fossil fuel burning and fertilizer production) (Vitousek et al., 1997). In forested ecosystems, increases in atmospheric nitrogen (N) deposition have been of particular concern, because a variety of negative environmental consequences, such as reduced forest growth, eutrophication, acid rain, and biodiversity loss, have been attributed to increases in Nr (Hietz et al., 2011; Houlton et al., 2013). Despite global-scale changes to N cycling, it has been difficult to pinpoint effects of Nr on a local scale in terrestrial ecosystems, due to an additional suite of activities that affect local N cycling such as management practices, intensive logging, disturbance regimes, alteration of species composition, and regional-scale variability in climate (Kareiva et al., 2007; McLauchlan and Craine, 2012).

Although understanding how these factors affect the N cycle is of paramount importance to understanding recent changes in forest dynamics, long-term records of N cycling in forests are rare and generally restricted to modern measurements that might span a few decades at most (Gerhart and McLauchlan, 2014). Long-term monitoring of N cycling metrics such as stream nitrate export indicates an unexpected ability of many terrestrial ecosystems to retain added N, with stable or declining trends in N availability since monitoring began in the late 20th century (Bernal et al., 2012). A more temporally complete understanding of the modern state and trajectory of N cycling in forests requires extending records back in time prior to settlement by Euro-Americans (Galloway et al., 2004). This retrospective approach, which uses N cycling proxies preserved in wood or sedimentary archives, has supported and extended the long-term monitoring studies. Some retrospective studies have indicated that regional and local-scale processes may be altering N availability to varying degrees during the past 500 years (McLauchlan et al., 2013a).

While our understanding of N availability in terrestrial ecosystems has improved, the lack of long-term records and relatively poor spatial coverage limits the ability to fully assess the consequences of anthropogenic disturbance to the N cycle. Fortunately, analysis of the standardized natural abundance ratios of ^{15}N to ^{14}N (δ^{15}N) stored in tree rings is a relatively new technique that serves as a proxy record for the history of N availability in past terrestrial ecosystems (Gerhart and McLauchlan, 2014). Of the approximately 50 published wood δ^{15}N studies so far, the majority have been in secondary forests, with trees less than a century old (e.g. Poulson et al., 1995; Bukata and Kyser, 2007; Hietz et al., 2010; Beghin et al., 2011; Stock et al., 2012; McLauchlan and Craine, 2012). The oldest published wood δ^{15}N value is from a sample dated to 1835 C.E. (McLauchlan et al., 2007). Because secondary forests are accruing biomass, with high demand for N, these types of sites potentially alter conclusions about the biogeochemical consequences of anthropogenic N deposition.

Interpretation of wood δ^{15}N trajectories depends on the relationship between soil N availability, foliar δ^{15}N, and wood δ^{15}N, providing another proxy for measuring N availability in soils through tree ring analysis (Craine et al., 2009). Briefly, stable N isotopes preserved in wood reflect multiple fractionating pathways within the N cycle. In forests, high δ^{15}N values are found in soils and leaves of ecosystems with high rates of nitrification (Pardo et al., 2006), high rates of denitrification (Houlton et al., 2006), partial nitrification followed by nitrate leaching (Pardo, 2002), and low reliance on mycorrhizal fungi for plant N uptake (Hobbie and Colpaert, 2003; Cuoto-Vazquez and Gonzalez-Prieto, 2010). Stable N isotopes of wood from dated tree rings can produce high-resolution terrestrial records of past N cycling at specific locations that extend back in time several centuries. Thus, wood δ^{15}N provides a useful proxy for analysing spatio-temporal patterns of terrestrial N availability.

Old-growth forests dominated by red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) once covered large areas of the north-central US Today, protected remnants of these forests provide valuable information regarding the role of natural disturbances like fire and windstorms in determining vegetation dynamics (Peet, 1984; Webb, 1989). Pre-settlement *P. resinosa* stands exhibit a variety of age structures (Fraver and Palik, 2012), with maximum tree ages observed to be approximately 200 to 300 years old (D'Amato et al., 2010; Silver et al., 2013). The disturbance regimes have been typically dominated by low-intensity surface fires that maintain an open understory, with occasional high-intensity stand-replacing fires (Clark, 1988, 1989). During the past 100 years, *P. resinosa* forests have experienced substantial regeneration declines, expansion of hardwood species, and the development of dense undergrowth composed of pyrogenic species like fir (*Abies balsamea*) (Frissell, 1973). Increases in deer populations, along with severe drought episodes have also hindered regeneration of pine species. As a result, neither *P. resinosa* nor *P. strobus* have been reproducing successfully since fire suppression began in the early 1920s (Ahlgren, 1976). One of the best-protected areas of old-growth *P. resinosa* occurs at Itasca State Park in northern Minnesota (Minnesota DNR). Due to significant logging and intensification of agriculture in the region, Itasca is considered a relict of the vast northern coniferous forests. Additionally, given the well documented timeframe of park establishment (1891) and implementation of fire suppression (∼ 1920s), N availability can be analyzed prior to and following human involvement, providing insight into how anthropogenic drivers can influence biogeochemical cycles in local terrestrial ecosystems.

Here, we analyze the spatio-temporal characteristics of N availability of *P. resinosa* within a mixed coniferous forest in Itasca State Park located in northwest Minnesota through use of nitrogen isotopes in tree rings. Our main objectives were to assess the long-term (century-scale) trajectory of N availability through isotopic analysis and additionally determine the influential drivers across space and time. We hypothesized: (1) nitrogen availability to the dominant tree species, *P. resinosa,* would be declining toward present at most sites within the watershed due to management-driven changes in fire regime in the early 20th century, and (2) there would be spatial heterogeneity within the temporal trend in the watershed, with individual *P. resinosa* trees exhibiting variable δ^{15}N trajectories based on location and geographic features.

2 Methods

2.1 Study site

Itasca State Park (ISP) in northern Minnesota is a large park (13 229 ha) and lies on the Itasca moraine, deposited by the Laurentide Ice Sheet 13 K YBP (47°14′ N 95°12′ W). The upland soils of ISP are a mixture of sandy outwash and glacial till. Climate is typical of a northern temperate forest, with approximately 65 cm of annual precipitation and a mean annual temperature of 3 °C. The vegetation prior to Euro-American settlement in the region was a mixture of red pine (*P. resinosa*), white pine (*P. strobus*), and jack pine (*P. banksiana*) forests and savannas, prairie openings, deciduous northern hardwood forests, and boreal bogs. Our study site, the Deming Lake watershed, lies within a mixed coniferous forest of Itasca State Park. It is a relatively small lake (5.4 ha surface area) (Fig. 1). The fire return interval during the presettlement period in ISP was approximately 22 years (Clark, 1988; Frissell, 1973), with stand-initiating fires occurring approximately every 10 years during the 1800s (Spurr, 1954). In recent years, several deciduous hardwood species have been increasing in abundance, including *Acer saccharum* (sugar maple), *Betula papyrifera* (paper birch), *Corylus cornuta* (beaked hazel), *Populus tremuloides* (aspen), *P. grandidentata* (big-toothed aspen), *Quercus borealis* (northern red oak), and *Tilia americana* (basswood). *Corylus cornuta* now dominates the understory (Kurmis and Sucoff, 1989). In the last 20 years, prescribed burns have been implemented in an attempt to stimulate regeneration of *P. resinosa* and reduce fuel loads (Santoro et al., 2001).

2.2 Field and laboratory methods

Increment cores of 5.15 mm diameter were obtained at 1 m above the forest floor from twenty-four individual *P. resinosa* trees surrounding the Deming Lake watershed in March 2014 with a Haglöf borer. *P. resinosa* was the only species sampled because of its dominance, its importance and legacy to the area, and the need to use a single species to test our hypotheses. Samples were gathered from five stands comprising four to five trees with aspects of west, north, east, and south (Fig. 2). Trees were sampled at different elevations, slopes, and proximity to the shoreline to capture the spatial variation in δ^{15}N that may arise from small-scale topographic features or geographical position.

The cores were stored in plastic bags and dried at 65 °C. Each core was sanded then scanned at 1200 dpi. Ring widths of the cores were analyzed using both Cybis and the CDendro software (Saltsjöbaden, Sweden). The pith was reached on 11 out of the 24 samples, therefore the absolute age could not be determined for most trees but could nevertheless be dated based on cross dating techniques and the last ring formation of 2013. The longest chronology contained 237 rings, while the shortest had

79 rings. Cores on average contained 145 rings. Following ring width analysis, cores were weighed and divided into 10 mg segments along ring boundaries that maximized temporal resolution while maintaining enough N in the sample for mass spectrometry. The wood samples were not subjected to any chemical pretreatments based on results from (Doucet et al., 2011). On average, wood samples comprised 2 or 3 annual rings, with a total of 1224 samples measured. Two cores were lost during measurement, and two were not sent out, therefore a total of 20 trees were used for subsequent analysis (Table 1).

The standardized ratio of $^{15}N:^{14}N$ relative to air ($\delta^{15}N$) was determined for segments of wood at the University of Maryland Center for Environmental Science, Central Appalachian Stable Isotope Facility (CASIF) Laboratory. The instrument is a ThermoFisher Delta V+ isotope ratio mass spectrometer fitted with sequential traps of $MgClO_4$, NaOH on solid support (Carbosorb), and a cold trap in liquid N_2.

2.3 Statistical analyses

In order to develop a spatio-temporal understanding of N cycling within the watershed, a number of statistical methods were employed. Tests for differences between group means were employed based on individual trees, stands sampled, and geographic location relative to Deming Lake. For the Kruskal–Wallis Tests the raw $\delta^{15}N$ values were used, as it was important to determine how location and other geographic features can influence mean values in the watershed. For temporal analyses, we calculated standardized values by subtracting the mean $\delta^{15}N$ from each sample for each core, giving each a core a mean value of 0 ‰. This is essentially a Z-score treatment, used in other isotopic analysis (McLauchlan et al., 2007; Craine and McLauchlan, 2010). To test hypothesis #1 (evidence of trend), simple linear regression along with the rank-based, non-parametric Mann–Kendall Trend Test (MK Test) were applied to each sample. Given its robustness for non-normally distributed data, the MK Test is frequently applied to hydroclimatic time series data. The MK Test determines the presence of a monotonic increasing or decreasing trend (given by the MK Tau value), along with the magnitude of the slope calculated through the Sen's Slope estimator. Trends determined by the test were deemed significantly different from zero if p values were < 0.05 (Mann, 1945; Sen, 1968).

After determining the trends and slopes of each core, a supplemental analysis sought to determine the date range of when the potential shift in mean occurred. This allowed us to test hypothesis #2, about the spatial variability in wood δ^{15}N among trees. Time-series related studies, particularly in the climate and atmospheric sciences, often employ change point analysis using a suite of tests. We applied four separate tests of change in the mean in order to improve bolster confidence that a change in mean does exist. The Pettit's Test (Pettitt, 1979), Buishand's Bayesian Test (Buishand, 1984), the standard normal homogeneity test (Alexandersson, 1986) as well the Cumulative deviation test (Rebstock, 2002) were applied to all samples. Relevant to our study, we used these tests to aid in our determination of whether a detectable human disturbance signature exists in the record. A great deal of research has been dedicated towards the study of detection procedures for identifying a potential change point in a data series. Many have argued that trends must be removed prior to detection of inhomogeneities, as trends (or autocorrelation) can create synthetic change points in a dataset (Beaulieu et al., 2012). However, other studies have claimed that removing the trend component has the same adverse affect (Guerreiro et al., 2013). In our study we manipulated the data as little as possible (the exception being standardization) and applied no detrending methods prior to tests for shifts in mean. Regardless, using a diverse suite of change-in-mean tests allows for comparison of different tests on the same datasets. The use of multiple analyses allows a rigorous test of whether a detectable shift in δ^{15}N values exists.

3 Results

3.1 Trends in δ^{15}N

Within the Deming Lake watershed, wood δ^{15}N has been significantly declining over the period of record as evident by the trajectories of individual trees. Of the twenty trees sampled, 18 demonstrated significantly declining trends toward present ($p < 0.05$) based on both simple linear regression and the MK Test. Trends were significantly positive in the other two trees. The steepest declines tended to occur in trees located in stands two and five (northeast and south areas of the lake), although no clear cohesive spatial pattern could be detected (Table 2). Similarly, the length of the chronology had no apparent effect on the steepness of slope of the samples, as trees with similar ring counts had different rates of change.

To test our first hypothesis – that management practices have influenced N availability in *P. resionsa* in this watershed – we employed four statistical analyses to detect temporal breakpoints in the wood δ^{15}N time series. Of the 18 trees with negative trajectories, a significant breakpoint ($p < 0.05$) could be detected based on each test in 15 cases. In 13 of the 15 trees, a similar breakpoint for each individual tree (within 1 data point) was evident for the four tests (Table 3). In the case of S2TA where significant break points were evident but the timing differed, extreme values occurring within a 20 year period more than likely distorted the signal creating the differences, as removal of the outliers in the period resulted the temporal agreement of a breakpoint.

Breakpoint tests were then applied to larger-scale watershed-level wood δ^{15}N based on averaging the time series for all trees. Using this chronology, a significant breakpoint of 1927 C.E. was detected (Fig. 3). A piecewise regression was also applied to the time series to show the varying trajectories prior to and post-1927 C.E. A slight positive trend exists (not significant) prior to 1927 C.E., and the major decline in wood δ^{15}N did not begin until the 1930s.

Both parts of our first hypothesis are supported by these results, if tests for breakpoints are good estimates of when shifts in mean occurred. Fire suppression began in the 1920s, and in 13 cases a change in mean could be detected within the period of 1920 to 1947. It is important to note that it would take time for the potential mechanisms affecting levels of N availability to change after a change in disturbance regime. As a result, there would be a lagged effect from the time of altered disturbance regime to when significant declining N availability would be evident in the wood δ^{15}N record of already established species such as *P. resinosa*. Without using homogeneity tests to assess whether a change-point exists, trees with sufficient data records prior to 1925 C.E. ($>$ 15 samples before 1925) were divided into two periods: δ^{15}N prior to 1925, and δ^{15}N after 1925. Tests for trend were applied to the two time series to see if slopes significantly differed. Indeed, in the analysis of the 15 trees used, 10 exhibited no significant trend ($p > 0.5$), three trees had significantly increasing trends, while two had significantly downward trends. Tests of the data following 1925, however, reveal similar trends to those discussed initially, with 16 trees having significantly negative trends, one tree with a negative trend, two trees with significantly upward trends, and one with no significant trend. Therefore, even without removing any trends, it is clear that these trees exhibit breakpoints in wood δ^{15}N trajectories, with a negative shift beginning the in 1920s.

3.2 Spatial Characteristics of δ^{15}N

To test our second hypothesis, we examined the spatial patterns of wood δ^{15}N values at several levels of spatial organization. First, for individual trees, raw δ^{15}N values exhibited a high degree of heterogeneity and spatial variation, with maximum δ^{15}N values for an individual tree ranging from 3.46 (S1TC) to −0.06 ‰ (S5TD) and minimum values ranging from −1.76 (S4TE) to −4.38 ‰ (S2TC) (Fig. 4a). The average SD for all trees sampled was 1.22 ‰. Tests among all trees revealed significantly different mean δ^{15}N ($p < 0.00001$), not surprising given the multitude of environmental factors that alter levels of N availability. With significantly different variances in the dataset detected, the Games–Howell Test was used in the post-hoc tests. Means of δ^{15}N for each tree significantly differed on average from 9 (8.7) other trees. Outliers in the post-hoc tests included tree S1TD, located in Stand One on the east end of the lake, and S5TC located in Stand Five on the south end of the lake. The former significantly differed from only two trees, while the latter significantly differed from 18 trees.

Second, spatial patterns were also analysed at the level of the stand, a group of neighboring trees. An initial ANOVA Test based on group means of the five stands sampled once again revealed significant ($p < 0.00001$) differences among stands, although post-hoc analysis indicated that only Stand Three, consisting of those trees on the north end of the lake, significantly differed from the other four groups. The trees within this stand by far had the lowest δ^{15}N average (by over 1 ‰) and the least amount of variation (Fig. 4b).

Third, we conducted a set of further tests based on geographic covariates such as distance from the lake shoreline, elevation, and slope. Sampled trees ranged in distance from the shoreline from approximately 10 to 26 m. Samples were separated into three groups based on their distributions: those within 13.7 m of the shoreline (7 trees), between 13.7 to 16.8 m (7 trees) and greater than 16.8 m (6 trees). Three groups were selected in an attempt to provide an adequate number and equal distribution of samples. Tests of the group means showed significant differences between the three groups ($p < 0.00001$), but only those trees closest to the lake significantly differed from the other two groups.

One unexpected result from the proximal tests was a change in average wood δ^{15}N value with distance from the shoreline. Values of wood δ^{15}N for trees closest to Deming Lake averaged −1.54 ‰, followed by −0.77 ‰ for the second closest group, and finally −0.64 ‰ for the group furthest from the lake. Inversely, higher variation in δ^{15}N was present in those trees furthest away from Deming Lake (1.47 SD), followed by 1.26 for the intermediate distance group and 1.10 for the trees closest to the lake. Interestingly, an increase in distance from the shoreline did not necessarily equate to higher elevations or steeper slopes. In fact, the highest elevations occurred in the group of trees located between 13.7 and 16.8 m from the lake. Similarly, the trees four trees residing on the steepest slopes (i.e > 20 %) were also in the two groups closest to the shoreline. Of course, variation in elevation and slope throughout the watershed is not surprising, but in general we expected that elevation along a straight path would decrease as distance from the shoreline decreased.

In terms of the variability in trajectories based on location and geographic features, the tests for breakpoints struggle to agree on breakpoint timing for the two groups closest to Deming Lake. Albeit significant, the timing of the breakpoints vary anywhere from 1927 to 1973. Conversely, for the trees furthest from the lake all tests agree on a significant 1924 breakpoint ($p < 0.0001$). The inability to agree on a similar breakpoint value more than likely results from averaging the δ^{15}N values for trees in a similar group, creating incredible variability making it difficult to assess whether a change in mean exists. Indeed, using a 5 year smoothing filter results in much better agreement among breakpoint tests for the two groups, with values in the 13.7–16.7 m group varying from 1926–1941, while the closest group of trees having a breakpoint value of 1926 based on all tests ($p < 0.0001$). Relative to the group trajectories, based on simple linear regression only the slope of the closest group of trees significantly differed from the others ($p < 0.0001$). The steepest decline was also present in this group. Conversely, when assessing the slopes after 1925, the most negative slopes occurred in the group of trees within 13.7–16.8 m, followed by the group < 13.7 m to the lake. Only the group furthest away significantly differed from the other two in terms of their trajectories following 1925. The two trees with increasing trajectories toward present appear to have no obvious landscape characteristics that explain those patterns. With respect to the trajectory based on the incline of the surface, once again three groups were created based on the criteria locations with > 19 % slope, between 14–19 % slope, and finally < 14 %. Trees with the highest % slope had significantly different slope values than the other two groups. While a similar breakpoint could be agreed upon with the two latter groups listed above (1926 and 1927 at $p < 0.0001$), a breakpoint could not be determined for trees with the highest slopes. Once again this may result from a decreased sample size within the group. The largest decline also occurred within this group, followed by trees residing on terrain with 14–19 % slope. In addition to there being significant spatial differences in wood δ^{15}N demonstrated in this study within a spatial extent of 676 m^2, our second hypothesis, about spatial differences in wood δ^{15}N trajectories, appears to be supported as well despite the overall agreement of declining δ^{15}N.

3.3 Terrestrial and Lacustrine records

Given the strong signal of declines in terrestrial δ^{15}N, we compared the wood δ^{15}N record to a previously-published sediment record from Deming Lake for the portion of temporal overlap – approximately the last 250 years (McLauchlan et al., 2013b). There is remarkable coherence between these two records. The most noticeable characteristic of both time series is the noticeably similar steep decline of δ^{15}N beginning in the 20th century. The same breakpoint tests used on the wood δ^{15}N were applied to sedimentary δ^{15}N using the period of data from 1750 to 2004 C.E. In three of the four tests, a change point of 1930 C.E. was detected (all significant at $p < 0.01$). The values of terrestrial δ^{15}N, on average, are smaller (more negative) than values of sedimentary δ^{15}N. While it would be ideal to test a larger portion of the sedimentary time series to accurately identify the change in mean, the two datasets share a remarkable degree of similarity during the past ~ 250 years (Fig. 5).

4 Discussion

Available nitrogen has clearly been declining over time in *P. resinosa* within the Deming Lake watershed. A robust set of breakpoint analyses identify the early 1920s as the time when a synchronous decline in wood δ^{15}N values began. Declines in wood δ^{15}N values toward present have been described in a number of studies and attributed to a variety of causes, described below (Gerhart and McLauchlan, 2014). Because of the synchrony of the breakpoint, the timing, and the direction of change (decline toward present), we believe the primary reason for the substantial decline in δ^{15}N over the past century has been management practices within the state park, namely fire suppression that began in the late 1910s. Disturbance regimes, both human and natural, can have profound impacts on nutrient cycling resulting from complex spatial and temporal patterns that affect primary productivity and biomass accumulation (Clark, 1988). In the case of fire, disturbance can influence N availability both on short and long-term scales. In the short term, fire impacts organic-matter pools (Wang et al., 2012), while on longer time scales fire can alter species composition subsequently influencing total carbon and N pools (Clark, 1990b; Nave et al., 2011).

Fire suppression could have the net effect of reducing N availability through the following mechanisms. Fire suppression of the type of low intensity ground fires common to *P. resinosa* forests allows for competing understory species to increase in abundance, both increasing plant demand for N and increasing annual litter input to the forest floor, thereby lowering the availability of nitrogen for tree species dependent on a semi-regular fire regime (Brisson et al., 1988; Tappeiner and Alm, 1975). Indeed, fire suppression of ponderosa pine forests in the western US has been demonstrated to reduce N availability up to 130 years after the onset of fire suppression through reduced net N mineralization and nitrification potential (MacKenzie et al., 2006).

We suggest that these changes in nutrient status may be contributing to the regeneration problems previously documented for *P. resinosa* in the upper US Natural fire occurrences are a key component to *P. resinosa* maintenance, as frequent, low-intensity burns eliminate competing understory species as well as improve the seedbed by reducing the forest floor depth (Flannigan and Bergeron, 1998). After a burn, *P. resinosa* invades burned regions by seeding from other trees nearby which were unaffected by the fire. It has been suggested that the old-growth pine forests of not only Itasca but much of the northern United States may eventually succeed to northern hardwoods, as regeneration attempts of pine species in the region have failed with fire suppression (Zenner and Peck, 2009).

Altered biogeochemistry would explain the sharp declines in wood δ^{15}N in many of the trees following the implementation of a no-burn policy in the 1920s. Significant declines in wood δ^{15}N of many of the trees sampled here did not begin until the earlymid 20th century. It is logical to believe that if this practice did in fact alter nutrient cycling at Deming Lake, it would have been a lagged effect. Undergrowth development and significant changes in ecosystem composition would take years to develop, and the resulting N pool would not be disrupted until years later. Bukata and Kyser (2007) analyzed the effects of tree-clearing and land-use change on *Quercus alba* (white oak) and *Quercus rubra* (red oak) in forest stands in Ontario, Canada. Their results showed that trees on the outer edges of the stand showed a marked increase in δ^{15}N compared to those in the center, coinciding with the tree-clearing event and land-use change. This study emphasizes the role of shifting ecosystem composition on δ^{15}N values resulting from human activity.

There are several alternative explanations for declining wood δ^{15}N values that have been published in the literature (see Gerhart and McLauchlan, 2014 for a summary). Similar patterns of decline in wood δ^{15}N observed elsewhere have been attributed to increases in atmospheric N deposition. This might be plausible if δ^{15}N in NO_x is much lower compared to soil δ^{15}N, and if the quantity of deposited N was sufficient to alter either the isotopic signature or cycling of soil N. Poulson et al. (1995) first hypothesized that a decreasing trend over time of δ^{15}N in rings of *T. canadensis* (eastern hemlock) stemmed from increased deposition of depleted ^{15}N compounds due to an increase of NO_x and NH_3 emissions in the late 20th century. At Deming Lake, with low levels of atmospheric N deposition, and the declines predating widespread human manipulation of the global N cycle, it is difficult to posit this as a viable explanation for the patterns evident at this site.

Declining δ^{15}N may also be attributed to a physiological process in plants or a time course of ecosystem processes in soils. As a tree ages, uptake of N switches from an open cycle to a closed cycle resulting from decreasing nutrient losses and increasing stand age (Jussy et al., 2000). Perhaps the sources supplying N to the tree change with age as well, with sources in the most recent growth years contain N depleted in ^{15}N than those which supplied the tree in the early stages of its life (Hobbie and Hobbie, 2006). More than likely some physiological factors influence N cycling within

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◂◂ ▸▸
◂ ▸
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

P. resinosa, but physiological-related explanations fail to account for the rapid step-change in δ^{15}N seen in a majority of the trees beginning in the 1920s. With age ranges anywhere from ~ 70 to ~ 240 years, the fact that both old-growth and younger trees are exhibiting a similar timeline of rapidly declining δ^{15}N, an external rather than internal force must be driving this macro-level change.

Despite the overall synchronous trajectory among trees, certain geographical differences resulted in different spatial signatures of δ^{15}N. In old-growth *P. resinosa* forests, Clark (1990a) had previously identified topographic position as an important driver of N mineralization rates, with spatial variation in soil moisture correlated with microbial activity. In our study, trees on the north side of the lake in a more open stand structure had the lowest average levels of wood δ^{15}N. Scattered and large *P. resinosa* dominated this area (highest average DBH among stands) with relatively few tree/shrub species in the understory present. Average levels of δ^{15}N also differed based on proximity to the lake, with samples furthest away containing the highest averages and variances compared to those closer to water body. It would be pertinent in future studies to further investigate the role landscape position plays in δ^{15}N signatures of both soil and plants. Given the high degree of spatial complexity of δ^{15}N in this watershed, the fact that the majority of trees exhibit significantly declining trends in the past century again supports the idea of a macro-scale process that has resulted in decreasing δ^{15}N and thus N availability over time.

Additional questions arise as the result of the striking similarities between the δ^{15}N values of the sediment record analysed in McLauchlan et al. (2013b) and our results. The marked decline in δ^{15}N in the latter part of the sediment record had been attributed to internally driven processes occurring within the lake, particularly the development of anaerobic conditions in the deeper areas of the lake. Over the past 500 years, δ^{15}N in the sediment record has been declining markedly, although a somewhat stable period is present from 1600 to 1900 followed by a drastic decline in the 20th century. The identical temporal pattern of nearby wood δ^{15}N suggests either different mechanisms driving the same pattern in the two records, or a need to reanalyze the contribution of terrestrial inputs to the sedimentary record. This result, of dendrochronological and sedimentary δ^{15}N records from the same small catchment showing strong agreement in their respective trajectories, has also been seen at an oligotrophic lake in New Hampshire (McLauchlan et al., 2007) and a high-elevation lake in the western US (Wolfe et al., 2013).

Overall, the results of our study analysing the spatial–temporal characteristics of δ^{15}N in a pine-dominated forest of northwest Minnesota demonstrate declining N availability for the past 80 years, which we believe to be caused by implementation of fire suppression in the park beginning the early 20th century. This study is the longest wood δ^{15}N chronology published, with δ^{15}N values from wood dated to 1775 C.E. (~ 238 years ago). Although selection of a single tree species (*P. resinosa)* provided an intriguing spatial and temporal picture of δ^{15}N, it would be useful to sample additional old-growth forests, and wood δ^{15}N of some of the understory species that became abundant with fire suppression, to obtain a more complete answer about the mechanism of these declines in δ^{15}N, and the role of changing environmental conditions in altering N cycling on local spatial scales.

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Table 1. List of the trees sampled, ring counts, the number of δ^{15}N samples obtained from that tree, elevation in meters, and distance from shore in meters.

Tree	Ring Counts	#δ^{15}N Samples	Elevation (m)	Distance from Shore (m)
S1TC	238	99	468	23.69
S1TD	122	44	469.5	20.63
S1TE	215	84	472.2	16.58
S2TA	175	98	474.5	14.28
S2TB	158	74	467.1	14.31
S2TC	162	55	465.2	12.57
S2TD	158	63	464.8	17.00
S2TE	79	50	467.7	13.20
S3TA	99	60	467	13.65
S3TC	118	49	469.5	10.29
S3TD	128	45	471.2	11.97
S4TA	95	35	470.4	9.35
S4TB	86	78	471	17.77
S4TC	171	64	468	16.82
S4TD	178	56	458	14.88
S4TE	159	51	466.1	9.30
S5TA	132	69	462.2	20.50
S5TB	110	68	462.2	20.50
S5TC	153	45	465.8	22.12
S5TD	166	37	469.5	14.64

Table 2. Slope based on simple linear regression (m), Sen's Slope and Kendall's Tau value based on Mann–Kendall Trend Test for each tree. The Hamed and Rao method takes into account autocorrelation and adjusts the Sen's Slope estimate.

Tree	m	*p* value	Sen's Slope (Hamed and Rao method)	Kendall's Tau
S1TC	−0.0196	< 0.0001	−0.029	−0.600[c]
S1TD	0.0101	< 0.0001	0.064	0.638[c]
S1TE	−0.0067	< 0.0001	−0.024	−0.355[c]
S2TA	−0.0085	< 0.0001	−0.022	−0.418[c]
S2TB	−0.0163	< 0.0001	−0.041	−0.657[c]
S2TC	−0.0105	< 0.0001	−0.045	−0.532[c]
S2TD	−0.0150	< 0.0001	−0.043	−0.518[c]
S2TE	−0.0101	< 0.0001	−0.080	−0.532[c]
S3TA	0.0061	< 0.05	0.017	0.214[a]
S3TC	−0.0078	< 0.0001	−0.037	−0.461[c]
S3TD	−0.0077	< 0.0001	−0.051	−0.554[c]
S4TA	−0.0003	NS	−0.003	−0.025NS
S4TB	−0.0170	< 0.0001	−0.042	−0.576[c]
S4TC	−0.0145	< 0.0001	−0.038	−0.587[c]
S4TD	−0.0014	< 0.05	−0.013	−0.176[a]
S4TE	−0.0075	< 0.0001	−0.039	−0.442[c]
S5TA	−0.0095	< 0.0001	−0.050	−0.546[c]
S5TB	−0.0156	< 0.0001	−0.040	−0.606[c]
S5TC	−0.0128	< 0.0001	−0.044	−0.674[c]
S5TD	−0.0094	< 0.001	−0.058	−0.371[b]

Tau values with [a] indicate $p < 0.05$, [b] $p < 0.01$, and [c] $p < 0.0001$, NS = not significant.

Table 3. Estimated breakpoint for each tree based on the four homoegeneity tests. Asterisk indicates a significant break point ($p < 0.05$) detected by that test, regardless of whether the tests agree.

Tree	Buishand's Test	CUSUM	Pettit's Test	SNTH Test
S1TC	1941*	1942*	1941*	1942*
S1TE	1925*	1925*	1925*	1925*
S2TA	1928*	1942*	1927*	1949*
S2TB	1930*	1930*	1930*	1930*
S2TC	1935*	1935*	1935*	1935*
S2TD	1958*	1956*	1956*	1958*
S2TE	1973*	1975*	1973*	1983*
S3TC	1942*	1942*	1942*	1942*
S3TD	1917*	1917*	1920*	1917*
S4TA	1980	1996	1980	2008
S4TB	1947*	1947*	1926*	1947*
S4TC	1943*	1943*	1933*	1943*
S4TD	1941*	1941*	1941*	1941*
S4TE	1968*	1968*	1968*	1968*
S5TA	1941*	1941*	1943*	1939*
S5TB	1924*	1923*	1923*	1923*
S5TC	1923*	1923*	1929*	1923*
S5TD	1927*	1927*	1927*	1927*

Figure 1. The Deming Lake watershed, looking west-southwest. *P. resinosa* and *P. strobus* are the most common species in this area, though understory vegetation includes smaller hardwoods, shrubs and various grasses. Photo credit: Amy Myrbo.

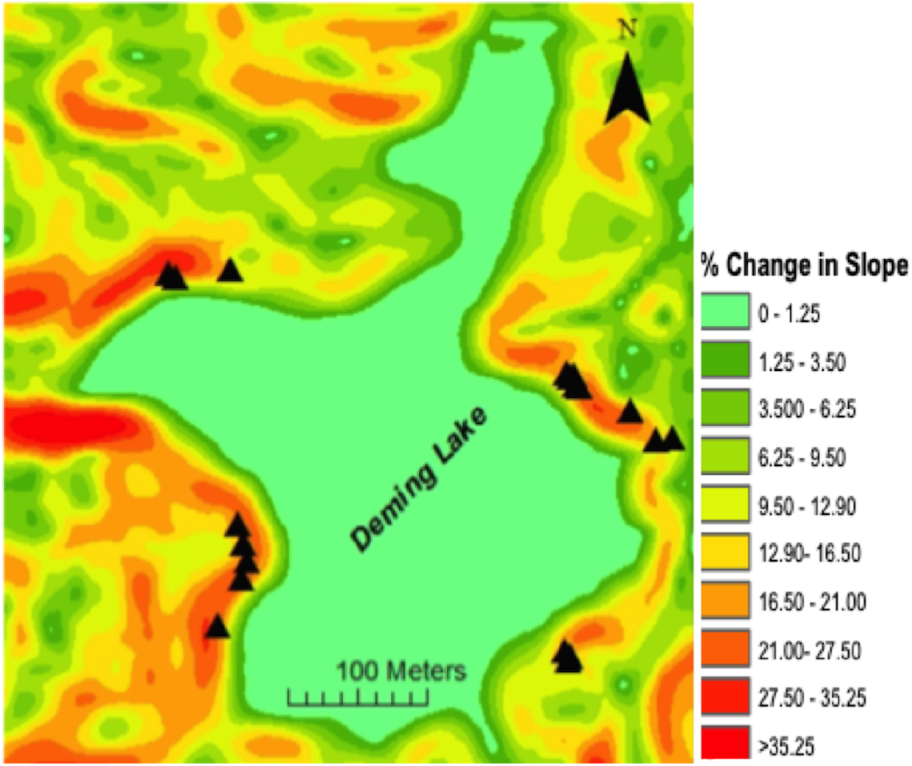

Figure 2. Map of Deming Lake with location of trees sampled and calculated slope values. A number of trees were sampled in relative close proximity to one another within the same stand and therefore symbols may represent more than one tree.

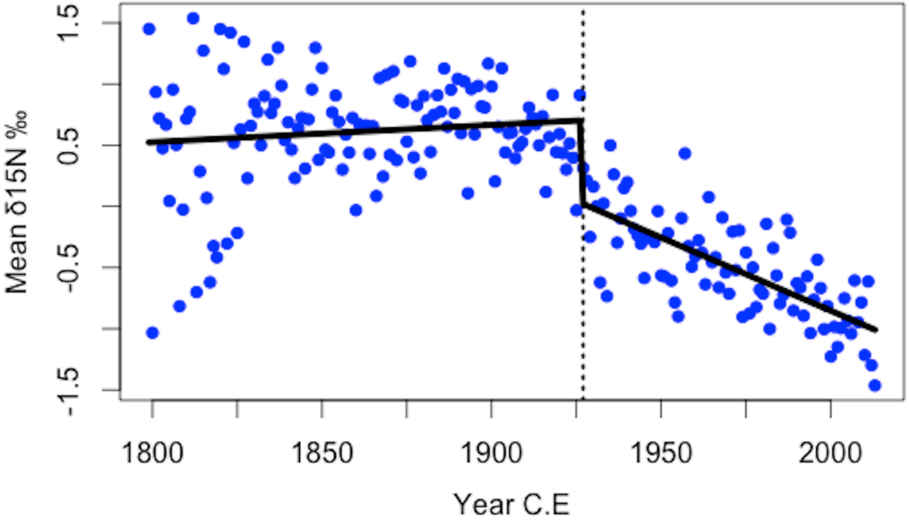

Figure 3. Piecewise regression line fit to the standardized δ^{15}N for the entire study site. For purposes of larger sample size, data for the period 1800–2013 were selected. Dashed line represents the significant change point of 1927 determined by change point tests. Sen's Slope prior to the determined 1927 breakpoint based on Mann–Kendall Trend Test is slightly positive albeit not significant ($p = 0.972$). The period of 1927–2013 has a significant ($p < 0.00001$) Sen's Slope of −0.012.

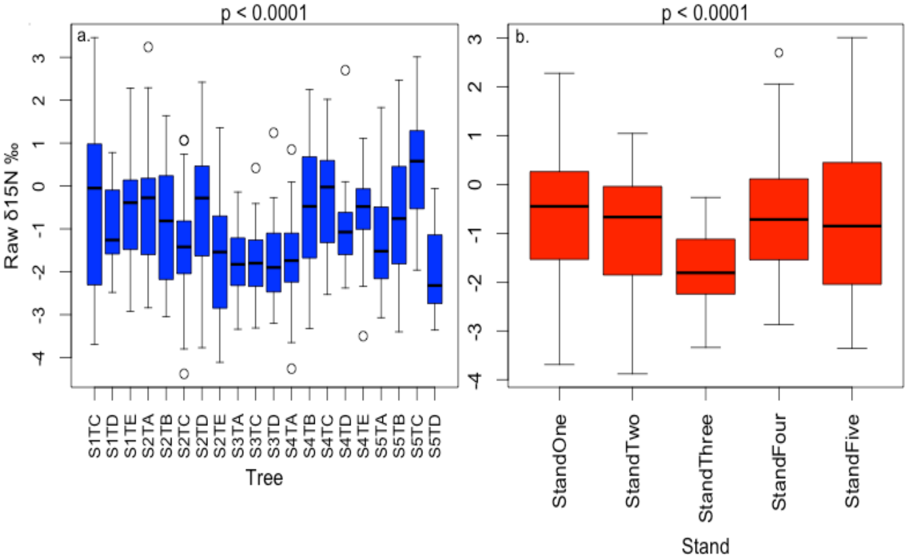

Figure 4. Comparison of N15 record with a 5-year smoothed raw wood N15 record. Blue indicates the WOOD N15 record (1775–2013), black indicates sediment N15 record (1749.5–2004.7)

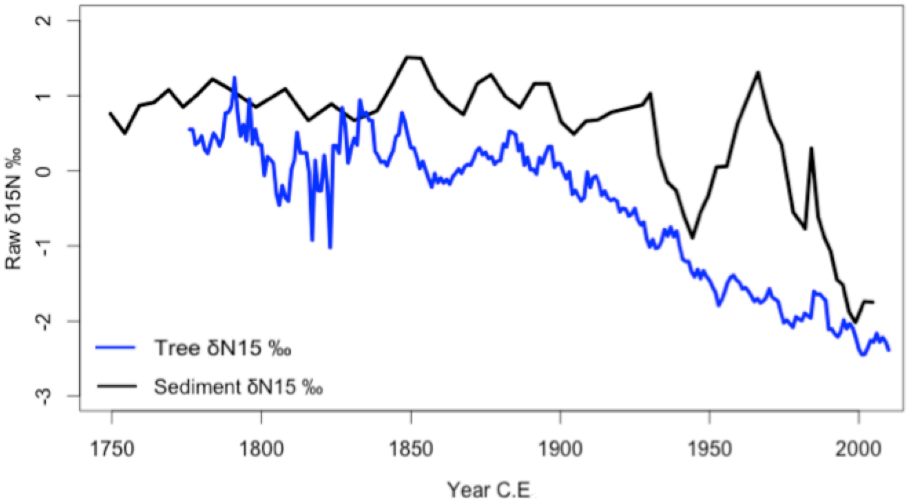

Figure 5. Comparison of sediment δ^{15}N record with a 5 year smoothed raw wood δ^{15}N record. Blue line indicates the sediment δ^{15}N record (1749.5–2004.7), black line indicates smoothed wood δ^{15}N record (1776–2013).

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀▮ | ▶▮
◀ | ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion