**Biogeosciences
Discussions**

# Species-specific trajectories of nitrogen isotopes in Indiana hardwood forests, USA

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**Nitrogen isotopes in hardwood forests**

K. K. McLauchlan and
J. M. Craine

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◀ | ▶

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Abstract

Humans have drastically altered the global nitrogen (N) cycle, and these alterations have begun to affect a variety of ecosystems. In North America, N deposition rates are highest in the Central US, yet there are few studies that examine whether N availability has been increasing to different tree species in the forests of the region. To determine the species-specific trajectories of N availability in secondary temperate forests experiencing high N deposition, we measured the N concentrations and composition of stable N isotopes in wood of four tree species from six hardwood forest remnants in Northern Indiana, USA. Annual nitrogen deposition rates averaged 5.8 kg ha$^{-1}$ from 2000 to 2008 in this region. On average, wood $\delta^{15}$N values in *Quercus alba* have been increasing steadily over the past 100 yr. In contrast, wood $\delta^{15}$N values have been declining in three other hardwood species – *Acer saccharum*, *Carya ovata*, and *Fagus grandifolia* – over the same time period. The species-specific trends suggest a change in the partitioning of ammonium and nitrate among species, a change in nitrification rates, and/or offsetting changes in the dependence of species on mycorrhizal fungi. With no apparent net change in wood $\delta^{15}$N over the past century at the stand level, on average there appears to have been little change in N availability for these forests despite high levels of N deposition in the region.

## 1 Introduction

Modern temperate forests are experiencing an unprecedented variety of anthropogenic changes on a global scale, such as increasing levels of atmospheric $CO_2$, increased temperature, and increased deposition of reactive forms of nitrogen (N) from the atmosphere (Kareiva et al., 2007). In addition to these regional- to global-scale changes, many forests are experiencing local changes in fire regimes, drought, and the introduction of non-native plants and animals while recovering from earlier logging and windthrow. Not only do many of these factors have the potential to interact in their

effects on forest processes, but they also have the potential to enhance or dampen N availability, which often limits primary productivity and influences forest species composition (Pepper et al., 2007). For example, experiments have suggested that elevated $CO_2$ may decrease terrestrial N availability (Johnson, 2006; Luo et al., 2004), while chronic N deposition may increase N availability to temperate forests (Aber et al., 2003).

Although understanding how global change factors affect the N cycle is of paramount importance to predicting 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 (Stoddard et al., 1999; Bernhardt et al., 2005). A more temporally-complete understanding of the modern trajectory of N cycling in forests requires extending records back in time beyond the modern record (Galloway et al., 2004). Analysis of the natural abundance ratios of $^{15}$N to $^{14}$N in wood of living trees can serve as a proxy record for the history of N cycling in terrestrial ecosystems (Bukata and Kyser, 2005, 2007; McLauchlan et al., 2007; Savard et al., 2009; Hietz et al., 2010). Although the N cycle is complex and the lack of direct climate information contained in N isotopes has previously hindered their use (McCarroll and Loader, 2004), recent analytical and conceptual advances suggest that N isotopic signatures in terrestrial ecosystems can be reliably interpreted (Savard, 2010; Houlton and Bai, 2009). Consensus is emerging that the standardized ratio of $^{15}$N to $^{14}$N ($\delta^{15}$N) in soil and leaves integrates a complicated terrestrial N cycle into a single metric that reflects terrestrial N availability (Craine et al., 2009). Briefly, there are a few major processes that alter the $\delta^{15}$N signature in plant material as compounds containing $^{15}$N are discriminated against in key steps of the N cycle (Högberg, 1997). The steps that fractionate most strongly are gaseous loss pathways, especially denitrification (Groffman et al., 2006; Menyailo and Hungate, 2006), gaseous loss during nitrification, and ammonia volatilization at high soil pH, and the transfer of N from mycorrhizal fungi to plants (Handley and Raven, 1992; Bedard-Haughn et al., 2003). Although there are many processes that discriminate against $^{15}$N, stand-level plant $\delta^{15}$N generally increases with increasing N availability,

here defined as the supply of N to terrestrial plants and soil microorganisms relative to their N demands (Schimel and Bennett, 2004). In forests, high $\delta^{15}$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 et al., 2002), and low reliance on mycorrhizal fungi for plant N uptake (Hobbie and Colpaert, 2003).

Wood in living trees provides a widespread and readily-available record of N isotopes associated with terrestrial ecosystems that can be used to reconstruct terrestrial N cycling. Wood has very low N concentrations, and most of the N in wood is located in proteins complexed with cellulose in cell walls (Bao et al., 1992; Showalter, 1993). A tiny proportion of N is mobile in sapwood, but most N is not mobile and N isotopes in wood have faithfully recorded clearance events in Ontario (Bukata and Kyser, 2005) and New Hampshire (McLauchlan et al., 2007), regional pollution in Eastern Canada (Bukata and Kyser, 2007; Savard et al., 2009), and short-term fertilization experiments in California (Hart and Classen, 2003) and France (Elhani et al., 2005). Ultimately, the analysis of natural abundance nitrogen isotopes in wood has the potential to elucidate whether forests are generally experiencing increased or decreased N availability.

In North America, some of the highest rates of N deposition occur in the Midwest region due to extensive inorganic fertilizer application to agricultural fields that began in the 1940s. The forests of this region are the most likely in North America to be experiencing eutrophication, but it is unknown how widespread this pattern might be or if all tree species in a forest respond similarly to the effects of N deposition. To better understand the changes in N cycling in temperate forests of the region, we obtained records of N isotopes, N concentrations, and ring widths from four tree species in six forest remnants in Northwestern Indiana. We expected to see an increase in wood $\delta^{15}$N in all hardwood tree species beginning in the mid-20th century. Alternatively, stand-level declines in wood $\delta^{15}$N would likely signal declines in N availability, while the lack of significant changes would indicate that N availability was not changing. We also analyzed the dendroisotopic records separately for each species, to assess whether

**Nitrogen isotopes in hardwood forests**

K. K. McLauchlan and J. M. Craine

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

there are species-specific trajectories of N isotopes that might signal species-specific changes in N availability or reliance on mycorrhizal fungi.

## 2  Methods

### 2.1  Study site

Increment bores were collected from six forest remnants in Northwest Indiana (Fig. 1). All sites are within 50 km of one another, in the Southern Great Lakes forests ecoregion (Olson et al., 2001). Extensive hardwood forests dominated by *Quercus alba* were common in the region prior to Euro-American settlement (Cowell and Hayes, 2007). These forests were cleared rapidly and converted to agricultural fields during the mid-19th century, and today the region is known as the Corn Belt, dominated by industrial agriculture. Each forest remnant contained a mix of species, generally with oaks (*Quercus* spp.) at all sites, shagbark hickory (*Carya ovata*) abundant in the drier sites, and sugar maple (*Acer saccharum*) and/or beech (*Fagus grandifolia*) abundant in the more mesic sites. N deposition in this area is among the highest in the US. The average amount of inorganic N deposited each year at these locations was 5.8 kg ha$^{-1}$ from 2000 to 2008 (National Atmospheric Deposition Program; http://nadp.sws.uiuc.edu). The source of this deposition is primarily inorganic N fertilizer applied to intensive corn and soybean agriculture in the region.

### 2.2  Increment bores: sampling, dating, and mass spectrometry

Sampling consisted of a 5.15 mm diameter increment bore that spanned the entire radius of each tree acquired 1 m above the forest floor. Replication focused on the region, so three individual living trees were sampled at each site, generally *Quercus alba*, *Carya ovata*, *Acer saccharum*, or *Fagus grandifolia* (hereafter referred to by genus only). Trees of different ages allowed us to test for temporal effects independent of tree

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

age (Hietz et al., 2010). Each increment bore was stored in a paper straw and dried at 60 °C until no further mass loss was observed. The face of each increment bore was sanded to increase the contrast between rings and then scanned at 1200 dpi. Each image was analyzed for ring width with Cybis CDendro software (Saltsjöbaden, Sweden).

5 The heartwood-sapwood boundary was determined visually on all but one increment bore. An age was assigned to each ring after cross-dating and close visual examination of the increment bore. After determination of ring width, each bore was weighed and divided into 30 mg segments along ring boundaries, providing enough N for mass spectrometry while maximizing the temporal resolution of the record and limiting the carbon

10 content and risk of incomplete combustion. The wood samples were not subjected to any chemical pretreatments based on results from (Bukata and Kyser, 2005; Hietz et al., 2010). The standardized ratio of $^{15}$N : $^{14}$N relative to air ($\delta^{15}$N) was determined for segments of wood at the Stable Isotope Mass Spectrometry Laboratory at Kansas State University on a ThermoFinnigan Delta Plus mass spectrometer interfaced with

15 a Carlo Erba 1110 elemental analyzer with Conflo II interface (Thermo Fisher Scientific Inc., Waltham, MA, USA), fitted with sequential traps of $MgClO_4$, NaOH on solid support (Carbosorb), and a cold trap in liquid $N_2$. Generally, every third segment of wood was analyzed resulting in an average length of time represented by a segment of 4.5 yr with 426 segments analyzed.

20 ## 2.3 Statistical methods

The data from the increment bores (wood $\delta^{15}$N, N concentration, and ring width) were manipulated as little as possible to reveal trends that might be obscured with detrending or statistical treatments that are applied temporally (Gavin et al., 2008). Average wood $\delta^{15}$N was standardized to the same mean value for each site. Extensive analysis of

25 the differences in chemical composition between heartwood and sapwood have been conducted (Savard et al., 2009; Hietz et al., 2010), and based on these results, N concentrations in wood deposited after 2000 C.E. were excluded from further statistical analyses. Wood N concentrations and $\delta^{15}$N for each increment bore were analyzed

with simple linear regression against age for all wood with dates after 1900 C.E., which helped account for different ages among individual trees and species and to facilitate comparisons among sites. Piecewise linear regressions were performed to identify potential breakpoints in the record, such as during the mid-20th century when inorganic fertilizer application began. We did not constrain the intercept for each portion of the record identified with piecewise linear regression.

## 3  Results and discussion

### 3.1  Long-term records of stable N isotopes

On average, values of wood $\delta^{15}$N for *Quercus* were 1.85‰ lower than the other three species ($-1.52$‰ vs. 0.33‰, $P < 0.001$) with no significant differences in average wood $\delta^{15}$N values among the other three species ($P = 0.77$). Standardizing wood $\delta^{15}$N among sites produced similar differences between the two species groups: *Quercus* wood $\delta^{15}$N values were 1.73‰ lower than those in the other hardwood species.

   Temporal trends in wood $\delta^{15}$N differed among the four hardwood species examined (Fig. 2). After standardizing wood $\delta^{15}$N so that all the sites had the same mean $\delta^{15}$N (0‰) from 1900–2008, *Quercus* wood $\delta^{15}$N increased over time with an inflection point (1986.5 ± 7.4) after which wood $\delta^{15}$N increased even faster. Before 1986, $\delta^{15}$N increased at a rate of 0.004‰ yr$^{-1}$. From 1987 on, *Quercus* wood $\delta^{15}$N increased by 0.055‰ yr$^{-1}$. In contrast, wood $\delta^{15}$N for the other three species – *Carya*, *Fagus*, and *Acer* – declined at a rate of 0.012‰ yr$^{-1}$ before 1980 and 0.045‰ yr$^{-1}$ after 1980. The point of inflection for these three species was 1980.5 ± 8.1. Analyzing the linear rates of change over the entire period of analysis, there was no significant difference among the three species in their trends ($P = 0.78$) (Fig. 2, Table 1). Thus, there are contrasting trends where *Quercus* wood $\delta^{15}$N has increased over time while wood $\delta^{15}$N for other hardwoods has decreased. All species experienced an acceleration of these isotopic trends, in opposite directions, in the 1980 s.

## 3.2 Wood N concentration

All species had higher N concentrations in wood formed after 2000 C.E., which was sapwood. Before 2000, N concentrations increased over time for both sets of species ($P < 0.01$ for both), but N concentrations increased more for *Quercus* (0.0056 mg g$^{-1}$ yr$^{-1}$) than for other species (0.0015 mg g$^{-1}$ yr$^{-1}$) ($P < 0.001$) (Fig. 3). Sapwood has been shown to have higher N concentrations than heartwood in several tree species (Merrill and Cowling, 1966), and this pattern is consistent in both un-treated wood and wood treated to remove water- and lipid-soluble compounds (Hietz et al., 2010). Thus, the higher N concentrations in sapwood than heartwood cannot be entirely explained by the higher proportion of labile N-containing compounds in liv-ing cells, and future research should help identify under what conditions a chemical extraction procedure might be useful and describe standardized methods for wood treatment prior to N isotopic analysis in environmental research. Wood N concentra-tions and $\delta^{15}$N values for each increment bore are shown in Fig. 4. The position of the heartwood-sapwood boundary varies among individual increment bores.

## 3.3 Age of trees and ring-width increments

Differences in temporal trends in wood $\delta^{15}$N values between the two sets of species were not due to differences in the ages of trees. The oldest wood sampled for all trees ranged from 1855 to 1953 C.E. (Table 1). The oldest wood we sampled for *Quercus* averaged 1898 C.E. among trees, compared with 1880 C.E. for *Carya*, 1922 C.E. for *Acer*, and 1916 C.E. for *Fagus*. Nor were there marked differences in radial increment trajectories for the two sets of species. On average, since 1900 C.E. the ra-dius of *Quercus* trees increased by $2.34 \pm 0.04$ mm yr$^{-1}$, while other species increased at just $1.66 \pm 0.03$ mm yr$^{-1}$. Yet, radial increment for all species declined over time, with *Quercus* radial increment decreasing at a rate of 0.01 mm yr$^{-1}$ and other species at 0.005 mm yr$^{-1}$ ($P = 0.003$). All six sites exhibit expected trends of reduced radial growth over time.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

The demography of nearby old-growth forest stands in Indiana indicates that the composition of tree species will be shifting in the near future, as canopy species such as *Quercus* spp. are replaced by subcanopy species such as *Acer saccharum* (Cowell and Hayes, 2007). High mortality in the subcanopy and a limited role of canopy gaps for favoring *Quercus* spp. may complicate these dynamics, however (Cowell et al., 2010). Our results indicate that altered nutrient dynamics in these forest remnants surrounded by agriculture are not substantially influencing these normal demographic processes.

## 3.4 Potential processes in this region

The different trajectories in wood $\delta^{15}$N between *Quercus* and the other hardwood tree species could be caused by several factors. The *Quercus* wood $\delta^{15}$N consistently increased at all sites over the duration of the record, which if it were typical of stand-level signatures would indicate increasing N availability, either through enrichment of N sources to the trees or reduced reliance on mycorrhizal fungi. Yet, the increases in *Quercus* wood $\delta^{15}$N were accompanied by decreases in wood $\delta^{15}$N of *Acer*, *Fagus*, and *Carya* species from the same stands. There are few single factor explanations that can explain the pairing of the two opposite $\delta^{15}$N trajectories.

One possibility is a partitioning of N sources among tree species. There is some evidence that herbaceous plant species partition sources of N such that consistent, interpretable differences among species in foliar $\delta^{15}$N are maintained (Kahmen et al., 2008). Over time, this could lead to species-specific trajectories of $\delta^{15}$N in plant tissue, as the type and quantity of N sources vary. However, there has been little evidence for this effect in wood $\delta^{15}$N to date. When the wood $\delta^{15}$N of two or more species have been studied in the same locations, trees generally exhibit the same trends in isotopic composition over time, even species with different growth forms, secondary compounds, wood anatomy, ecology, and function such as conifers and hardwoods (Savard et al., 2009). This could be a function of spatial scale, where the relative strength of regional processes such as N deposition and local processes such as species interactions determines the direction and type of signal in wood $\delta^{15}$N values.

Nitrification, the conversion of ammonium to nitrate, is a strongly fractionating step that results in isotopic enrichment of $NH_4^+$ and depletion of $NO_3^-$. On average, the $\delta^{15}N$ values of *Quercus* wood were lower than those of *Acer*, *Fagus*, and *Carya*, which would suggest a greater reliance of *Quercus* on $NO_3^-$ than $NH_4^+$ (Kahmen et al., 2008).

5 If *Quercus* took up less $NO_3^-$ over time and the other species took up more $NO_3^-$ over time, then this would lead to a gradual enrichment of wood $\delta^{15}N$ in *Quercus* and a depletion of wood $\delta^{15}N$ in the other species. Similarly, if N mineralization rates relative to plant demand were constant over time and nitrification rates became higher, this would also likely lead to a narrowing of the difference in wood $\delta^{15}N$ between the two sets

10 of species. The type of mycorrhizal association varies among these hardwood tree species: *Quercus*, *Fagus*, and *Carya* form associations with ectomycorrhizal fungus, while *Acer* forms associations with arbuscular mycorrhizal fungus. Although this hypothesis requires further testing, ectomycorrhizal *Quercus* seedlings have been shown to have a greater relative preference for $NO_3^-$ over $NH_4^+$ when compared to *Acer* (Tem-

15 pler and Dawson, 2004).

Other potential explanations for patterns in wood $\delta^{15}N$ over time are possible, but are generally less parsimonious. For example, plant species that rely on ectomycorrhizal fungi are much more depleted in $^{15}N$ than other species as a result of the fungi transferring depleted N to the plants. The increase in *Quercus* wood $\delta^{15}N$ since 1900 C.E.

20 could be driven by a reduction in the reliance of the *Quercus* species on mycorrhizal fungi, but this would not explain the concomitant decline in $\delta^{15}N$ of *Acer*, *Fagus*, and *Carya*. Another alternative explanation is that the hardwood tree species are taking up different amounts of the deposited N, such that the recent wood $\delta^{15}N$ signatures reflect the isotopic signature of deposited N. This is also somewhat unlikely because there is

25 high variability in the isotopic signature of N deposited from fossil fuel sources. The $\delta^{15}N$ values for deposited nitrate are circumneutral but range from $-8.1\,‰$ to $3.2\,‰$ in the Eastern US (Elliott et al., 2007). Additionally, a N-deposition explanation fails to account for two aspects of the data: the past divergence of the wood $\delta^{15}N$ values between *Quercus* and the other hardwood species (almost $3\,‰$ in 1900 C.E.) and the

lack of a mid-century breakpoint when fertilizer use, and anthropogenic N deposition, commenced in the region.

When comparing temporal trends between regions, the absolute amount of N deposition could be important. A deposition station close to the Indiana forest locations has been averaging approximately $6\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ of inorganic N wet deposition over the past decade, and the sites we studied receive approximately 5.76 to $6\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ (Fig. 1). In a New Hampshire secondary forest, wood $\delta^{15}$N had consistently declined among five species from 1929 to 2005 C.E., with no indication of wood $\delta^{15}$N significantly increasing for any species (McLauchlan et al., 2007). This decline in wood $\delta^{15}$N was consistent with the hypothesis that N availability had been declining due to forest regrowth. N deposition rates are approximately 20 % higher in Northwest Indiana than they are in New Hampshire, yet there has been no evidence of consistent increases in wood $\delta^{15}$N in the Indiana forests. In Brazil, with very low anthropogenic N deposition, wood $\delta^{15}$N has generally been increasing during the 20th century (Hietz et al., 2010).

In all, determination of whether stand-level $\delta^{15}$N for these forests is increasing or decreasing will require more precise weighted mass-balance assessments, but there is currently little evidence for consistent trends in stand-level N availability over time in the Indiana forests. Regardless, the analyses of the wood $\delta^{15}$N in these Indiana forests reveals clear species-specific trajectories that may reflect differences in resource partitioning. Future research on patterns of dendroisotopic $\delta^{15}$N should include a range of species in a given stand and not assume that patterns for one species are representative of others. In addition, mechanistic work that investigates the role of N fertilizer, associations with mycorrhizal fungus, and progressive N limitation at different spatial scales is likely to be necessary to begin to separate the various hypotheses about the species-specific trajectories for these forests.

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**Nitrogen isotopes in hardwood forests**

K. K. McLauchlan and
J. M. Craine

Title Page

| Abstract | Introduction |
| Conclusions | References |
| Tables | Figures |

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Houlton, B. Z. and Bai, E.: Imprint of denitrifying bacteria on the global terrestrial biosphere, P. Natl. Acad. Sci. USA, 106, 21713–21716, doi:10.1073/pnas.0912111106, 2009.

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**Nitrogen isotopes in hardwood forests**

K. K. McLauchlan and J. M. Craine

Title Page

| Abstract | Introduction |
| Conclusions | References |
| Tables | Figures |

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 1.** Simple linear regressions between wood $\delta^{15}$N and year of wood formation for eighteen trees sampled in Indiana, USA. The slope is since 1900. Tree diameter (diam) is based on the length of increment bore. First year is the earliest date for wood analyzed, not the pith date or year established.

| Site | Species | First year (C.E.) | Diam (cm) | $r^2$ | $m$ | $P$ |
|------|---------|-------------------|-----------|-------|-----|-----|
| Black Rock Barrens | *Carya ovata* | 1943 | 26 | 0.91 | −0.038 | < 0.001[*] |
| | *Quercus alba* | 1920 | 45 | 0.00 | 0.001 | 0.83 |
| | *Quercus alba* | 1938 | 22 | 0.33 | −0.013 | 0.03[*] |
| Bryan Woods | *Carya ovata* | 1872 | 44 | 0.37 | −0.014 | 0.002[*] |
| | *Acer saccharum* | 1948 | 30 | 0.71 | −0.027 | < 0.001[*] |
| | *Quercus alba* | 1855 | 74 | 0.16 | 0.010 | 0.05[*] |
| Cumberland Woods | *Carya ovata* | 1861 | 45 | 0.29 | −0.011 | 0.05[*] |
| | *Acer saccharum* | 1938 | 55 | 0.69 | −0.017 | < 0.001[*] |
| | *Quercus alba* | 1881 | 19 | 0.01 | 0.002 | 0.68 |
| McCormick Woods | *Carya ovata* | 1872 | 80 | 0.61 | −0.008 | < 0.001[*] |
| | *Acer saccharum* | 1893 | 33 | 0.65 | −0.017 | < 0.001[*] |
| | *Quercus alba* | 1893 | 42 | 0.36 | 0.013 | 0.001[*] |
| Purdue Arboretum | *Fagus grandifolia* | 1916 | 44 | 0.30 | −0.015 | 0.01[*] |
| | *Acer saccharum* | 1922 | 46 | 0.55 | −0.011 | < 0.001[*] |
| | *Quercus alba* | 1939 | 46 | 0.55 | 0.028 | < 0.001[*] |
| Rosebank Woodlot | *Carya ovata* | 1856 | 74 | 0.66 | −0.018 | < 0.001[*] |
| | *Quercus alba* | 1863 | 37 | 0.62 | 0.019 | < 0.001[*] |
| | *Acer saccharum* | 1953 | 33 | 0.62 | −0.039 | < 0.001[*] |

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

⏮ | ⏭

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Nitrogen isotopes in hardwood forests**

K. K. McLauchlan and
J. M. Craine

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

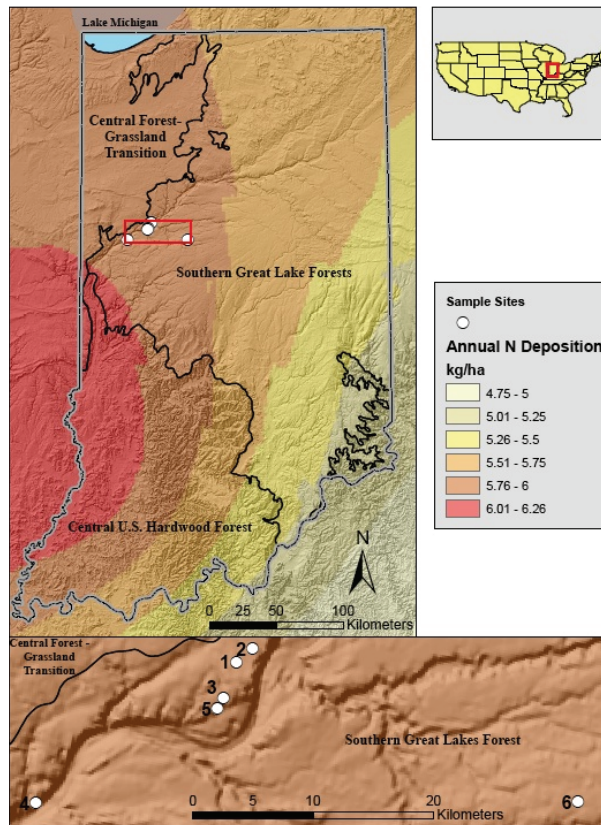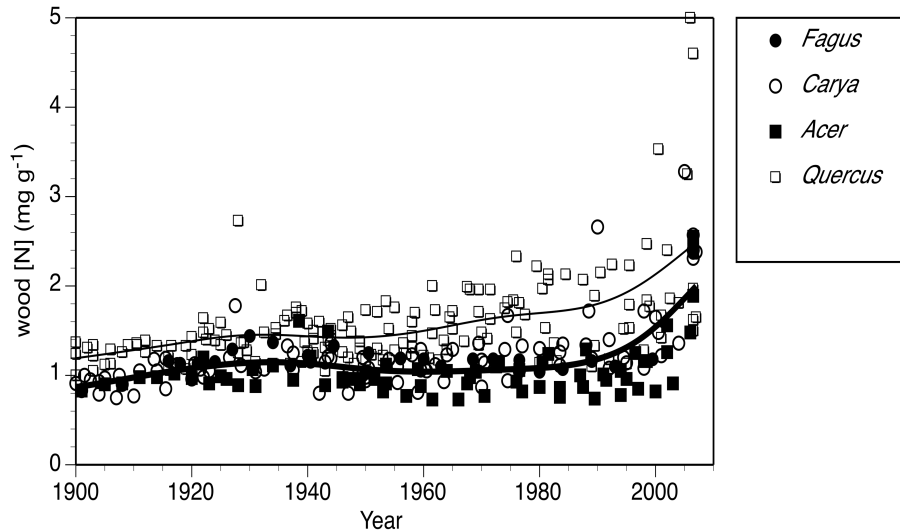Printer-friendly Version

Interactive Discussion



**Fig. 1.** Locations of six study sites in Indiana, with interpolated N deposition from the National Atmospheric Deposition Program, ecoregions delineated by the World Wildlife Fund, and topography from the United States Geological Survey. On the lower panel, 1 is Cumberland Woods, 2 is Rosebank Woods, 3 is McCormick Woods, 4 is Black Rock Barrens, 5 is Purdue Arboretum, and 6 is Bryan Woods.

Full Screen / Esc
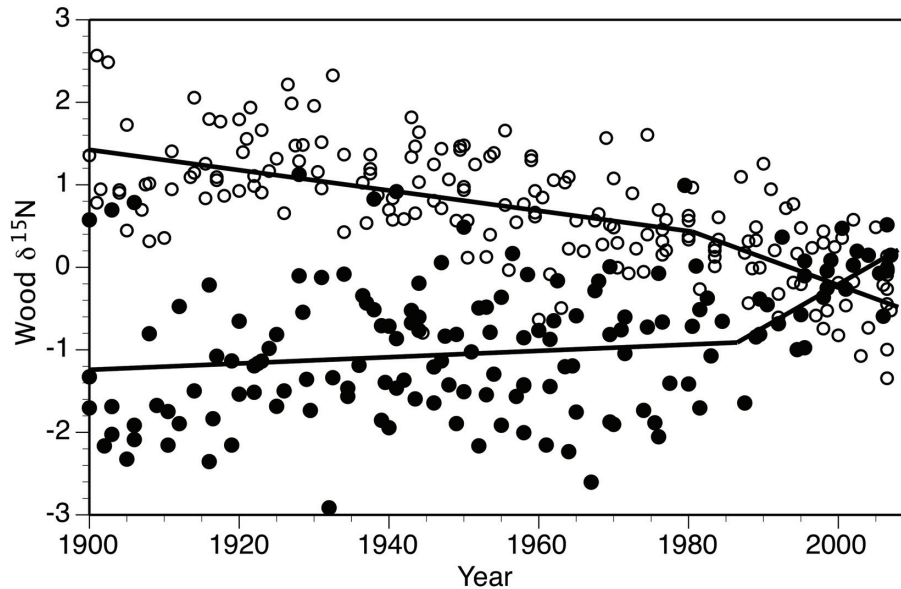
**Fig. 2.** Wood $\delta^{15}$N over time standardized to the same mean (0‰) across sites for *Quercus alba* (solid circles) and three other hardwood species (*Carya ovata*, *Fagus grandifolia*, and *Acer saccharum*, open circles). Lines represent piecewise linear regression. Inflection dates are 1986 for *Quercus alba* and 1980 for the other species.

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Fig. 3.** Wood (N) over time. The thin line is a spline fit for *Quercus* wood, while the thick line is a spline fit for the three other hardwood species.

Full Screen / Esc

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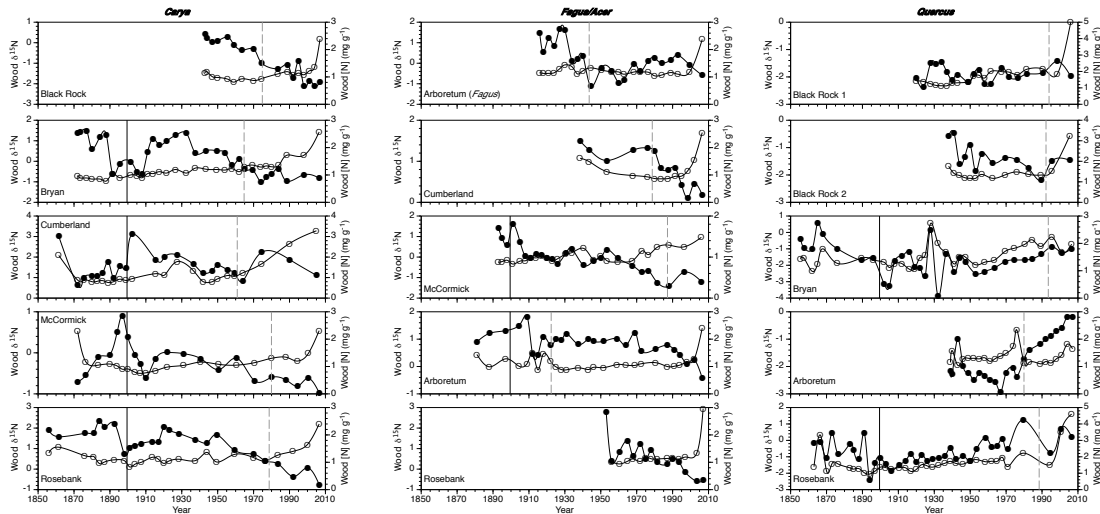
Interactive Discussion



**Fig. 4.** Nitrogen characteristics of wood samples from each individual tree sampled. For each increment bore, solid circles indicate wood $\delta^{15}$N, open circles are wood N concentrations, the solid line is 1900 C.E. and the dashed line is the heartwood-sapwood transition.