

## Altered Ecosystem Nitrogen Dynamics as a Consequence of Land Cover Change in Tallgrass Prairie

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**ABSTRACT.**—In recent decades, substantial areas of North American tallgrass prairie have been lost to the establishment and expansion of woodlands and forests, including those dominated by eastern redcedar (*Juniperus virginiana*). This shift in dominant plant life form, from C<sub>4</sub> grasses to coniferous trees, may be accompanied by changes in productivity, standing stocks of biomass and nutrients and biogeochemical cycles. The goal of this study was to quantify and compare major pools and fluxes of nitrogen in recently established ( $\leq 80$  y) redcedar forests and adjacent native grasslands. Three former grassland sites in the Flint Hills region of Kansas that developed closed-canopy redcedar forests in the recent past were paired with adjacent grassland sites on similar soil type and topographic position ( $n = 3$  sites/land cover type), and selected soil and plant nitrogen pools and fluxes were measured in replicate plots ( $n = 6$ /site) along transects in each forest or grassland site over a 20-mo period. We found few significant differences in median soil inorganic N pools or net N mineralization rates between the forest and grassland sites, though there was a trend for greater concentrations of inorganic N in grassland sites on most sample dates, and cumulative growing season net N mineralization averaged 15% less in forest sites ( $14.3 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ) than in grassland sites ( $16.9 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ). Mean aboveground plant productivity of forest sites ( $9162 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) was about 2.5 $\times$  greater than that of comparable grasslands (similar soils and topographic position), in spite of similar levels of soil N availability. This resulted in an ecosystem-level nitrogen use efficiency (ANPP:litterfall N) in forests that was more than double that of the grasslands they replaced. Additional changes in N cycling associated with redcedar forest development included large accumulations of N in aboveground biomass and transfer to the forest floor via litterfall; redcedar aboveground biomass contained  $617 \text{ kg N/ha}$ , forest floor litter N was  $253 \text{ kg N/ha}$ , and litterfall N flux was  $41 \text{ kg ha}^{-1}\cdot\text{yr}^{-1}$ . These are substantial increases in aboveground biomass N accumulation, surface litter N inputs, and surface litter N accumulation compared to the native grasslands characteristic of this region. These fundamental shifts in ecosystem patterns and processes have the potential to alter regional biogeochemistry and both nitrogen and carbon storage throughout areas of the eastern Central Plains where coverage of redcedars is increasing.

### INTRODUCTION

In the last several decades, the ecological impacts of land cover and land-use change have received increasing attention. Land cover and land-use changes can have a wide variety of ecological effects (Meyer and Turner, 1992; Vitousek *et al.*, 1997), including alteration of ecosystem functioning (*e.g.*, biogeochemical fluxes) (Houghton *et al.*, 1999; Tilman *et al.*, 2000) and the distribution and diversity of species (Dobson *et al.*, 1997; Chapin *et al.*, 1998). An important land cover change occurring in grasslands worldwide is an increase in the abundance and cover of woody plant species (Archer, 1995; McPherson, 1997; Gill and Burke, 1999; Briggs *et al.*, 2005). Hypothesized drivers for this vegetation shift include climate change (Archer, 1993), increasing atmospheric CO<sub>2</sub> concentration (Polley *et al.*, 1994; Bond and Midgely, 2000), and changes in land use including fire suppression and increased

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grazing intensity (McPherson *et al.*, 1993; Scholes and Archer, 1997; Brown and Archer, 1999; Van Auken, 2000; Briggs *et al.*, 2002). Some of the ecological consequences of woody vegetation expansion into grasslands include losses of grassland biodiversity and productivity (Hoch and Briggs, 1999; Van Auken, 2000), increased soil nutrient availability and cycling (Hibbard *et al.*, 2001), decreased soil CO<sub>2</sub> flux (Smith and Johnson, 2004) and altered soil C storage (Jackson *et al.*, 2002) and increased nutrient (especially C) storage in woody biomass (Gill and Burke, 1999; Houghton *et al.*, 1999; Tilman *et al.*, 2000; Norris *et al.*, 2001b).

In the productive tallgrass prairies of central North America, there have been two predominant patterns of increased woody vegetative cover (Briggs *et al.*, 2005). First, riparian gallery forests have expanded farther up slope in stream valleys, increasing in cover in some areas by 69% from 1939 to 2002 (Knight *et al.*, 1994; Briggs *et al.*, 2005). Second, reductions in fire frequency have facilitated the establishment and spread of woody vegetation including several species of shrubs and eastern redcedar (*Juniperus virginiana* L., redcedar hereafter) into drier upland sites that were historically grass dominated (Bragg and Hulbert, 1976; Towne and Owensby, 1984; Engle *et al.*, 1988). In these grasslands, local plant community dynamics are controlled largely by disturbance regimes including grazing and burning (Hartnett and Fay, 1998; Bakker *et al.*, 2003). Frequent fires in these grasslands hinder woody plant establishment and growth, enhance productivity of the dominant C<sub>4</sub> grasses, and affect species diversity (Bragg and Hulbert, 1976; Knapp and Seastedt, 1986; Gibson and Hulbert, 1987; Collins, 1992; Briggs and Knapp, 1995).

Redcedar is characterized by rapid growth and high reproductive output, which enables the development of monospecific, closed-canopy stands in as little as 40 y (Blan, 1970; Hoch and Briggs, 1999; Briggs *et al.*, 2002). This has contributed to substantial increases in abundance and cover of redcedar, both locally and regionally throughout the eastern Central Plains. Schmidt and Leatherberry (1995) noted the rapid expansion of redcedar in four states of the lower Midwest and estimated that it occurred in nearly 2 m ha of forestland in 1993, a 113% increase since the previous inventory just two decades earlier. In an 8000 ha study region of eastern Kansas, Hoch (2000) projected that closed-canopy redcedar forests could increase 34% in cover from 1997 to 2011 based on rates of expansion in the recent past. The expansion of redcedar cover may result in additional loss of native tallgrass prairie and valuable grazing lands, with concomitant changes in ecosystem processes including soil nutrient cycling and availability, which have potential feedbacks to plant community composition and primary productivity.

This research focused on documenting some of the biogeochemical consequences of the conversion of tallgrass prairie to eastern redcedar forest. Our specific objectives were to: (1) quantify key aspects of ecosystem N pools and fluxes such as plant biomass N, forest floor N, total and available soil N and ecosystem-level nitrogen use efficiency (NUE) in recently established, closed-canopy redcedar forests and (2) compare these measurements with similar data collected in paired adjacent grassland sites (soil N pools and fluxes) or with data from similar grasslands at the nearby Konza Prairie Biological Station (ecosystem-level N budgets and NUE).

## METHODS

### SITE DESCRIPTION

This research was conducted in the Flint Hills of eastern Kansas, where the landscape consists of stream-dissected hills eroded in a complex dendritic pattern. Vegetation in the

TABLE 1.—Descriptions of eastern redcedar forest study sites, including tree age, density, above-ground biomass, litterfall rates and ANPP (data from Norris *et al.*, 2001a, 2001b)

Site	Location	Approx. age (yr)	Tree density (trees/ha)	Aboveground total biomass (kg/ha)	Litterfall production (kg/ha/yr)	ANPP (kg/ha/yr)
1	Scenic Dr. 39°17'N, 96°34'W	35	1733	114120	5193	9796
2	Tuttle Cr. Dam 39°10'N, 96°39'W	80	860	210952	4503	7247
3	Randolph 39°27'N, 96°45'W	40	1900	120738	5159	10442

Flint Hills reflects a complex dynamic affected by geology, climate, fire, grazing and other human activities. The native vegetation of the region is primarily tallgrass prairie, dominated by warm-season ( $C_4$ ) grasses (*e.g.*, *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparius*, *Panicum virgatum*), which co-occur with a diverse assemblage of cool season ( $C_3$ ) graminoids and forbs (Freeman, 1998). Bands of deciduous forest border streams in the valley bottoms, and shrub thickets occur at the upper reaches of draws and on slopes around limestone outcrops (Freeman, 1998). Soil properties of the region are most influenced by prairie vegetation and organic matter accumulation. In general, soils are characterized as cherty silty clay loams (Ransom *et al.*, 1998). The climate is characterized as temperate mid-continental. Mean annual temperature is 13 C. Annual precipitation is 835 mm of which about 75% occurs during the growing season. This amount of precipitation is sufficient to support the growth of woody vegetation and, as a result, land-use practices play a major role in affecting land-cover (Briggs *et al.*, 2005).

Three paired forest-grassland study sites in the Flint Hills were selected within a 40 km radius of Manhattan, Kansas, and have been previously described by Norris *et al.* (2001a, b). Each study site included a closed-canopy redcedar forest (Table 1) paired with an adjacent grassland site. The forest stands at these sites ranged in age from approximately 35 to 80 y old, as determined by both historical aerial photographs and tree ring analysis (Hoch, 2000). Based on historical photographs and  $^{13}C$  analysis of soil organic carbon pools (Smith and Johnson, 2003), these sites were grass-dominated prior to redcedar encroachment, which presumably occurred as a result of changes in land use (particularly reductions in fire frequency). These forests, representing the current endpoint (most advanced stage) of redcedar encroachment into tallgrass prairie, are now dominated by eastern redcedar with very little understory vegetation. Herbaceous biomass in the forests averaged only 0.18 g/m<sup>2</sup> (Briggs *et al.*, 2002).

The individual grassland sites paired with each forest site were used primarily for soil N measurements in this study. These sites were located adjacent to a forest site, usually separated by only a fence. Each was grazed by cattle and frequently burned (approximately once every 3 y), representing the predominant land-use for grasslands in this region. Plant communities were characteristic of the region, dominated by  $C_4$  grasses co-occurring with a variety of  $C_3$  grasses and forbs (Freeman, 1998). By choosing paired forest and grassland sites that were adjacent to one another and on similar soils and topographic positions (slope, elevation, aspect), and with historically similar vegetative cover, we assumed that any differences in soil N pools or processes between forest and grassland represented a change that occurred as a consequence of land-use change (*e.g.*, reductions in fire frequency) and the associated change in land cover, from grasslands to redcedar forests. Because the paired grassland sites were all grazed, which precluded estimating ANPP and potential biomass

accumulation, we used data from ungrazed upland tallgrass prairie at the nearby Konza Prairie Biological Station for comparisons of potential ANPP and standing stocks of plant and litter N in redcedar forests and grasslands. Detailed descriptions of the Konza Prairie site are available in Knapp *et al.* (1998).

#### SOIL N FLUXES

At each forested site, soil sampling was done in six plots ( $2 \times 2$  m) spaced evenly along a 200 m transect bisecting the interior portion of the forest stand. Transects of equal length were established in each adjacent grassland site, in areas with similar soil type and topographic position relative to the paired forest transect. Extractable inorganic soil N and in situ net N mineralization rates were measured in each of the six sample plots ( $n = 4$  cores per plot, 24 per transect) year round from May 1998 through Dec. 1999 using an intact soil core incubation method (Blair, 1997 modified from Raison *et al.*, 1987). Soil cores (5 cm diameter, 10 cm deep) were collected for measurement of initial inorganic N concentrations, and adjacent cores, contained in polyvinyl chloride (PVC) sleeves, were incubated in the field for approximately 30-d intervals during the growing season (May through Oct.) and longer periods (2–3 mo) during the remainder of the year. A soil depth of 10 cm was used because this was the maximal depth that could be consistently sampled at all sites due to the occurrence of shallow limestone layers. The upper 10 cm in these grasslands typically includes 44% of grassland belowground plant biomass (Rice *et al.*, 1998) and the greatest concentrations of soil organic matter and microbial biomass (Dodds *et al.*, 1996). Before collecting initial soil samples or installing in situ cores, identifiable surface litter ( $O_i$  horizon) in the forest sites was excluded from both the initial samples and the incubated soil cores to facilitate comparisons with mineralization rates in grassland sites, where surface litter was generally absent due to frequent fires and grazing. Comparisons of forest cores with and without surface litter horizons indicated no significant differences in net N mineralization rates (McKinley, 2006). Field-moist soil from both the initial and incubated cores was sieved (4 mm screen) and subsamples extracted with 2 mol/L KCl. Concentrations of inorganic N ( $\text{NH}_4\text{-N}$  and  $\text{NO}_2/\text{NO}_3\text{-N}$ ) in the extracts were measured colorimetrically using an Alpkem FlowSolution analyzer. Additional subsamples of soil were dried at 60 C to determine gravimetric soil water content and extractable soil N concentrations were converted to  $\mu\text{g N/g}$  dry soil. Daily net N mineralization rates for specific incubation periods were calculated as  $(N_F - N_I)/\text{days}$ , where  $N_F$  is the final concentration of total extractable N ( $\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$ ) in post-incubation PVC cores and  $N_I$  is the initial concentration of total extractable N in the adjacent core taken at the start of the incubation period. Cumulative N mineralized over the growing season was calculated by summing net N mineralization rates from specific incubation periods, and extrapolating values for the short periods between incubations. Extractable N concentrations and net N mineralization rates were converted to a kg/ha basis using site-specific bulk density measurements (Smith and Johnson, 2003).

#### N POOLS

Standing stocks of N in plant biomass, litter and soil were quantified in the forest sites and compared either to data collected from the adjacent grassland sites as part of this study (soil N), or to published data from the nearby Konza Prairie Biological Station (plant biomass and litter N). Data from Konza Prairie Biological Station provided an index for potential plant productivity and accumulation of biomass N in the absence of grazing. Allometric equations relating diameter at breast height (dbh) to aboveground biomass N (Norris *et al.*, 2001b) were applied to three 0.02 ha plots equally spaced along the sample transects in each

forest site to determine standing stocks of aboveground tree biomass N. We did not measure belowground biomass directly in the forest sites, but estimated redcedar belowground biomass assuming a root:shoot ratio of 0.25 (Cairns *et al.*, 1997) and applying a mean root N concentration of 0.50% (Norris *et al.*, 2001a). Estimates of forest floor (O<sub>i</sub> horizon) N mass were obtained by collecting twenty 0.1 m<sup>2</sup> litter samples consisting of identifiable litter along each sample transect (corresponding to the litter removed from soil cores for inorganic N analysis). Total soil N to a depth of 10 cm was quantified in both forest and grassland sites using soil samples from the initial N mineralization cores collected on two dates (May 1998 and Oct. 1999). Litter and soil samples were dried for 48 h at 60 C, weighed, ground and analyzed for N content on a Carlo Erba NA 1500 Analyzer (Carlo Erba, Milano, Italy).

#### NITROGEN USE EFFICIENCY

In order to compare forests and grasslands developed under the same climate and on similar soils, we calculated nitrogen use efficiency (NUE) for each forest site using data collected in this study and compared their NUE to that of a typical grassland site in this region using data from the Konza Prairie Biological Station. Ecosystem-level NUE was calculated two ways, using ANPP:litterfall N, an index of the amount of aboveground biomass produced per unit of N lost (Vitousek, 1982; Reich *et al.*, 1997) and as ANPP:soil net N mineralized, an index of aboveground biomass produced per unit soil N available (Reich *et al.*, 1997). In the forest sites, ANPP was calculated using allometric regression equations (Norris *et al.*, 2001b) and litterfall N determined through the use of litter collectors and analysis of subsamples for N content (Norris *et al.*, 2001a). Grassland NUE was calculated using average ANPP (obtained by harvesting end-of-season aboveground biomass), litterfall (collected using 1 m long troughs on the soil surface) and standing dead N values from an annually burned upland site at Konza Prairie Biological Station (Seastedt, 1988; Knapp *et al.*, 1998; Blair *et al.*, 1998). Both surface litterfall N and standing dead N were used since both represent sources of annual N loss via litter production in grasslands.

#### DATA ANALYSIS

Soil N measurements (total N, inorganic N, and mineralization rates) within a particular site were characterized by high spatial variability. For these measurements, we used median values from each site for our analyses to diminish the influence of extreme values (Zar, 1996). A repeated measures ANOVA was used for the inorganic N and mineralization data to determine land cover effects over the course of the entire study. A mixed model was used to incorporate the random effect of blocking on location with the fixed effect of land cover type (Proc mixed, SAS Institute, Cary, NC). The analysis included the determination of an appropriate covariance structure while accounting for unequal spacing between sample dates (Littell *et al.*, 1996). Differences between forests and grasslands at each date were evaluated by *t*-tests using a Bonferroni correction. Soil moisture was considered as a possible covariate; however, including it did not aid in the analysis. Results are reported in the text as significant where  $P < 0.05$ .

### RESULTS

#### SOIL NITROGEN AVAILABILITY

Mean measurements of soil N pools and fluxes in both the grassland and forest sites were characterized by a large amount of spatial heterogeneity. Across all dates, the effect of land cover type on inorganic N concentrations was only marginally significant ( $P = 0.0889$ );

however, there was a fairly consistent trend for inorganic N to be slightly higher in grassland sites on most sample dates (Fig. 1A). The greatest margin of difference between net N mineralization rates in forest and grassland sites occurred in May of both years when the grasslands exhibited greater mineralization rates than forested sites (Fig. 1B); however, this was only significant on one date (May 1999,  $P = 0.0237$ ) and there was no overall effect of land cover type on mineralization rates across all dates. Cumulative net N mineralized was calculated at the end of the first year (May 1998–Apr. 1999) and again after the second growing season (May–Oct. 1999) (Fig. 1C) and although not significantly different, forest sites mineralized on average 15% less N ( $14.3 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ) than adjacent grassland sites ( $16.9 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ). Values for both the forest and grassland sites are within the range previously reported for tallgrass prairie sites at the nearby Konza Prairie Biological Station (Blair, 1997; Turner *et al.*, 1997).

#### NITROGEN POOLS

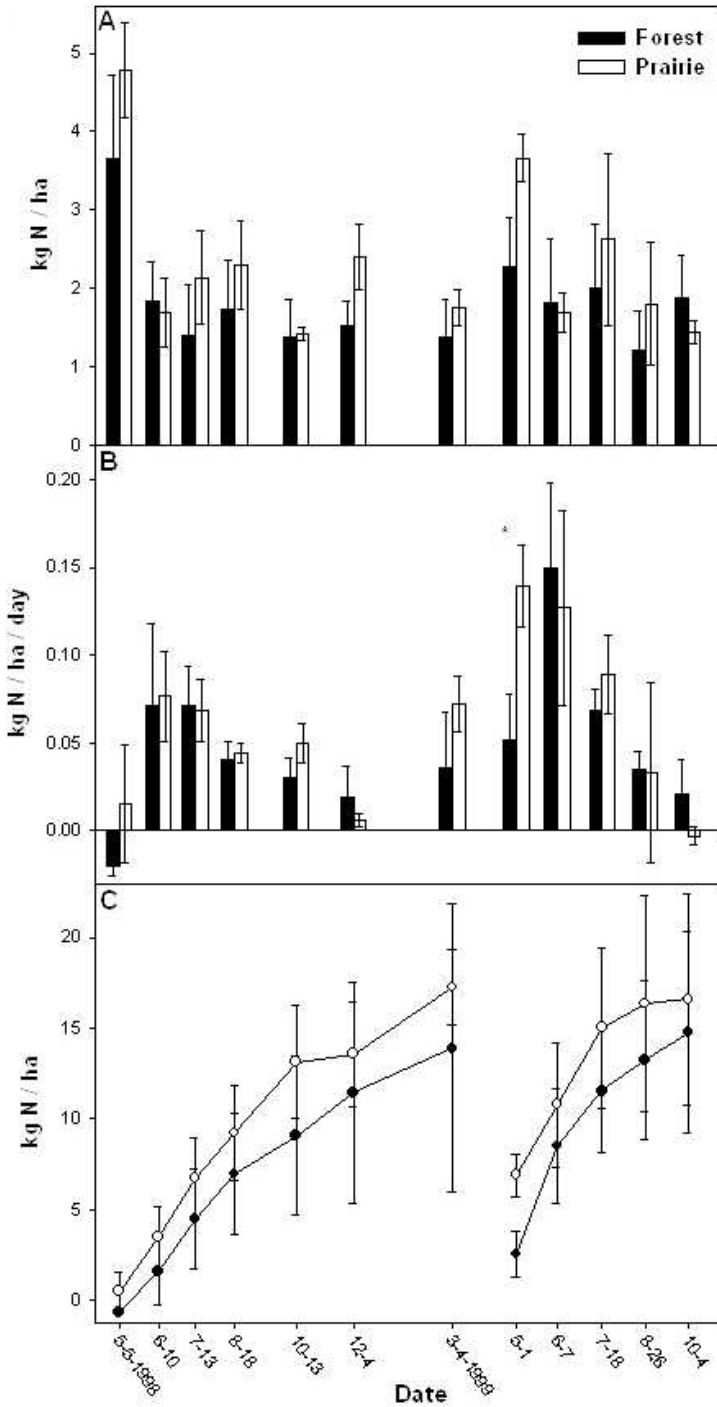
Redcedar forests stored considerable quantities of N in aboveground biomass and surface litter compared to the grassland sites they replaced. The forest sites had 20–27% of total ecosystem N in plant biomass (depending on stand age), most of which was aboveground (Fig. 2). This was substantially more than the proportion of ecosystem N sequestered in plant biomass in ungrazed grassland sites (approximately 3.6%). In forest sites, we estimated mean aboveground biomass N to be  $617 \text{ kg N/ha}$  (Norris *et al.*, 2001b), which was approximately 15× greater than typical shoot N in local tallgrass prairie ( $40 \text{ kg N/ha}$ , Blair *et al.*, 1998). Additionally, litter accumulations on the forest floor ( $O_i$  horizon) contained, on average,  $253 \text{ kg N/ha}$ , which was substantially more than the litter pool in grasslands, which is subject to frequent removal by burning (Norris *et al.*, 2001a). Averaged across all three sites, total soil N content (0–10 cm) was not significantly different between forest and grassland sites although the mean proportion of total ecosystem N residing in the soil was higher in grasslands (96.4%) than in forests (77.6%).

#### NITROGEN USE EFFICIENCY

Perhaps the greatest difference between the grassland and forest sites was their nitrogen use efficiency (NUE). Estimates of ecosystem-level NUE, calculated as ANPP ( $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ) per unit N returned in litterfall ( $\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ), were 223 ( $\pm 21$ ) for the redcedar forest sites and 93 for grassland sites (no standard error is included for grasslands sites, since we used the long-term mean of ANPP at upland, burned grassland sites and a mean annual litterfall value for this calculation). Estimates of NUE calculated as ANPP:soil N mineralized ( $\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ) were 1151 ( $\pm 459$ ) for forest and 256 ( $\pm 62$ ) for grasslands. Differences in NUE between forest and grassland were due to the much greater average ANPP in redcedar forests ( $9162 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ , Norris *et al.*, 2001b) relative to comparable upland grassland sites ( $3700 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ , Knapp *et al.*, 1998) coupled with the relatively minor differences in litterfall N and soil N mineralized.

#### DISCUSSION

Despite the extreme land cover change associated with the coniferous afforestation of tallgrass prairie, changes in soil nitrogen availability and net N mineralization in surface soils of recently established stands ( $\leq 80 \text{ y}$ ) of closed canopy redcedar forest were relatively small compared to adjacent grasslands sites. Although there were only a few statistically significant differences between forest and grassland sites for either measure of soil N availability (extractable inorganic N or net N mineralization) across all sites, the data did



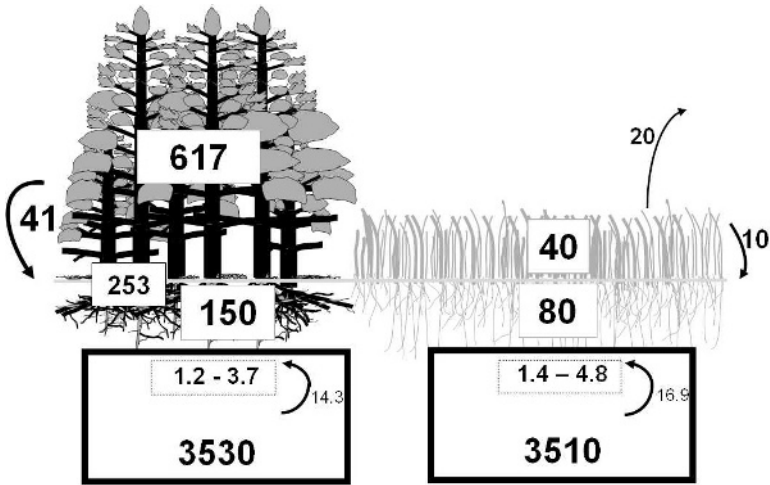


FIG. 2.—Major pools (kg/ha) (boxes) and fluxes (kg·ha<sup>-1</sup>·yr<sup>-1</sup>) (arrows) of nitrogen in recently established (35–80 y old) redcedar forests and comparable grasslands, including aboveground and belowground biomass, litterfall, forest floor (forest), volatilization (prairie), and within the soil box (0–10 cm): total soil N, annual net N mineralization rate, and available N (in the interior box). Values for forest sites are the mean of the three forest sites studied here, as are the grassland soil N values. Other data for grasslands represent mean values for frequently burned, ungrazed upland prairie, based on data from the Konza Prairie Biological Station

suggest a modest reduction in N availability as a consequence of conversion of grasslands to forests, driven primarily by early season differences between land cover types (Fig. 1). It is important to note that grassland management may play a role in affecting these comparisons. The paired grasslands used in this study were all subject to long-term grazing, which is a dominant land-use for native prairie in the Flint Hills region. Grazing has been shown to significantly increase N availability in these grasslands, relative to non-grazed tallgrass prairie (Johnson and Matchett, 2001). Thus, the relative comparisons of soil N availability were likely affected by both differences in land-use (*i.e.*, fire and grazing) as well as the changes in land-cover type that occur once fire and grazers are excluded from these grasslands.

The relatively small changes in soil N availability observed in this study contrasts with other studies of woody encroachment into North American grasslands, which often indicate significant increases in rates of nutrient cycling, availability, and accumulation (*e.g.*, Schlesinger *et al.*, 1990; Wilson and Kleb, 1996; Hibbard *et al.*, 2001); however, there are limited studies in temperate grasslands that involve coniferous species and an evaluation of soil nutrient consequences. In southern Texas (Brown and Archer, 1989; Archer, 1995; Hibbard *et al.*, 2001) and in Arizona (MacPherson *et al.*, 1993), land cover change has been

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FIG. 1.—A.) Inorganic nitrogen (nitrate and ammonium) extracted from initial N mineralization samples, B.) daily net nitrogen mineralization rates, and C.) cumulative net N mineralized from May 1998 through Dec. 1999. Bars represent the mean ±1 SE with n = 3. Using a repeated measure analysis, there were no significant main effects of land cover type (forest vs. grassland) across dates. An asterisk (\*) denotes a significant difference (P < 0.05) between forest and grassland for a particular date

well documented following the invasion of honey mesquite (*Prosopis glandulosa* Torr.). This leguminous species obtains at least 50% of total N requirements from symbiotic N<sub>2</sub>-fixation (Rundle *et al.*, 1982; Boutton *et al.*, 1992) and has a foliar N concentration of 5.2% (Barnes and Archer, 1996), more than 4× the live foliage nitrogen content of redcedar (1.25%). Despite increases in foliar inputs and litter quality, a modeling exercise showed that landscape changes in soil carbon associated with the mesquite-dominated uplands did not vary significantly from heavily grazed soils until well after 30 y of woody plant development (Hibbard *et al.*, 2003).

The redcedar stands in our study were relatively young and may continue to alter soil N dynamics as they mature, especially considering the relatively low quality and slow decomposition of redcedar litter (Norris *et al.*, 2001a). The oldest forest site at Tuttle Cr. Dam, double the age of the younger sites, exhibited greater soil N concentrations and mineralization rates relative to the younger forests and usually the grassland sites as well. For instance, average annual net N mineralized at the Tuttle Cr. Dam forest was 27.8 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> compared to 8.5 and 6.7 at the other forest sites and 16.9 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> in the grasslands. These data suggest a potential time lag on the scale of decades of soil nutrient responses associated with this land cover change and that these sites have yet to reach equilibrium. Clearly, in order to explain the patterns of change in ecosystem processes associated with redcedar forest expansion, we need a better understanding of plant-soil interactions and the temporal dynamics of this afforestation.

In contrast to the relatively minor changes in soil N pools and processes, there were substantial increases in aboveground biomass and surface litter N pools associated with the conversion of grassland to forest. Likewise, large increases in ANPP (Norris *et al.*, 2001b) led to dramatic increases in NUE in grassland sites converted to redcedar forests, providing an interesting metric for comparisons of these two land cover types. Previous studies of NUE have often found that NUE increases with diminishing N availability (Gosz, 1981; Lennon *et al.*, 1985; Escudero *et al.*, 1992; Reich *et al.*, 1997). However, in this case, differences between forest and grassland do not appear to be linked to differences in soil N availability, but rather to intrinsic characteristics of the species themselves, providing an opportunity to evaluate how changes in plant life form can alter ecosystem-level patterns of NUE on sites of similar fertility and nutrient availability.

The comparatively low NUE in grassland, relative to redcedar forest, is particularly interesting given the efficiency of the C<sub>4</sub> photosynthetic pathway and ability of the dominant grasses to operate under conditions of low N availability (Knapp and Seastedt, 1986), typically the nutrient most limiting to grassland productivity (Risser and Parton, 1982; Seastedt *et al.*, 1991; Blair *et al.*, 1998) due to a strong interaction between frequent disturbances (*e.g.*, fire, grazing) and N (Ojima *et al.*, 1994; Blair, 1997). Conifers also possess traits that result in a high NUE, including conservative N cycling due to poor litter quality (*e.g.*, low leaf N, high lignin), slow decomposition rates, and high internal redistribution of N (Gosz, 1981; Reich *et al.*, 1992). Leaf longevity is a simple factor related to each of these mechanisms (Chapin, 1980; Reich *et al.*, 1995; Aerts and Chapin, 2000) and it is probable that differences in the leaf life-span of redcedar stands (3–6 y) (Norris, 2000) and tallgrass prairie (5–6 mo) contribute to observed patterns of N cycling and NUE.

It is also interesting to note the changes in total ecosystem nitrogen associated with the conversion of grassland sites to forest. If we examine the major pools and fluxes of N in these mature redcedar forests and in frequently burned grassland (Fig. 2), there was no significant change in total soil N pools, but a substantial increase in N stored in aboveground biomass and the litter layer. We recognize that the changes in aboveground

biomass might be offset or augmented by changes in belowground biomass which we did not measure directly. However, our estimates of plant biomass N belowground magnify the differences between N sequestered in plant total biomass in forest and grassland, as redcedar root N mass was estimated to be 150 kg N/ha compared to about 80 kg N/ha for root mass N in native tallgrass prairie. These estimates of root biomass in redcedar forest stands are first approximations that will require verification, but they suggest the importance of both above- and below-ground biomass in N accumulation in new redcedar forests.

Since the establishment of these forests, these sites appear to have accumulated 910 kg N/ha in total ecosystem N (15 to 23 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>) relative to grassland. It is not uncommon for aggrading forests to accumulate nitrogen as a result of conservative nutrient cycling (Bormann and Likens, 1979; Pearson *et al.*, 1987). In the case of conversion of tallgrass prairie to redcedar forest, the elimination of fire and associated N losses may account for at least a portion of the accumulated N. Two additional potential explanations for the high rate of N accumulation include enhanced N inputs via N<sub>2</sub>-fixation (Bormann *et al.*, 1977, 1993) or more efficient capture of atmospheric deposition by coniferous trees (Lovett and Lindberg, 1984, 1993). While we cannot discount these two mechanisms for additional N accumulation, they are believed to be minor relative to other inputs (*e.g.*, bulk precipitation) (Vance *et al.*, 1983; Grant and Binkley, 1987; Heath *et al.*, 1988). The apparent increase in N storage may also reflect a redistribution of existing N pools following the conversion of grasslands to redcedar stands as soil N from deeper depths is depleted and redistributed into plant biomass and litter. This seems unlikely, however, as these forests occurred on relatively shallow soils and we observed no significant difference in total N stored in the upper 10 cm of soil in grassland and forest sites.

This study highlights some important changes in ecosystem-level NUE and nitrogen storage as a result of land-cover change from native tallgrass prairie to redcedar forest. However, understanding the mechanisms underlying these changes in N cycling will require better knowledge of several processes. In particular, root production and turnover have not been quantified directly in comparable grassland and redcedar sites, but are likely responsible for the majority of total N turnover (Cox *et al.*, 1978). In addition, a more detailed assessment of the temporal dynamics of change may provide insights into the apparent differences in N dynamics between forest sites of different age, as suggested by a possible stand age factor in net N mineralization rates. Lastly, identifying the mechanisms by which these forests have accumulated a substantial amount of N relative to the grasslands they replaced may shed light on the controls of biomass and C sequestration in these newly established forests. In summary, the establishment of redcedar forests in areas formerly dominated by native grasslands results not only in decreased biodiversity (Hoch and Briggs, 1999), but also significant changes in productivity (Norris *et al.*, 2001b) and ecosystem N storage. The increases in productivity as well as N and C storage with redcedar encroachment are consistent with the reported effects of other types of woody plant expansion in the Midwestern U.S. (Tilman *et al.*, 2000; Hughes *et al.*, 2006), indicating that this land cover change may have important impacts on regional biogeochemistry (Pacala *et al.*, 2001; Jackson *et al.*, 2002). However, the long-term dynamics of these newly established ecosystems, with respect to disturbance (*e.g.*, fire) and climate (*e.g.*, drought and climate change), are still unknown and deserve further attention, as the current rates of biomass and nutrient accumulation will likely not be sustainable.

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