JGR Biogeosciences

Nitrogen Cycle Patterns During Forest Regrowth in an African Miombo woodland Landscape

Marc Mayes[1,2,3] (iD), Jerry Melillo[2] (iD), Christopher Neill[4,2], Cheryl Palm[5], Jack Mustard[1], and Gerson Nyadzi[6]

[1]Department of Earth, Environmental and Planetary Sciences, Brown University, Providence, RI, USA, [2]The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, USA, [3]Present address: Earth Research Institute, University of California, Santa Barbara, CA, USA, [4]The Woods Hole Research Center, Falmouth, MA, USA, [5]Institute for Sustainable Food Systems, University of Florida, Gainesville, FL, USA, [6]Millennium Promise Tabora, Tabora, Tanzania

Abstract Tropical dry forests in eastern and southern Africa cover 2.5×10^6 km^2, support wildlife habitat and livelihoods of more than 150 million people, and face threats from land use and climate change. To inform conservation, we need better understanding of ecosystem processes like nutrient cycling that regulate forest productivity and biomass accumulation. Here we report on patterns in nitrogen (N) cycling across a 100-year forest regrowth chronosequence in the Tanzanian Miombo woodlands. Soil and vegetation indicators showed that low ecosystem N availability for trees persisted across young to mature forests. Ammonium dominated soil mineral N pools from 0- to 15-cm depth. Laboratory-measured soil N mineralization rates across 3- to 40-year regrowth sites showed no significant trends and were lower than mature forest rates. Aboveground tree N pools increased at 6 to 7 kg N·ha^{-1}·yr^{-1}, accounting for the majority of ecosystem N accumulation. Foliar δ^{15}N <0‰ in an N-fixing canopy tree across all sites suggested that N fixation may contribute to ecosystem N cycle recovery. These results contrast N cycling in wetter tropical and Neotropical dry forests, where indicators of N scarcity diminish after several decades of regrowth. Our findings suggest that minimizing woody biomass removal, litter layer, and topsoil disturbance may be important to promote N cycle recovery and natural regeneration in Miombo woodlands. Higher rates of N mineralization in the wet season indicated a potential that climate change-altered rainfall leading to extended dry periods may lower N availability through soil moisture-dependent N mineralization pathways, particularly for mature forests.

Plain Language Summary In dry tropical Miombo woodlands of sub-Saharan Africa, forests have experienced high rates of clearing and degradation from growing demands for land and resources (e.g., charcoal, firewood). A lack of knowledge regarding controls on forest regrowth, such as nutrient cycling, has limited development of recommendations for managing regrowth as part of forest landscape restoration. This work studied patterns of ecosystem nitrogen (N) availability with regrowth, and how the sensitivity of N availability from an important soil decomposition process (N mineralization) varied between wet and dry seasons in the Tanzanian Miombo. Across 12 sites spanning a 100-year regrowth chronosequence, increases in ecosystem N stocks were dominated by aboveground vegetation (trees). Soil N mineralization of regrowth sites did not recoup rates of mature forests. Sources and processes whereby trees accumulated N were unclear from the data, but evidence suggested the importance of redistribution of N from soil to vegetation and a possible role for N fixation. We also found in lab measurements that N mineralization rates were 2 to 3 times higher in the wet than dry season. For management of regrowth and forest landscape restoration, results indicated the importance of maintaining aboveground biomass in regrowth forests for conserving ecosystem N resources.

1. Introduction

The Miombo woodlands contain the largest tropical dry forest regions in southern Africa (>2.5 M/km^2) and provide food, water, energy, and income to >150 million people across 11 nations (Frost, 1996; Rudel, 2013). By 2050, the population of Miombo region countries is projected to more than double to >350 M, equivalent to adding the total present population of western Europe to the region in 35 years (United Nations, Department of Economic and Social Affairs, 2015). Although Miombo landscapes are mosaics of mature forest, shifting cultivation, grazing lands, and regrowing forests that have historically experienced high rates of

disturbance, recent increases in resource demands greatly threaten the extent and integrity of regional forests (Rudel, 2013). Miombo regions have experienced globally high forest clearing rates since 2000, and many tree species valuable for human use as timber or other ecological services are endangered (Hansen et al., 2013; Rudel, 2013; Schwartz et al., 2002). Growing demand for wood-derived biomass energy is also a significant threat to forests in fast-growing Miombo-region countries such as Tanzania, where charcoal is the primary cooking fuel of up to 80% of urban households (Mwampamba, 2007) and up to 30% of deforestation in Tanzania has been attributed to charcoal production (Chidumayo & Gumbo, 2013).

Climate changes involving increased temperature and altered rainfall regimes may also affect forest capacity for regrowth in such water-limited systems (Wang et al., 2015). Recent climate model projections all predict altered timing and duration of rainy seasons and more episodic rainfall regimes in the Miombo region (Dunning et al., 2018; Lyon & DeWitt, 2012; Ongoma, Chen, et al., 2018). Such changes stand to affect dynamics of ecosystem moisture availability for tree and grass productivity, litter decomposition and soil nutrient cycling processes, and other ecosystem services (Wang et al., 2015).

Controls on forest regrowth and recovery from disturbance are not well understood in the Miombo woodlands. Forest landscape restoration programs that include management for natural regeneration alongside agricultural development are expanding across southern and eastern Africa and have potential to maintain Miombo forests and their services (Chazdon, 2008; WRI, 2016). Improved knowledge of ecosystem processes, such as the recovery and maintenance of nutrient cycling during forest growth, can inform decisions regarding management strategies to conserve Miombo forest areas.

Established paradigms predict that phosphorus (P) ultimately limits productivity in tropical forests on highly weathered soils (Chadwick et al., 1999; Davidson et al., 2007). More recent experiments and regrowth sequences in Neotropical humid and dry forests indicate that the supply of plant-available mineral N (ammonium (NH_4^+) and nitrate (NO_3^-)) in soil limits forest regrowth following disturbance, but this limitation diminishes as forests mature (Davidson et al., 2004, 2007; Saynes et al., 2005; Waring, Becknell, et al., 2015). Because forest areas in the Miombo are woodlands with mixed tree-grass cover and frequent fire, it is unclear if they exhibit low-N conditions as found in tropical savannas such as the Brazilian Cerrado, or more rapid recovery of N availability with regrowth as seen in moister tropical forests (Bustamante et al., 2004; Davidson et al., 2007; Saynes et al., 2005). Decades of research indicate that N availability is often low in dry tropical regions (Wang et al., 2015) and limits plant productivity in agriculture and agroforestry in southern Africa (Sileshi & Akinnifesi, 2008; Vitousek et al., 2009). Low N availability also likely limits rates of Miombo forest regrowth, but this has not been studied in detail.

There are reasons to suspect Miombo woodlands have low N supplies relative to tree N demand, and that land use and climate-change pressures may negatively affect N availability for forest growth. A substantial fraction (about 40%) of Miombo woodlands grow on ancient, highly weathered terrains with sandy to sandy loam soils (Ultisols, Acrisols) that are low in organic matter (soil organic carbon (SOC) < 2%) and experience strong water and nutrient limitation (Batjes, 1996; Frost, 1996; Martinelli et al., 1999; Palm et al., 2007). Sandy to sandy loam soil textures limit buildup of soil organic matter that stores soil N (Palm et al., 2007; Schmidt et al., 2011). The Miombo has a seasonally dry climatology, defined as location with between 250- and 2,000-mm annual rainfall and a three- to four-month or longer dry season with erratic rainfall distribution (Murphy & Lugo, 1986). This makes extended periods of low soil moisture common and limits decomposition and release of organically bound N through mineralization (Palm et al., 2007; Schimel & Bennett, 2004). Fire can further exacerbate N loss through volatilization and retard soil N accumulation (Frost, 1996). Long-term, widespread shifting smallholder agriculture has occurred throughout the Miombo region, and this has resulted in estimated annual N "mining" from soil because N removed from crop biomass exceeds nutrient inputs (Vitousek et al., 2009). It is also unclear what processes contribute significant N inputs to Miombo ecosystems as forest regrow. Candidates include N fixation, which is estimated to provide 2–6 kg N ha^{-1} yr^{-1} in the dry tropics (Houlton et al., 2008), or atmospheric deposition, estimated to supply 3–5 kg N·ha^{-1}·yr^{-1} over eastern and southern Africa, although this is uncertain and variable (Bobbink et al., 2010; Lamarque, 2013).

Here we report on patterns in N cycle indicators across a forest regrowth chronosequence spanning more than 100 years in the Tanzanian Miombo woodlands. Combining data on canopy structure, foliar tissue, and soils, we evaluated indicators of ecosystem N availability across regrowth and mature forest sites, and

between wet and dry seasons, over a 400-km^2 region. Our hypothesis was that ecosystem N availability would remain low relative to tree demand in regrowing forests in this landscape, and reflect broad influences of low N inputs from woody vegetation productivity, frequent disturbance, and edaphic factors linked to sandy soils and fire that limit accumulation of plant-available N. To explore evidence for N fixation across regrowth sites, we focused our foliar sampling to compare foliar N concentrations and N stable isotope composition (δ^{15}N) among a canopy tree species shown to actively fix N in Miombo ecosystems (*Pterocarpus angolensis*; Högberg, 1986; Mehl et al., 2011), and two non-N-fixing trees, a canopy dominant (*Brachystegia spiciformis*) and a pioneer species (*Terminalia sericea*).

2. Materials and Methods

2.1. Study Region and Experimental Design

Our study landscape in Tabora, Tanzania, is located in the northeastern range of the Miombo woodlands (Figure 1). Tabora has a seasonally dry tropical climate, with mean annual temperature of 23.9 °C, and annual precipitation ranging from 700 to 900 mm/year. Rain typically falls from November to May, with a six-month dry season (for an example rainfall record to visualize the seasonal pattern; see M. T. Mayes et al., 2015). Woodlands in Tabora occur predominantly on sandy, highly weathered, nutrient-poor Ultisols derived from ancient granite and gneissic parent material, interspersed with low-lying drainages (mbuga) dominated by grasses and poorly draining Vertisols (Frost, 1996). Dominant woodland trees include species of the *Brachystegia* and *Julbernardia* genera, along with canopy trees such as *P. angolensis* in which past research has confirmed nitrogenase activity in root nodules indicating active N fixation (Högberg, 1986).

This study took advantage of numerous abandoned agricultural lands undergoing natural regeneration around Tabora to study the evolution of N cycling with forest regrowth. Complex patterns of agricultural land use, grazing, disturbance, and abandonment since the late 1800s has created a matrix of varying-age woodland stands across the Tabora region. Population growth and increasing demand for forest resources has resulted in increasing land use pressures on local woodlands. Central Tabora's population (2.3 million, 2012) has grown at rates over 2% per year (URT, 2014). It experienced a 15% net loss of forest area between 1995 and 2011 largely caused by expansion of smallholder agriculture in this region, but also from land-clearing for charcoal production, which is on the rise as demand grows in urban markets of Tabora town and other distant cities, and paving of national roads increases market accessibility. Interestingly, forest areas that had regrown since 1995 comprised 16% of Tabora regional forest cover in 2011(M. T. Mayes et al., 2015). Increasing proportions of standing forest cover represent recent (<30 years) naturally regenerated woodland stands. Aside from regions such as a local army base, to which open access was prohibited, most mature and regrowth forests experience some degree of grazing pressures from cows and goats, particularly in the dry season when browse and forage is scarce in grasslands.

2.2. Field Site Locations and Layout

We identified forest chronosequence sites through a combination of remote sensing analyses (M. T. Mayes et al., 2015), field visits, and interviews with local people about land use and fire histories (Figure 1b). We chose regrowth forest sites that represented widespread shifting agricultural practices prior to regrowth, which included the following conditions: (1) sites were previously cultivated with maize for at least 20 years during the period they were actively farmed and (2) did not experience fire within two to three years prior to sampling. All forest sites experienced grazing pressure from cattle and goats to some degree. Since information on past agricultural, fire history, and grazing pressures was ascertained by informal survey of land-holders. A key assumption in site selection was that the influences of past cultivation, fire, and grazing processes was "controlled" and that the main covariate among all was regrowth age. In effort to check farmer responses, all interviews were done with at least two people present, the current landowner and a village elder familiar with the region for at least 40 years or more, and sites having regrown since 1990 were cross-checked with remote sensing analyses (Mayes et al., 2015; Mayes et al., 2017). We took pilot soil cores to a depth of 190 cm for basic soil property characterization as we searched for accessible regrowth chronosequence sites. Pilot soil cores were taken at five mature forest sites, four regrowth forest sites of mixed ages (10–30 years since agricultural abandonment), and four sites in active maize cultivation. Predominant features of regrowth chronosequence sites included location on flat terrain (slope <2%), sandy soil texture
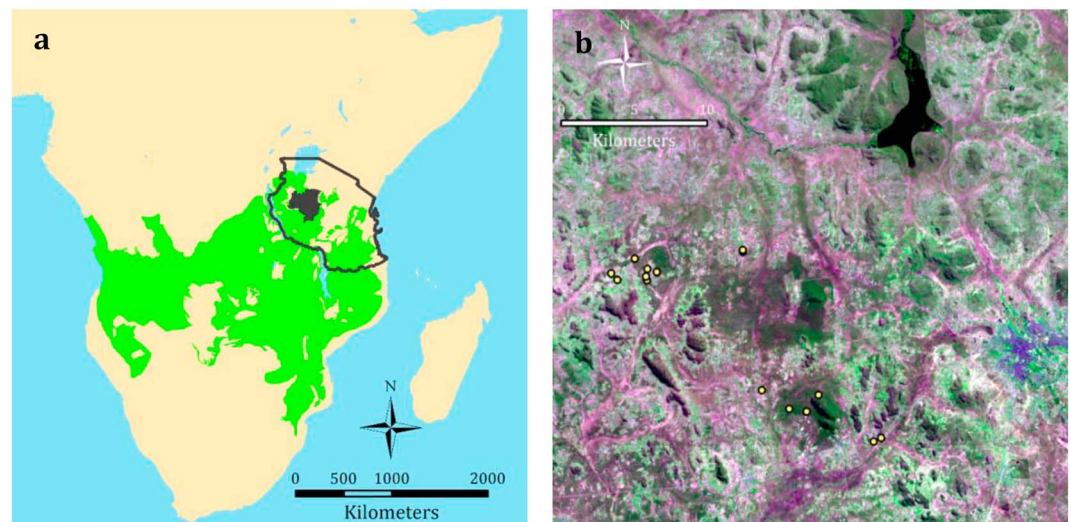
Figure 1. Location of the study region and forest chronosequence sites in Tabora, Tanzania. (a) Miombo woodlands are shown in green (dry tropical forest-containing regions in sub-Saharan Africa subset from the Nature Conservancy Ecoregions data set, http://maps.tnc.org/gis_data.html). The national boundary of Tanzania is shown in black, and Tabora Province shown in solid black. (b) The Tabora woodlands studied here are located in the center of Tabora Province, with field sites indicated by yellow dots against a June 2014 Landsat 8 false-color image. The Landsat 8 false color image (14 June 2015) shows in red-green-blue colors band 6 (shortwave-infrared 1.57–1.65 µm), band 5 (near-infrared 0.85–0.88 µm), and band 7 (shortwave-infrared 2.11–2.29 µm).

(surface soils >70% sand), and approximately 20-year histories of maize cultivation prior to abandonment and subsequent forest regrowth. For the main study, we chose 12 sites for vegetation and soil measurements: nine regrowth sites aged 3 years (two sites), 4, 10, 16, 24, 30, and 40 years (two sites) and three mature forest sites >100 years. Field sites were laid out as 50 × 50-m plots, with four 10-m-radius circular subplots distributed in a stratified random sampling design. This field site layout had previously been determined as efficient for representing the spatial variability of aboveground carbon stocks in woody vegetation in prior studies of carbon accumulation with regrowth in Miombo woodlands of Mozambique (Williams et al., 2008).

2.3. N Cycle Indicators in Soils and Vegetation

Our goal for field data collection was to sample major soil and vegetation indicators of ecosystem N availability for tree growth across the chronosequence, over the sequence of a complete growing season (wet and dry seasons, 2015). The soil N cycle indicators we measured included soil total organic carbon (C), total N, soil mineral N (ammonium (NH_4^+) + nitrate (NO_3^-)) concentrations and lab-measured mineralization potentials over 14-day incubations, and soil $\delta^{15}N$. To evaluate vegetation-based evidence for the prevalence of N fixation with regrowth, we focused sampling on three trees. These included a documented canopy N-fixer *P. angolensis* (family Fabaceae), and two non-N-fixing species, a common Miombo canopy dominant *B. spiciformis* (family Caesalpiniaceae) and a local pioneer species, *T. sericea* (family Combretaceae; Frost, 1996; Högberg, 1986).

2.3.1. Soil Data

At the 12 main regrowth sites, we sampled soils at four points per field site (center points of each circular subplot), at 0–5- and 5–15-cm depths, in wet (March–April 2015) and late dry seasons (September–October 2015), and measured soil temperatures at the time of sampling. Soils were sieved (2 mm) and composited across cores within each site. We measured soil moisture via oven-drying for gravimetric water loss over 48 hr at 105 °C immediately after sampling in Tabora, Tanzania. We measured soil organic carbon, total nitrogen, and soil $\delta^{15}N$ via subsequent analyses, at the Marine Biological Lab Stable Isotope Laboratory on a Europa ANCA-SL elemental analyzer-gas chromatograph preparation system, interfaced with a continuous-flow Europa 20-20 gas source stable isotope ratio mass spectrometer. Soil mineral N (ammonium and nitrate) was assessed via 24-hr potassium chloride (KCl) extraction subsequent analyses of the extracts.

For mineral N concentrations, soil KCl extractions were performed in Tabora, Tanzania immediately after sampling, transported frozen, and analyzed at Marine Biological Lab. We assessed soil N mineralization via 14-day aerobic laboratory incubations in a dark room at ambient temperature (~28 °C) in Tabora, begun on the same day as sampling, with repeat KCl extracts performed after 14 days.

At pilot sites, soils were sampled in a single coring location per site away from field edges and forest boundaries. Soils were bulked in six depth increments: 0–15, 15–30, 30–50, 50–100, 100–150, and 150–190 cm. Soil texture analyses were only possible for the pilot soil cores with depth (not the regrowth transect sites). Soil texture was measured with a basic field texture kit consisting of settling tubes (LaMotte #77330, Chestertown, MD, USA) and pH was measured in water with a pH electrode. Bulk soil organic carbon and total nitrogen were measured in the laboratory as for the 12 main regrowth sites above. As these sites were sampled only in one location per field site and at different depth increments, we analyzed these data separately from the main-line chronosequence sites.

2.3.2. Vegetation Data

The vegetation N cycle indicators we measured included those based on tree woody biomass, foliar samples (leaf %N and δ^{15}N), and those combining foliar and canopy structure data (leaf specific mass (LAI)) to represent N demand for leaf production at field-site scales. For N contained in stem woody biomass, we inventoried trees >5 cm dbh within the four circular subplots, measured diameter at breast height (dbh), and used Miombo-specific allometric equations and wood chemistry to estimate stem wood carbon (C) and N pools normalized over the total subplot areas (Frost, 1996; Williams et al., 2008). Wood biomass N was calculated using tree inventory data across sites, and published values for wood percent N in Miombo trees (0.57%; Chidumayo, 1994). For foliar N indicators, we sampled three leaves from five individuals of N-fixing *P. angolensis* and non-N-fixing *B. spiciformis* and *T. sericea* in the middle of the growing season (March–April 2015). Leaf-specific mass was assessed by punching out fixed areas of leaves per tree dividing differenced wet-oven dry (105 °C) mass by leaf area. Leaf %N and δ^{15}N were measured via dry combustion and GC-MS analyses similarly to soils.

To scale foliar %N to canopy-level estimates of N use for leaf production, we multiplied foliar %N by specific mass and the wet-dry season leaf-area difference. We took optical measures of leaf-area using a LICOR-2200 at six points per circular subplot during wet season maximum (March–April 2015) and mid-dry season (July 2015) minimum leaf cover conditions to calculate dry season leaf-area difference (wet-dry) as an estimate of the area of annual leaf production.

2.4. Statistical Analysis

Across main regrowth chronosequence sites, one-factor ANOVA was used to test effects of regrowth site age on canopy dry season leaf-area difference and tree N demand for leaf production. ANOVA or ANCOVA with Tukey's honest significant difference tests or Kruskal-Wallis tests with Wilcoxon rank-sum tests were used to assess effects of regrowth site age and tree species on foliar data, and regrowth site age and depth on soil data. Following an analytical approach used by Davidson et al. (2007), we assessed N cycling indicators across regrowth chronosequences both as ranked categories, and the logarithm of site age on N cycling indicators. We conducted our analyses with data encompassing all regrowth and mature forest sites, and the data set excluding mature forests, in order to test for age effects among regrowth sites alone (Table S4). Soil temperature and moisture were also included as covariates in ANCOVA analyses of age effects on soil nutrient cycling indicators.

Pilot soil data were analyzed via ANOVA or Kruskal-Wallis sum-rank tests for effects of site class (mature forest, agriculture) and depth on texture, bulk soil carbon, total nitrogen, and C:N ratios, to basic biogeochemical characterization of forest surface soils into context with agricultural soils and the broader soil profile.

All analyses were completed using R (R Core Team, 2017) and R studio (RStudio Team, 2016).

3. Results

3.1. Soil Characterization From Pilot Cores

Soils from pilot soil cores to 2-m depth were sandy (mean texture 82.2 ± 0.9% sand, 9.77 ± 0.1% silt, 8.09 ± 0.8 clay), acidic (mean pH = 5.03 ± 0.004), and had SOC concentrations less than 0.50% and total nitrogen (TN)

Table 1
Physical and Chemical Characteristics of Pilot Soil Cores to 2-m Depth Across a Miombo Woodland Landscape, Tabora, Tanzania

Site class	N sites	Depth (cm)	Sand	Silt + clay	pH	C g/kg	N g/kg	C:N ratio
Agriculture	4	0–15	0.788 ± 0.033	0.212 ± 0.034	5.16 ± 0.260	4.01 ± 0.246	0.326 ± 0.026	14.4 ± 0.679
		15–30	0.808 ± 0.023	0.192 ± 0.023	5.05 ± 0.212	2.85 ± 0.105	0.244 ± 0.017	13.8 ± 0.565
		30–50	0.788 ± 0.026	0.212 ± 0.026	4.91 ± 0.199	1.85 ± 0.127	0.180 ± 0.016	12.1 ± 0.506
		50–100	0.753 ± 0.036	0.247 ± 0.039	4.85 ± 0.159	1.05 ± 0.078	0.134 ± 0.009	9.04 ± 0.250
		100–150	0.733 ± 0.047	0.266 ± 0.047	5.01 ± 0.128	0.759 ± 0.065	0.106 ± 0.008	8.31 ± 0.338
		150–190	0.680 ± 0.049	0.320 ± 0.047	5.17 ± 0.157	0.864 ± 0.269	0.089 ± 0.011	10.95 ± 2.84
Regrowth forest *Mixed age classes*	4	0–15	0.845 ± 0.032	0.154 ± 0.032	5.06 ± 0.113	3.60 ± 0.204	0.273 ± 0.015	15.4 ± 0.214
		15–30	0.853 ± 0.033	0.146 ± 0.033	4.90 ± 0.076	2.80 ± 0.264	0.215 ± 0.021	15.2 ± 0.408
		30–50	0.868 ± 0.031	0.131 ± 0.031	4.94 ± 0.074	1.83 ± 0.173	0.166 ± 0.018	13.0 ± 0.719
		50–100	0.868 ± 0.037	0.132 ± 0.037	4.92 ± 0.069	1.11 ± 0.165	0.122 ± 0.018	10.6 ± 0.346
		100–150	0.810 ± 0.032	0.19 ± 0.032	4.92 ± 0.010	0.673 ± 0.091	0.091 ± 0.014	8.81 ± 0.438
		150–190	0.855 ± 0.040	0.145 ± 0.040	5.03 ± 0.102	0.520 ± 0.063	0.073 ± 0.011	8.54 ± 0.462
Mature forest	5	0–15	0.873 ± 0.020	0.127 ± 0.020	5.02 ± 0.172	4.73 ± 0.541	0.344 ± 0.025	15.9 ± 0.698
		15–30	0.876 ± 0.017	0.138 ± 0.023	5.01 ± 0.175	2.67 ± 0.183	0.203 ± 0.002	15.4 ± 0.940
		30–50	0.865 ± 0.032	0.135 ± 0.032	5.04 ± 0.200	1.60 ± 0.114	0.139 ± 0.013	13.6 ± 0.652
		50–100	0.835 ± 0.031	0.165 ± 0.031	5.19 ± 0.197	1.08 ± 0.162	0.112 ± 0.013	11.4 ± 1.15
		100–150	0.855 ± 0.014	0.145 ± 0.014	5.12 ± 0.147	0.655 ± 0.031	0.081 ± 0.007	9.60 ± 0.595
		150–190	0.841 ± 0.027	0.158 ± 0.027	5.18 ± 0.133	0.553 ± 0.036	0.064 ± 0.005	10.3 ± 0.713

Note. Soil texture data listed as proportions. Values listed are averages with standard error of the mean.

concentrations less than 0.04% (Table 1). Soil texture differed slightly but significantly among site land cover types (Kruskal-Wallis chi-square 23.3, d.f. = 2, $p < 0.05$). Agricultural sites had the lowest mean %sand (75.8 ± 0.3%) and showed a trend of fining texture toward sandy clays by 150-cm depth (Table 1). Mean soil texture did not differ significantly between regrowth forest sites (85.0 ± 0.2%) and mature forest sites (85.8 ± 0.1%), and showed little variability with depth (Table 1). Across all pilot soil cores, ANOVA models with depth and land cover as explanatory variables accounted for significant variability in SOC (ANOVA adjusted $r^2 = 0.893$, $F = 106.8$, $p < 0.05$) and TN (adjusted $r^2 = 0.845$, $F = 72.3$, $p < 0.05$). SOC concentrations declined significantly with depth ($F = 149$, $p < 0.05$) but showed no dependence on land cover type ($F = 1.34$, $p = 0.266$). TN showed similar trends, although averaged across all depths, agriculture sites had slightly but significantly higher TN concentrations ($F = 6.11$, $p = 0.003$) than regrowth and mature forest sites, which did not differ from one another. There were no significant correlations between SOC and soil texture or TN and soil texture. C:N ratios were similar across all sites and showed no significant differences across land cover types, but showed significant differences with depth at all sites (Kruskal-Wallis chi-square 60.8, $p < 0.05$), decreasing from about 15 at surface soils to 10 by 150–190 cm (Table 1).

3.2. N Cycle Indicators in the Regrowth Chronosequence

Total N stocks for 0–15-cm depth were less than 1.0 Mg N/ha (range 0.59–0.98 Mg N/ha) and did not increase significantly with regrowth site age (Table 2 and Figure 2a). Ammonium dominated soil extractable mineral N ($NH_4^+ + NO_3^-$), with ammonium:nitrate concentration ratios of ≥50:1 at 0–5-cm depths and ≥20:1 at 5–15-cm depths (Figure 2b and Table S1). Soil mineral N ($NH_4^+ + NO_3^-$) concentrations at 0–5- and 5–15-cm depths differed significantly by depth in all models (Table S4), but did not increase with site age across regrowth classes (Figure 2c and Tables S1 and S4). Meanwhile, soil mineral N concentrations of mature forest sites were significantly higher than 10–24-year sites (Tukey HSD, $p = 0.021$) and 30–40-year sites ($p = 0.026$; Figure 2c and Tables 2 and S1). Soil $\delta^{15}N$ did not increase with regrowth site age; rather, a significant age effect in all AN(C)OVA and log-age models ($p < 0.001$) was driven by enriched soil $\delta^{15}N$ at the youngest regrowth sites (Tables 2 and S4). Analytical precisions, based on replicate analyses of international reference materials, are ±0.1‰ (1 sigma) for both $\delta^{13}C$ and $\delta^{15}N$.

In laboratory incubations, soil N mineralization potential rates (Nmin) differed significantly by season, but not regrowth age (Figure 3 and Table S1). For mature forests, wet season Nmin potentials (5.54 ± 0.51 (S.E.) kg N·ha^{-1}·14 d^{-1}) were 3 times higher and significantly different than dry season Nmin potentials (1.98 ±

Table 2
Physical and Chemical Characteristics of Surface Soils Across Miombo Forest Regrowth Chronosequence Sites by Depth

Regrowth site age class	N sites	Depth (cm)	Bulk density (g/cm^3)	C g/kg	N g/kg	δ^{15}N o/oo	C:N ratio (mol)	SOC (Mg/ha)	Total N (Mg/ha)
3–4 years	3	0–5	1.60 ± 0.05	5.80 ± 1.28	0.49 ± 0.13	4.62 ± 0.68	14.0 ± 0.67	4.60 ± 0.89	0.390 ± 0.092
		5–15	1.57 ± 0.05	4.63 ± 1.07	0.37 ± 0.01	4.82 ± 0.91	14.5 ± 0.62	7.22 ± 1.50	0.581 ± 0.125
		0–15	na	na	na	na	na	11.8 ± 2.37	0.970 ± 0.216
10–24 years	3	0–5	1.52 ± 0.09	4.14 ± 0.13	0.30 ± 0.02	3.14 ± 0.51	15.9 ± 0.61	3.16 ± 0.25	0.233 ± 0.027
		5–15	1.61 ± 0.03	3.11 ± 0.07	0.22 ± 0.01	4.00 ± 0.37	16.3 ± 0.67	5.01 ± 0.15	0.360 ± 0.025
		0–15	na	na	na	na	na	8.17 ± 0.40	0.594 ± 0.052
30–40 years	3	0–5	1.56 ± 0.07	9.35 ± 2.36	0.61 ± 0.14	2.73 ± 0.43	17.6 ± 0.45	7.30 ± 1.83	0.479 ± 0.111
		5–15	1.63 ± 0.01	4.81 ± 0.95	0.31 ± 0.05	3.62 ± 0.37	18.1 ± 1.17	7.85 ± 1.48	0.502 ± 0.079
		0–15	na	na	na	na	na	15.2 ± 3.30	0.981 ± 0.188
Mature >100 years	3	0–5 5–15	1.54 ± 0.07	7.58 ± 1.43	0.53 ± 0.08	3.51 ± 0.23	16.5 ± 1.12	5.88 ± 1.31	0.412 ± 0.075
		0–15	1.59 ± 0.02	3.97 ± 0.40	0.28 ± 0.02	3.83 ± 0.68	16.6 ± 1.00	6.30 ± 0.61	0.445 ± 0.036
			na	na	na	na	na	12.2 ± 1.90	0.857 ± 0.103

Note. Values listed are averages with standard error of the mean. Accompanies Figure 1.

1.03 kg N·ha^{-1}·14 d^{-1}; $p < 0.05$; Wilcoxon sum rank tests (Figure 3 and Tables S1 and S4)). Averaged across all regrowth sites, wet season Nmin potentials (average 3.02 ± 0.44 kg N·ha^{-1}·14 d^{-1}) were about 2 times higher than the dry season (average 1.54 ± 0.41 kg N·ha^{-1}·14 d^{-1}). Wet season Nmin rates among regrowth sites (average 3.02 ± 0.31 kg N·ha^{-1}·14 d^{-1}) were >50% lower and significantly different than mature forest Nmin rates (average 5.54 ± 0.51 kg N·ha^{-1}·14 d^{-1}; $p < 0.05$, Wilcoxon sum rank tests).

3.3. Aboveground Tree N Pools and Foliar N Indicators

Contrasting trends in soils, trees accrued significant quantities of N in woody biomass and N demand for canopy leaf production increased markedly with regrowth (Figures 2e and 2f and Tables 3 and 4). Age effects were significant for regrowth site wet-dry season LAI differences (ΔLAI wet-dry; Figure 2e), gross canopy N demand (Figures 2e and 2f and Table S4), and N in woody biomass (Tables 4 and S4). From 3–4-year sites to 30–40-year sites, N in woody biomass increased at a rate of 8.0–11 kg N·ha^{-1}·yr^{-1}, and from 40-year regrowth to mature forests, by 5.6 kg N·ha^{-1}·yr^{-1} (Table 4). These N accumulation rates accompanied an average woody biomass carbon (C) increment of 0.6 Mg C·ha^{-1}·yr^{-1} across 3–4- to 40-year sites (Figure S1). N demand for canopy leaf production increased sixfold with regrowth, driven by increasing LAI with regrowth site age (Tables 3 and 4). The total N embodied in wood stocks and demand for canopy leaf production for mature forest sites, 654 ± 160 (S.E. across sites) kg N/ha, is 633 kg N/ha larger than the N at three- to four-year regrowth sites (21.3 ± 9.2 kg N/ha).

In foliar chemistry data across regrowth sites, species effects dominated those of regrowth site age effects. Site-averaged foliar %N and δ^{15}N did not differ with regrowth site age (Figures 2d and 2g). By species, foliar δ^{15}N averaged <0‰ for the documented canopy N fixer, *P. angolensis (Pa)* across all sites (range −0.16 ± 0.54 (S.E.)‰ to −1.31 ± 0.21‰; Figure 4a). These values were significantly depleted by 2–4‰ relative to foliar δ^{15}N of the nonfixers (*B. spiciformis (Bs)*, *T. sericea (Ts)*); Figure 4 and Tables S3 and S5). Foliar %N differed significantly across all species, with *Pa* averaging above 3%, *Bs* around 2.5%, and *Ts* approximately 2% dry weight N (Figure 4b and Table S4; $p < 0.001$ in all models).

4. Discussion

Evidence from soil and vegetation N cycle indicators showed that ecosystem N availability was low across Miombo forest sites of all ages, that ecosystem N accumulation with regrowth was driven by growth of aboveground tree N stocks, and that by 40 years of regrowth, ecosystem mineral N availability remained below that of mature forest sites. For soils 0–15 cm, bulk soil organic carbon (concentrations <1.0% or 10 g/kg; stocks <15 Mg/ha) and total N (concentrations <0.1% or 1.0 g/kg; stocks <1.0 Mg/ha) were lower than many other Neotropical and global tropical dry forest and savanna ecosystems with similar tree biomass of 50–150 Mg/ha at maturity. For comparison, at Mexican tropical dry forest soils 0–10 cm, SOC
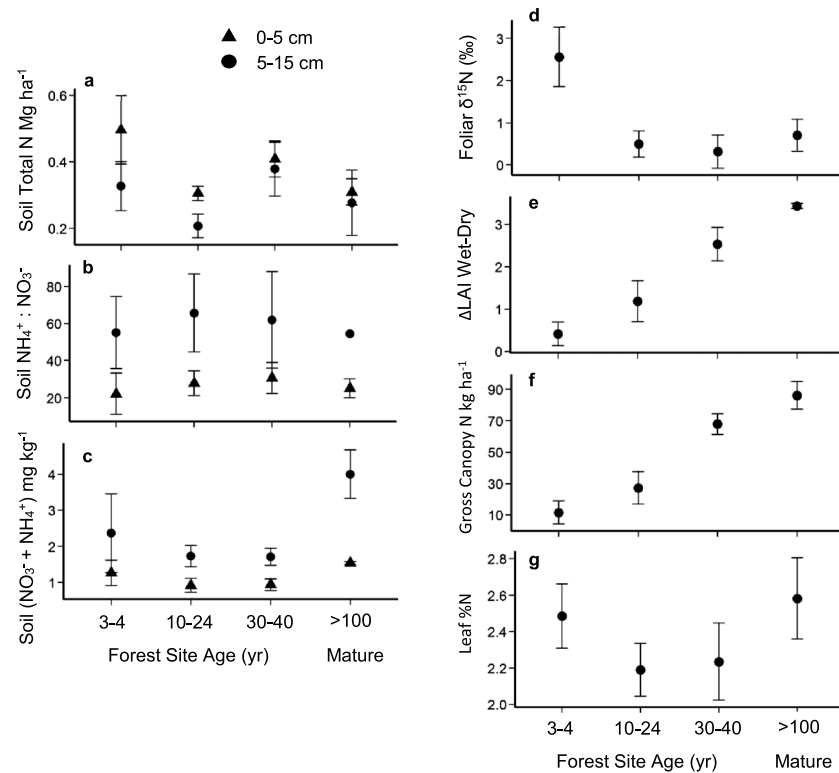
Figure 2. Indicators of N cycling show low ecosystem N availability and lack of recovery relative to tree N demand along a Miombo forest regrowth chronosequence. (a) Soil total organic N. (b) Soil ammonium:nitrate ratio. (c) Soil extractable mineral N (nitrate + ammonium) concentration by depth. (d) Foliar δ^{15}N. (e) Wet-dry season leaf-area difference (ΔLAI). (f) N demand for canopy leaf production. (g) Foliar mass percentage N. Error bars indicate SEM for data within each group. Forest age effects are significant in analyses of variance, covariance, or Kruskal-Wallis tests for soil extractable mineral N, foliar δ^{15}N, ΔLAI, and canopy N demand ($p \leq 0.05$; see Table S4). Soil, foliar, and canopy indicators (a–d, g) showed no increase in ecosystem N availability with regrowth, and contrasted significant increases in indices of tree demand for N for primary production during regrowth (e, f). See Table S4 for age and other effects on dependent variables.
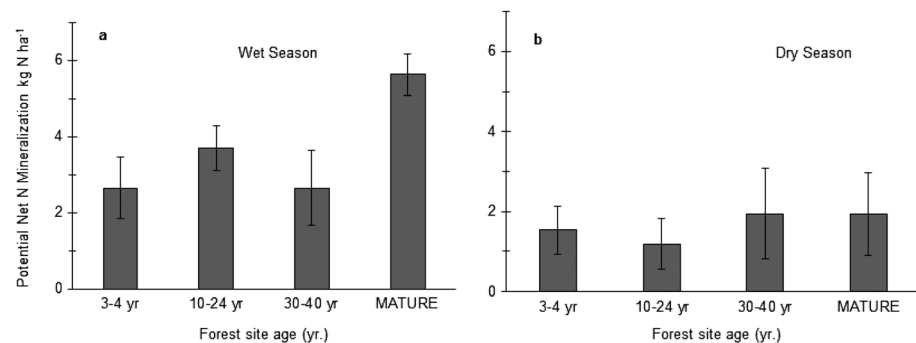

Figure 3. Soil N ($NH_4^+ + NO_3^-$) mineralization potentials (Nmin) in 14-day lab incubations, compared across Miombo forest regrowth chronosequence sites in wet and dry seasons. Lab-measured potential soil N ($NH_4^+ + NO_3^-$) mineralization production potentials for 0–15 cm in the (a) 2015 wet season (March–April) and (b) 2015 dry season (September–October). Error bars show group SEM. In ANOVA, Nmin differed significantly by season ($p = 0.032$); wet season Nmin rates averaged across all forest sites (average 3.65 kg N ha^{-1} 14 d^{-1} ± 0.47 SEM) were more than double those of dry season Nmin rates (average 1.65 kg N ha^{-1} 14 d^{-1} ± 0.38 SEM; $p < 0.05$, Tukey HSD tests; see Table S1 for bar chart results and Table S4 for detailed statistical results). Within the wet season (a), Nmin rates showed a lack of trend among regrowth forest sites. Wet season Nmin rates among regrowth sites (average 3.02 kg N ha^{-1} 14 d^{-1} ± 0.31 SEM) were >50% lower and significantly different than mature forest Nmin rates (average 5.54 kg N ha^{-1} 14 d^{-1} ± 0.51 SEM; $p < 0.05$, Wilcoxon sum rank tests; see Table S4).

Table 3
Average Foliar Chemistry and Canopy Data Grouped by Forest Regrowth Age Class

Regrowth site age class (n trees)	Foliar (N g/kg)	Foliar C:N (mol)	LAI$_{wet}$ March–April 2015	LAI$_{dry}$ July 2015	LAI$_{wet-dry}$	Canopy N (kg N/ha)
3–4 years (11)	24.9 ± 1.8	23.5 ± 1.7	0.63 ± 0.30	0.21 ± 0.02	0.41 ± 0.28	11.6 ± 7.4
10–24 years (18)	21.9 ± 1.4	27.7 ± 1.9	1.80 ± 0.50	0.61 ± 0.05	1.19 ± 0.48	27.3 ± 10.4
30–40 years (12)	22.3 ± 2.1	27.6 ± 3.1	3.35 ± 0.36	0.81 ± 0.04	2.53 ± 0.40	67.9 ± 6.6
Mature >100 years (12)	25.8 ± 2.2	24.3 ± 2.2	4.81 ± 0.03	1.38 ± 0.09	3.43 ± 0.06	86.1 ± 8.7

Note. Accompanies Figures 1e–1g. Values listed are averages with standard error of the mean.

and TN has been reported at 35–45 Mg C/ha and 0.9–2.5 Mg N/ha (Jaramillo et al., 2003; Saynes et al., 2005), approximately 2 to 3 times higher stocks than Miombo. SOC and TN concentrations 0–10 cm around Guanacaste, Costa Rica were 3 to 4 times higher than the Miombo sites we report on here (SOC, 30–40.7 g/kg; TN, 3.0–4.0 g/kg; Waring, Adams, et al., 2015). Compared to the Miombo sites, Hawaiian tropical dry woodland soils 0–10 cm had 5–10 times higher SOC and TN concentrations and stocks (SOC −108 g/kg, 52.0 Mg C/ha; TN 6 g/kg, 3.1 Mg/ha; D'Antonio et al., 2017). Miombo woodland SOC and TN stocks and concentrations were more similar to, but still 20–50% lower than tropical dry forests in India (SOC 12–18 g/kg, TN 1.1–1.3 g/kg; Chaturvedi et al., 2011). Miombo soils appeared most similar in bulk SOC and TN surface soil characteristics to dry tropical woodlands of Australia (SOC 4.2–12.5 g/kg, 30.0 Mg C/ha; TN 0.89 Mg/ha; Harms et al., 2005) and the Brazilian cerrado (SOC 4.4–6.7 g/kg, soils 0–5 and 5–10 cm; TN 0.33–0.39 g/kg; Frazão et al., 2010). In Australia and the Cerrado sites, comparably sandy soils derived from highly weathered parent materials and higher rates of fire are two edaphic factors shared in common with the Miombo that accounted for low N in the Miombo as well. Many fewer studies have reported N mineralization rates of soils in tropical dry forests, but Miombo rates were low in comparison. For example, Saynes et al. (2007) report potential N mineralization rates across Mexican tropical dry forests of 0.8–2.2 g·m^{-2}·d^{-1} (8.0–22 kg·ha^{-1}·d^{-1}) in the dry season and 4.5–5.3 g m^{-2} d^{-1} (45–53 kg ha^{-1} d^{-1}) in the wet season. These rates were 5–10 times higher than those we found across the Miombo chronosequence.

Low soil total N and lack of recovery of soil N with regrowth in the Miombo likely reflected edaphic limits on the buildup of soil carbon and organic matter, which holds the bulk of long-term soil N stock. Frequent and intense regimes of disturbance to topsoil including fire, as well as ecological factors such as high consumption rates of litter inputs by termites and ants, are factors in Miombo systems that may limit SOC and TN compared to Neotropical and other dry forests (Frost, 1996). Our findings indicated that sandy texture contributed to low SOC and TN across all sites, and limited capacity for regrowth forest soils to accumulate SOC and TN. With soils of 85% sand across mature and regrowth forest pilot sites, soil capacities in this region to retain SOC and TN were inherently low. Further, low site-to-site variability in the texture across forest pilot sites suggested that for the regrowth chronosequence as well, soil texture itself did not explain the differences in mature forest versus regrowth forest mineral N availability. From pilot soil core data at smallholder agriculture sites active longer than 15 years, which indicated little difference in bulk soil C:N ratios from regrowth or mature forest sites, it appeared that agricultural-related influences to soils before regrowth, such

Table 4
Nitrogen (N) Stocks in Surface Soils and Aboveground Tree Biomass Across a Forest Regrowth Chronosequence in the Miombo Woodlands, Tabora Tanzania

Regrowth site age class (n sites)	Soils		Trees	
	Total soil organic N[o] (0–15 cm kg ha^{-1})	N in woody biomass[i] (kg N/ha)	N demand for canopy leaf biomass[i] (kg N ha^{-1} yr^{-1})	Total N wood + canopy leaves[i] (kg N/ha)
3–4 years (3)	970 ± 216	9.75 ± 3.98 c	11.6 ± 7.40 b	21.3 ± 9.2 c
10–24 years (3)	594 ± 52	53.7 ± 4.94 b	27.3 ± 10.4 b	81.0 ± 14.1 bc
30–40 years (3)	981 ± 188	252 ± 35.3 ab	67.9 ± 6.6) ab	320 ± 47.9 ab
Mature >100 years (3)	857 ± 103	568 ± 158 a	86.1 ± 8.7 a	654 ± 160 a

Note. Site age effects on N resources were tested via ANOVA and log linear age models and are indicated in superscript as significant[i] or insignificant[o] ($p \leq 0.05$). During regrowth (3–4 to 30–40 years), N resource pools in aboveground woody biomass and canopy leaves increased significantly by rates of 8.1–11.1 kg N ha^{-1} yr^{-1}. Soil N resources showed no significant trends with site age. By column, quantities with different lowercase letters were different (Tukey honest significant difference tests, $p \leq 0.05$).
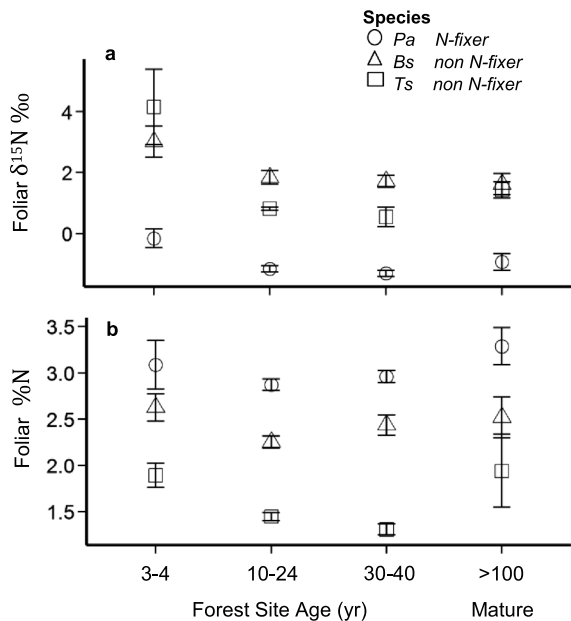
Figure 4. Differences in foliar N cycle indicators among an N-fixing tree (*Pterocarpus angolensis*, *Pa*) and non-N-fixing trees (*Brachystegia spiciformis*, *Bs*; *Terminalia sericea*, *Ts*) across a Miombo forest regrowth chronosequence. (a) Foliar δ^{15}N. (b) Foliar N concentration. Error bars indicate SEM for data within each species-site group. Indicators showed significant differences by species ($p < 0.05$ in Kruskal-Wallis tests; see Table S3 for values and Table S5 for statistical results). The N fixer had significantly lower foliar δ^{15}N <0 per mil (a) and higher %N (b) compared to non-N fixers grouped among all regrowth and mature forest classes. *Ts* showed significantly lower foliar %N in 30–40-year sites than mature forest sites ($p < 0.05$ in Kruskal-Wallis tests; see Table S3 for values and Table S5 for statistical results).

as physical soil disturbance from tilling and altered nutrient balance terms relative to forests (e.g., fertilizer input, crop biomass extraction), had little effect on bulk soil C:N stoichiometry. However, a caveat that limits the direct comparability of these pilot agricultural sites to sites in the regrowth forest chronosequence was that the agriculture sites had slightly but significantly less sandy soils, so their baseline SOC and TN content as forested sites may have been higher. Overall, in this landscape there was a trend of continuous agricultural land use occurring at locations with finer-textured soil, so regrowth forests occurring on extremely sandy soils likely reflecting a selection bias among farmers to choose soils with finer textures for continued cultivation. Further study of soil carbon and nitrogen dynamics on newly cleared forest areas on sandier soils, or regrowth and mature forests on less-sandy soils, might indicate more precisely how agriculture affects the biogeochemical soil template prior to forest regrowth.

In soil mineral N pools, the persistence of high ammonium:nitrate ratios across sites indicated that microbes and plants competed for a low supply of mineralized N from early forest regrowth through maturation (Schimel & Bennett, 2004). There was a lack of soil δ^{15}N enrichment with regrowth, indicating conservative microbial N cycling dynamics with low rates of recycling and turnover (Amundson, 2003; Davidson et al., 2007; Martinelli et al., 1999). Significantly higher soil mineral N concentrations and wet season N mineralization rates in mature forest sites, compared to regrowth forest chronosequence sites, indicated that by 40-year mineral N availability for plants in surface soils remained below that of mature forests. These results differ from findings of N cycle recovery with regrowth after several decades in Neotropical humid forests (Davidson et al., 2007) and Neotropical dry forests (Saynes et al., 2005). Our finding of incomplete recovery of soil N availability after 40 years of regrowth is an important juxtaposition and complement to studies of Miombo carbon and forest structure with regrowth, which have found aboveground tree biomass carbon and stem structure recovery on 20–40-year time scales (Kalaba et al., 2013; McNicol et al., 2015; Williams et al., 2008). Slower soil N cycle recovery, relative to that of aboveground stem C and N, implies that repeat disturbance of forests that removes woody biomass in regrowth stages retards subsequent forest recovery in part by removing N dominantly accumulating in woody biomass. An implication of these results for managing African dry tropical forests for long-term regrowth is that restricting removal of deadwood for firewood, and limiting partial or complete clearing for charcoal, may be important for conserving ecosystem N stocks that exist in woody biomass.

These patterns lead to the question of how trees acquire the more than 600 kg N found in mature forests across a century of growth, given the lack of clear indicators of increasing soil N supplies. Broadly, the two possible sources are (1) recycling and redistribution of N from soil to vegetation over time or (2) new inputs to the ecosystem, including N deposition and N fixation. Our data suggest that both sources contribute to tree N accumulation, including the possibility of N fixation throughout regrowth. Soil-to-woody vegetation recycling and redistribution of N is the most probable dominant source of N to trees—the variability in total soil N pools was large enough to accommodate some N redistribution to tree pools—but soil N pools were not large enough to account for the total N we found accumulating in trees by 100 years (654 kg N/ha) without some new ecosystem inputs. Given the clear trend in increases in canopy leaf production, the litter layer, which we were not able to measure, is a possible contributor to redistribution and accumulation of N if this litterfall N was tightly recycled around trees. Past research has found that up to 30% of foliar N in Miombo species is translocated between peak and end-of-rainy season (Chidumayo, 1994); the fate of the other 70% of leaf N through senescence and downstream litter layer nutrient cycling dynamics certainly warrant further study in Miombo systems. Foliar δ^{15}N from the canopy N-fixing tree, *P. angolensis* was <0 per mil across all regrowth and mature forest sites, indicating the possibility that active N fixation occurred in

this species at all forest sites age categories (Figure 4a and Table S3; Shearer & Kohl, 1988). This was consistent with past findings that *Pa* has root nodules with nitrogenase activity in Tanzania (Högberg, 1986). Foliar N concentrations of *P. angolensis* were also significantly higher than those of non-N fixers across all sites (Figure 4b and Table S3). However, caution is deserved because foliar $\delta^{15}N$ alone is not a conclusive sign of N fixation (Chalk et al., 2016; Soper et al., 2015). Even if N fixation occurred in one species with documented fixing capacities, it is unclear whether fixation of that species supported N accumulation of those specific species or the broader tree community. Further study of N fixing dynamics across more potential N-fixing trees in the African dry tropics, in the overstory and understory, may provide further insights. Strategies may include tree- and plot-scale experiments to assess N mass balance and residuals, alongside labeled N additions and use of natural abundance $\delta^{15}N$ (Soper & Sparks, 2017). Estimates of potential N fixation in the dry tropics (2–6 kg N ha^{-1} yr^{-1}; Houlton et al., 2008) are high enough to account for the tree N accumulation we observed in combination with a soil-vegetation recycling/redistribution process. Modeled N deposition rates (3–5 kg N ha^{-1} yr^{-1}; Lamarque, 2013) suggest that this process may also play a role, but this study did not make measurements addressing this question. Further study of soil-vegetation N cycle exchanges, including litterfall N decomposition rates, soil N pools, rates of N fixation, basal areas of N fixing trees, rooting depths of trees, N deposition, and N loss pathways including leaching and gaseous losses, could further constrain contributions of these N sources that contribute to tree N accumulation with regrowth. Because *P. angolensis* is endangered from tree poaching due to its value as a timber species (Schwartz et al., 2002), further research on its ecosystem function and management attention to its conservation is needed.

Results from laboratory incubations implied that climate changes, such as shorter rainy seasons with increasing proportions of rainfall occurring in fewer extreme events, may limit ecosystem N availability from soil N mineralization. N mineralization potentials were 2–3 times higher in soils sampled and incubated during the wet season than dry season. Wet to dry seasonal differences in Nmin potentials over 14 days at mature forest sites (3.56 kg N/ha) were larger than contrasts across the age gradient (2.52 kg N/ha). Given projected increases in dry periods regionally with climate change, due to shortening rainy seasons, and increasing proportions of rain falling in fewer extreme events (Dunning et al., 2018; Lyon & DeWitt, 2012; Ongoma, Chena, et al., 2018), longer periods of low-soil moisture conditions in the future may provide as much a shock to N mineralization activity as forest clearing/regrowth cycles. While illustrative, these results, based on soils sampled once per season, do not address the challenge of capturing characteristically pulsed dynamics of N processes in seasonally dry regions. Higher temporal resolution and longer-duration studies of N cycle processes in pulsed events are needed to more precisely address impacts of rainfall changes on N mineralization. Nevertheless, this first set of N mineralization assays between wet-dry seasons and regrowth sites across a Miombo woodland suggests that shortening rainy seasons and more episodic rainfall regimes will further limit N availability for trees via mineralization, potentially reducing regrowth capacity and carbon accumulation rates.

5. Conclusions and Implications for Management

This study was one of the first evaluations of N cycle changes across a forest regrowth chronosequence in the African dry tropics. Our findings showed that basic N cycling and low N-availability conditions in the Miombo were more similar to mixed tree-grass savanna systems such as the Brazilian cerrado and Australian tropical dry forests than to humid or other Neotropical dry tropical forests (Bustamante et al., 2004; Davidson et al., 2007; Saynes et al., 2005; Waring, Becknell, et al., 2015). N cycle recovery took longer than 40 years, longer than C stock or forest stem structure recovery, and longer than N cycle recover in humid tropical and Neotropical dry forests. During regrowth, ecosystem N accumulation occurred predominantly in aboveground vegetation pools (wood). A mixture of soil-vegetation recycling and redistribution and N fixation likely provide accumulating N, although further study is required to further constrain sources and dynamics of ecosystem N accumulation. N mineralization rates in laboratory-incubated soils in the wet compared to the dry season suggested that N availability from mineralization, particularly in mature forests, may be reduced by extended dry periods predicted with climate change from changing rainfall variability.

These results have important consequences for Miombo woodland forest management and conservation. Forest managers are looking for information to manage forest lands for regrowth, given increasing rates

forest cutting across mature and regrowth forests for charcoal production in the region (Chidumayo & Gumbo, 2013). Given that we found woodland regrowth from agricultural abandonment occurring on extremely sandy-textured soil regions, and the pervasive, low SOC and soil N content of these soils that did not vary significantly across agricultural, regrowth, and mature forests, we advocate that land management for forest regrowth should attempt to maximize ecosystem N retention by conserving tree and aboveground biomass. Strategies for conserving N could focus on discouraging the removal of tree biomass in regrowth sites, including selective cutting of live stems for charcoal or timber and removal of deadwood for firewood, management to reduce outbreaks of high-intensity fires that top-kill trees, and managing grazing in forest areas to minimize disturbance to the litter layer, topsoil, and understory.

Conservation of regrowth and mature African tropical dry forests and woodlands will face challenges from development pressures for agriculture and other land uses, demands for wood-based fuels including charcoal (Chidumayo & Gumbo, 2013), and other extractable resources (Searchinger et al., 2015). With over 200 million more people projected to be living in and depending upon resources and services of Miombo woodlands by 2050, proactively managing forest landscapes to maintain N supply will be an important step for promoting forest regrowth after disturbance and mature forest productivity amid increasing land use and climate change pressures.

References

Amundson, R. (2003). Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochemical Cycles*, *17*(1), 1031. https://doi.org/10.1029/2002GB001903

Batjes, N. H. (1996). Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science*, *47*(2), 151–163. https://doi.org/10.1111/j.1365-2389.1996.tb01386.x

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., et al. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*(1), 30–59. https://doi.org/10.1890/08-1140.1

Bustamante, M. M. C., Martinelli, L. A., Silva, D. A., Camargo, P. B., Klink, C. A., Domingues, T. F., & Santos, R. V. (2004). [15]N natural abundance in woody plants and soils of central Brazilian savannas (Cerrado). *Ecological Applications*, *14*(sp4), 200–213. https://doi.org/10.1890/01-6013

Chadwick, O. A., Derry, L. A., Vitousek, P. M., Huebert, B. J., & Hedin, L. O. (1999). Changing sources of nutrients during four million years of ecosystem development. *Nature*, *397*(6719), 491–497. https://doi.org/10.1038/17276

Chalk, P. M., Inácio, C. T., Balieiro, F. C., & Rouws, J. R. C. (2016). Do techniques based on ^{15}N enrichment and ^{15}N natural abundance give consistent estimates of the symbiotic dependence of N2-fixing plants? *Plant and Soil*, *399*(1–2), 415–426. https://doi.org/10.1007/s11104-015-2689-9

Chaturvedi, R. K., Raghubanshi, A. S., & Singh, J. S. (2011). Carbon density and accumulation in woody species of tropical dry forest in India. *Forest Ecology and Management*, *262*(8), 1576–1588. https://doi.org/10.1016/J.FORECO.2011.07.006

Chazdon, R. L. (2008). Beyond deforestation: Restoring degraded lands. *Communities*, *320*(5882), 1458–1460. https://doi.org/10.1126/science.1155365

Chidumayo, E. N. (1994). Phenology and nutrition of miombo woodland trees in Zambia. *Trees*, *9*(2), 67–72. https://doi.org/10.1007/BF00202124

Chidumayo, E. N., & Gumbo, D. J. (2013). The environmental impacts of charcoal production in tropical ecosystems of the world: A synthesis. *Energy for Sustainable Development*, *17*(2), 86–94. https://doi.org/10.1016/J.ESD.2012.07.004

D'Antonio, C. M., Yelenik, S. G., & Mack, M. C. (2017). Ecosystem vs. community recovery 25 years after grass invasions and fire in a subtropical woodland. *Journal of Ecology*, *105*(6), 1462–1474. https://doi.org/10.1111/1365-2745.12855

Davidson, E. A., de Carvalho, C. J. R., Figueira, A. M., Ishida, F. Y., Ometto, J. P. H. B., Nardoto, G. B., et al. (2007). Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature*, *447*(7147), 995–998. https://doi.org/10.1038/nature05900

Davidson, E. A., de Carvalho, C. J. R., Vieira, I. C. G., de O Figueiredo, R., Moutinho, P., Ishida, F. Y., et al. (2004). Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecological Applications*, *14*(4), S150–S163.

Dunning, C. M., Black, E., & Allan, R. P. (2018). Later wet seasons with more intense rainfall over Africa under future climate change. *Journal of Climate*, *31*(23), 9719–9738. https://doi.org/10.1175/JCLI

Frazão, L. A., Piccolo, M. d. C., Feigl, B. J., Cerri, C. C., & Cerri, C. E. P. (2010). Inorganic nitrogen, microbial biomass and microbial activity of a sandy Brazilian Cerrado soil under different land uses. *Agriculture, Ecosystems & Environment*, *135*(3), 161–167. https://doi.org/10.1016/J.AGEE.2009.09.003

Frost, P. (1996). The ecology of Miombo woodlands. The Miombo in transition: Woodlands and welfare in Africa. Retrieved from http://books.google.com/books?hl=nl&lr=&id=rpildJJVdU4C&pgis=1

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., et al. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*(6160), 850–853. https://doi.org/10.1126/science.1244693

Harms, B. P., Dalal, R. C., & Cramp, A. P. (2005). Changes in soil carbon and soil nitrogen after tree clearing in the semi-arid rangelands of Queensland. *Australian Journal of Botany*, *53*(7), 639. https://doi.org/10.1071/BT04154

Högberg, P. (1986). Nitrogen-fixation and nutrient relations in savanna woodland trees (Tanzania). *Journal of Applied Ecology*, *23*(2), 675–688. https://doi.org/10.2307/2404045

Houlton, B. Z., Wang, Y.-P., Vitousek, P. M., & Field, C. B. (2008). A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature*, *454*(7202), 327–330. https://doi.org/10.1038/nature07028

Jaramillo, V. J., Kauffman, J. B., Renteria-Rodriguez, L., Cummings, D. L., & Ellingson, L. J. (2003). Biomass, carbon, and nitrogen pools in Mexican tropical dry forest landscapes. *Ecosystems*, *6*(7), 609–629. https://doi.org/10.1007/s10021-002-0195-4

Kalaba, F. K., Quinn, C. H., Dougill, A. J., & Vinya, R. (2013). Floristic composition, species diversity and carbon storage in charcoal and agriculture fallows and management implications in Miombo woodlands of Zambia. *Forest Ecology and Management*, *304*, 99–109. https://doi.org/10.1016/J.FORECO.2013.04.024

Lamarque, J.-F. (2013). Multi-model mean nitrogen and sulfur deposition. *Atmospheric Chemistry and Physics Discussions*, *13*(3), 6247–6294. https://doi.org/10.5194/acpd-13-6247-2013

Lyon, B., & DeWitt, D. G. (2012). A recent and abrupt decline in the East African long rains. *Geophysical Research Letters*, *39*, L02702. https://doi.org/10.1029/2011GL050337

Martinelli, L. A., Piccolo, M. C., Townsend, A. R., Vitousek, P. M., Cuevas, E., McDowell, W., et al. (1999). Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests. *Biogeochemistry*, *46*(1–3), 45–65. https://doi.org/10.1007/BF01007573

Mayes, M., Mustard, J., Melillo, J., Neill, C., & Nyadzi, G. (2017). Going beyond the green: Senesced vegetation material predicts basal area and biomass in remote sensing of tree cover conditions in an African tropical dry forest (miombo woodland) landscape. *Environmental Research Letters*, *12*(8). https://doi.org/10.1088/1748-9326/aa7242

Mayes, M. T., Mustard, J. F., & Melillo, J. M. (2015). Forest cover change in Miombo Woodlands: Modeling land cover of African dry tropical forests with linear spectral mixture analysis. *Remote Sensing of Environment*, *165*, 203–215. https://doi.org/10.1016/j.rse.2015.05.006

McNicol, I. M., Ryan, C. M., & Williams, M. (2015). How resilient are African woodlands to disturbance from shifting cultivation? *Ecological Applications*, *25*(8), 2320–2336. https://doi.org/10.1890/14-2165.1

Mehl, J. W., Geldenhuys, C. J., Roux, J., & Wingfield, M. J. (2011). Die-back of kiaat (*Pterocarpus angolensis*) in southern Africa: A cause for concern? *Southern Forests: a Journal of Forest Science*, *72*(3-4), 121–132. https://doi.org/10.2989/20702620.2010.547244

Murphy, P. G., & Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology, Evolution, and Systematics*, *17*(1), 67–88. Retrieved from. www.annualreviews.org, https://doi.org/10.1146/annurev.es.17.110186.000435

Mwampamba, T. H. (2007). Has the woodfuel crisis returned? Urban charcoal consumption in Tanzania and its implications to present and future forest availability. *Energy Policy*, *35*(8), 4221–4234. https://doi.org/10.1016/J.ENPOL.2007.02.010

Ongoma, V., Chen, H., & Gao, C. (2018). Projected changes in mean rainfall and temperature over East Africa based on CMIP5 models. *International Journal of Climatology*, *38*(3), 1375–1392. https://doi.org/10.1002/joc.5252

Ongoma, V., Chena, H., & Gaoa, C. (2018). Projected changes in mean rainfall and temperature over east Africa based on CMIP5 models. *International Journal of Climatology*, *38*(3), 1375–1392. https://doi.org/10.1002/joc.5252

Palm, C., Sanchez, P., Ahamed, S., & Awiti, A. (2007). Soils: A contemporary perspective. *Annual Review of Environment and Resources*, *32*(1), 99–129. https://doi.org/10.1146/annurev.energy.31.020105.100307

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from. https://www.r-project.org/

RStudio Team (2016). *RStudio: Integrated Development Environment for R*. Boston, MA: RStudio, Inc. Retrieved from. http://www.rstudio.com/

Rudel, T. K. (2013). The national determinants of deforestation in sub-Saharan Africa. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*(1625), 20120405. https://doi.org/10.1098/rstb.2012.0405

Saynes, V., Hidalgo, C., Etchevers, J. D., & Campo, J. E. (2005). Soil C and N dynamics in primary and secondary seasonally dry tropical forests in Mexico. *Applied Soil Ecology*, *29*(3), 282–289. https://doi.org/10.1016/J.APSOIL.2004.11.007

Schimel, J., & Bennett, J. (2004). Nitrogen mineralization: Challenges of a changing paradigm. *Ecology*, *85*(11), 2917–2926. https://doi.org/10.1890/03-8021

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. a., et al. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, *478*(7367), 49–56. https://doi.org/10.1038/nature10386

Schwartz, M. W., Caro, T. M., & Banda-Sakala, T. (2002). Assessing the sustainability of harvest of *Pterocarpus angolensis* in Rukwa region, Tanzania. *Forest Ecology and Management*, *170*(1–3), 259–269. https://doi.org/10.1016/S0378-1127(01)00774-5

Searchinger, T. D., Estes, L., Thornton, P. K., Beringer, T., Notenbaert, A., Rubenstein, D., et al. (2015). High carbon and biodiversity costs from converting Africa's wet savannahs to cropland. *Nature Climate Change*, *5*(5), 481–486. https://doi.org/10.1038/nclimate2584

Shearer, G., & Kohl, D. H. (1988). Natural ^{15}N abundance as a method of estimating the contribution of biologically fixed nitrogen to N2-fixing systems: Potential for non-legumes. *Plant and Soil*, *110*(2), 317–327. https://doi.org/10.1007/BF02226812

Sileshi, G., & Akinnifesi, F. K. (2008). Meta-analysis of maize yield response to woody and herbaceous legumes in sub-Saharan Africa. *Plant and Soil*, *307*, 1–19. https://doi.org/10.1007/s11104-008-9547-y

Soper, F. M., Boutton, T. W., & Sparks, J. P. (2015). Investigating patterns of symbiotic nitrogen fixation during vegetation change from grassland to woodland using fine scale δ^{15}N measurements. *Plant, Cell and Environment*, *38*(1), 89–100. https://doi.org/10.1111/pce.12373

Soper, F. M., & Sparks, J. P. (2017). Estimating ecosystem nitrogen addition by a leguminous tree: A mass balance approach using a woody encroachment chronosequence. *Ecosystems*, *20*(6), 1164–1178. https://doi.org/10.1007/s10021-016-0100-1

United Nations, Department of Economic and Social Affairs, P. D (2015). World population prospects: Key findings and advance tables. *1*. https://doi.org/10.1017/CBO9781107415324.004

URT (2014). Basic demographic and socio-enomic profile statistical tables, Tanzania mainland. Dar es Salaam.

Vitousek, P. M., Naylor, R., Crews, T., David, M. B., Drinkwater, L. E., Holland, E., et al. (2009). Nutrient imbalances in agricultural development. *Science*, *324*(5934), 1519–1520. https://doi.org/10.1126/science.1170261

Wang, L., Manzoni, S., Ravi, S., Riveros-Iregui, D., & Caylor, K. (2015). Dynamic interactions of ecohydrological and biogeochemical processes in water-limited systems. *Ecosphere*, *6*(8), art133. https://doi.org/10.1890/ES15-00122.1

Waring, B. G., Adams, R., Branco, S., & Powers, J. S. (2015). Scale-dependent variation in nitrogen cycling and soil fungal communities along gradients of forest composition and age in regenerating tropical dry forests. *New Phytologist*, *209*(2), 845–854. https://doi.org/10.1111/nph.13654

Waring, B. G., Becknell, J. M., & Powers, J. S. (2015). Nitrogen, phosphorus, and cation use efficiency in stands of regenerating tropical dry forest. *Oecologia*, *178*(3), 887–897. https://doi.org/10.1007/s00442-015-3283-9

Williams, M., Ryan, C. M., Rees, R. M., Sambane, E., Fernando, J., & Grace, J. (2008). Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique. *Forest Ecology and Management*, *254*(2), 145–155. https://doi.org/10.1016/J.FORECO.2007.07.033

WRI (2016). AFR100: Africa restoring 100 million hectares of deforested and degraded land by 2030.