
Effects of Prescribed Fire on Nutrient Pools and Losses from Glades Occurring Within Oak-Hickory Forests of Central Kentucky

T. L. E. Trammell,^{1,2} C. C. Rhoades,^{3,4} and P. A. Bukaveckas^{1,5}

Abstract

Forest openings, also known as glades, arise through a variety of mechanisms including disturbance (fire and blow downs) and local variation in soil or bedrock geology. They are common in many forest types and are often dominated by locally rare herbaceous species. Prescribed burning is increasingly used as a management approach for maintaining glades although little is known about the effects of fire on these habitats. Of particular concern is the potential for nutrient loss during and after fire because glades are often characterized by nutrient-poor soils. We quantitated nutrient losses through combustion and leaching for glade and adjacent forest habitats subjected to a prescribed burn. Our findings suggest that spring burns do not result in appreciable loss of nutrient capital from glades in comparison with those observed in the surrounding forest. Fire

resulted in a substantial loss of litter mass (37%) in the forest but no measurable loss in the glade. Nitrogen losses through combustion were significant in the forest and were equivalent to 4.5 years of atmospheric inputs. Fire significantly increased soil nitrate pools in forest but not in glade plots. No detectable increases in nitrogen, phosphorus, or base cation leaching were observed in either forest or glade habitats within 4 months after the burn. These findings suggest that plant and microbial nutrient uptake rapidly reestablish control over leaching losses when burns are conducted at the start of the growing season. Biotic retention minimizes fire impacts on nutrient loss from the ecosystem.

Key words: combustion, Kentucky, leachate, nitrification, nitrogen mineralization, nutrient cycling, prescribed fire, restoration, soil nitrogen.

Introduction

Many forest and grassland ecosystems depend on periodic fire to maintain their vegetation composition (Boerner et al. 1988; Briggs & Knapp 1995; Gill & Williams 1996), and paleoecological records suggest fire has been prevalent in Appalachian forests for 4,000 years (Delcourt & Delcourt 1997). Periodic fires contribute to the formation and maintenance of forest openings (hereafter, glades; Anderson et al. 1999), and managers have begun to reintroduce fire to maintain the unique flora comprising glade communities. There have been many studies of fire effects on grasslands and forests (Boerner 1982; Mackensen et al. 1996; Boerner 2000; Thomas et al. 2000), but we know of no prior studies that have examined fire effects on glades in mid-latitude forests.

The impact of fire on nutrient cycling is dependent on the severity of the fire (intensity, aerial extent, and frequency) and on the characteristics of the ecosystem including dominant vegetation type and fuel load (Boerner 1982; Dudley & Lajtha 1993; Pyne et al. 1996). Fires promote nutrient loss from ecosystems through oxidation and volatilization of nutrients stored in vegetation, woody debris, and litter and through subsequent (post-fire) loss via soil leaching, surface run-off/erosion, and convection of ash (Fisher & Binkley 2000). Pathways of nutrient loss are element specific and depend in part on volatilization temperatures which are lower for carbon (C) and nitrogen (N) (approximately 200°C) than for phosphorus (P) and base cations (>500°C; Pyne et al. 1996). The low volatilization temperature for N increases the potential for loss through combustion (Boerner 1982), whereas higher volatilization temperatures for P and base cations result in their accumulation in fire ash (Kauffman et al. 1994). Ash is easily dissolved by rain and lost via leaching or run-off (Moore 1996; Thomas et al. 2000). Fire may also indirectly affect nutrient leaching through changes in soil microbial activity. Ash inputs and increased microbial mineralization after burning can result in elevated ammonium concentrations, higher rates of nitrification, and increased leaching losses (Fisher & Binkley 2000). Vegetation mortality or damage after fire will reduce plant nutrient uptake and increase the potential for leaching losses. The extent of

¹Department of Biology & Center for Watershed Research, Life Sciences 139, University of Louisville, Louisville, KY 40292, U.S.A.

²Address correspondence to T. L. E. Trammell, email tara.trammell@louisville.edu

³Department of Forestry, University of Kentucky, Lexington, KY 40506, U.S.A.

⁴Present address: U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, CO 80526, U.S.A.

⁵Present address: Department of Biology and Center for Environmental Studies, 1000 Cary Street, Virginia Commonwealth University, Richmond, VA 23284, U.S.A.

such changes and the rate of subsequent vegetation regrowth will determine the balance between nutrient retention and loss after fire.

Differences in vegetation structure between forest and glade communities may result in different pathways of nutrient loss after fire. Greater aboveground biomass and higher fuel loads in forests favor high combustion losses. If tree mortality is low, post-fire recovery is rapid and may act to minimize leaching losses particularly when burns are conducted at the start of the growing season. In glades, fine herbaceous litter predominates and fuel loads are lower. In contrast to the surrounding forest, low combustion losses within glades may be offset by high leaching losses.

Prescribed burns were conducted in early spring at three glades located at the Bernheim Arboretum and Research Forest near Louisville, Kentucky, U.S.A. The objective of this study was to quantitate nutrient losses due to leaching and combustion in the glades and surrounding forest. We hypothesized that (1) greater fuel load in forest plots would result in greater combustion losses; (2) leaching losses would predominate over combustion losses in glade plots; and (3) burning would increase inorganic soil N pools and net mineralization and nitrification in both forest and glade habitats.

Methods

Site Description

The study sites consisted of three isolated glades (650–2,900 m² in area) located within the Bernheim Arboretum and Research Forest. The Arboretum comprises 4,900 ha of second-growth hardwood forest and isolated abandoned agricultural fields within Kentucky's Western Knobs ecoregion (39 km south of Louisville; 37°52' N, 85°35' W). The mean annual precipitation for this region is 113 cm, and the mean annual maximum and minimum temperatures are 25 and 0°C, respectively. Agriculture and logging activities within the Arboretum occurred before 1929, and no prescribed burning has occurred since that time. The Kentucky Division of Forestry extinguishes infrequent human- and lightning-caused fires in the research forest (M. Shea, Bernheim Arboretum & Research Forest, 2000, personal communication).

The glades occur at an equal elevation on south-facing slopes. Their location corresponds to a band of interbedded limestone and dolomite that forms silty loam soils mapped as Caneyville-Rock and Caneyville-Beasley-Rock outcrop series with fine, mixed mesic Typic Hapludalfs classification (Soil Conservation Service 1986). A previous study conducted at these sites comparing soil properties of the forest and glades demonstrated that the glades are situated on alkaline soils (pH = 8) with extremely low plant-available soil phosphorus (Mehlich-III P: <0.1 g/m²), whereas soils in the surrounding forest are richer in total and available nitrogen (N) (Rhoades & Shea 2003).

The glades are dominated by *Schizachyrium scoparium* (little bluestem), *Sporobolus vaginiflorus* (dropseed), and *Danthonia spicata* (poverty oat grass) with scattered *Juniperus virginiana* (eastern redcedar) encroaching at the edge (Homoya 1999; Rhoades et al. 2004). The surrounding forest is unique to calcareous soils and consists mainly of *J. virginiana*, *Acer saccharum* (sugar maple), *Fraxinus quadrangulata* (blue ash), *Cercis canadensis* (eastern redbud), *Quercus muehlenbergii* (chinquapin oak), and *Quercus alba* (white oak) (Homoya 1999; Rhoades et al. 2004).

Burn Treatment

Prescribed burning was conducted on 29 March 2000. The air temperature was 13–17°C and relative humidity was 32–44%. Headfire flame length ranged 0.3–1.2 m and the backfire flame lengths were 0.15–0.30 m. Fire lines bisected the glades to restrict the fire to about 50% of each opening. At each site, burned areas encompassed grass-dominated glade interior, woody edge, and surrounding forest. Fire temperatures estimated with aboveground and buried (5 cm) temperature-sensitive paints (Tempilac, South Plainfield, NJ, U.S.A.) exceeded 500°C within the leaf litter layer but did not reach 50°C in the mineral soil (5 cm). To assess variability in burn cover, we established transects of 100 m in length and 10 m apart through the burned half of the glades. We measured burn presence at each meter point along the transects. Percent burn cover was calculated as the number of burned points divided by all the points sampled.

Sample Design

Fire effects on soil leachate losses were measured at two of the three glades, whereas combustion losses (herbaceous vegetation, litter, and woody debris), plant-available soil N pools (nitrate [NO₃⁻] and ammonium [NH₄⁺]), and N transformations were quantitated at all three sites. Four randomly selected transects bisected the glades and continued 50 m into the surrounding forest. Glade plots were established near the boundary between the glade and surrounding forest. Forest plots were located 10–20 m into the surrounding forest. For both the glade and the forest, plots were located within the burned and unburned (hereafter, control) areas.

Sample Collection

Soil Leachate. To estimate losses of N, P, and base cations, we analyzed the elemental content of soil water leachate from samples collected on multiple dates before and after the prescribed burn. Nutrient losses were compared to flux rates for a biologically conservative ion (chloride [Cl⁻]) to distinguish burn effects from seasonal and spatial variability. Two months before the first collection (October 1999), zero-tension lysimeters (305 cm²)

were buried at a depth of 10 cm (includes O-horizon and part of the A-horizon). The objective was to sample leachate loss where the majority of fine roots are located (Pregitzer et al. 2000), and shallow rooting depth is often characteristic of glade species (Anderson et al. 1999). In addition, the prevalence of rocky materials precluded lysimeter installation in deeper layers without substantial disturbance to the soil profile. Two replicate lysimeters were installed at burned and control areas in each of the forest and glade plots and at both study sites ($n=16$ lysimeters). Before anticipated rain events, we deployed 1-L acid-washed polyethylene bottles to collect outflow from the lysimeters. Rainfall and leachate samples were collected within 48 hr after each event. Eight events exceeding 2.54 cm of rainfall per 48 hr were sampled during the study period (October 1999 through July 2000; four collection dates before and after the burn). Solute concentrations were converted to aerial flux rates (mg/m^2) based on the volume of water collected and the area sampled by the lysimeter. This allowed comparison among study plots with different water yields. The sampling events represented a volume of precipitation (28 cm) equivalent to 26% of the total for the year (106 cm; Bernheim Arboretum Weather Station records). We assumed that our lysimeter collections underestimated annual leachate losses by a fraction equivalent to that represented by the proportion of rainfall occurring during these events. Lysimeter data for the eight events were summed and multiplied by the corresponding factor (3.8) to derive an annualized estimate of leachate loss.

Precipitation and leachate samples were filtered through Gelman 0.45- μm glass-fiber filters (Fisher Scientific, Hampton, NH, U.S.A.) and frozen until analysis. Samples were analyzed for Cl^- , NH_4^+ , nitrate (NO_3^-), total dissolved N (TDN), soluble reactive P (SRP), total dissolved P (TDP), and base cations (K^+ , Na^+ , Ca^{2+} , and Mg^{2+}). Chloride was analyzed using the manual modification of the automated ferricyanide method (APHA 1999). Nitrate, NH_4^+ , and TDN analyses were performed on a Skalar San Plus segmented flow water analysis system (Breda, the Netherlands) using cadmium reduction, phenate, and persulfate digestion methods, respectively (APHA 1999). Dissolved organic N (DON) was determined by subtracting the sum of NO_3^- and NH_4^+ from TDN. Total dissolved P samples were digested with persulfate then analyzed (as for SRP) using the manual, ascorbic acid, two-reagent method (APHA 1999). Base cations (K^+ , Na^+ , Ca^{2+} , and Mg^{2+}) were analyzed on a GBC Avanta atomic absorption spectrometer (Melbourne, Australia; APHA 1999). Analyses of pre-burn samples showed that NO_3^- accounted for 88% of TDN and that SRP accounted for 98% of TDP. Therefore, post-burn lysimeter samples were analyzed for NO_3^- and TDP only.

Litter and Woody Debris. We measured fuel load before and after the burn to quantitate combustion losses. Fuel load was estimated as the dry mass of litter and woody debris. Litter was collected from four (0.0625-m^2) subplots

in each of the habitat types (forest and glade) at all three study sites ($n=24$ subplots). Litter in grassland plots consisted of dead and living grass and leaf material and, in forest plots, of dead leaf material and fine woody debris (<0.1 cm diameter). Woody debris was partitioned into four size classes: small (<2.54 cm diameter), medium (2.54–7.6 cm diameter), large (7.6–20.5 cm diameter), and huge (>20.5 cm diameter) (Deeming et al. 1978). Small and medium woody debris were sampled in eight randomly selected plots per site. Plots covered 3×3 m except where patchy burning necessitated the use of 1×1 -m plots. Small and medium woody debris were counted in each plot. Before burning, all large and huge woody debris within the burned areas were counted and mapped. The volume, dry mass, and carbon (C) and N content were measured on a subset of samples (10% for volume; 1–5% for mass, C, and N) from each size class. Litter samples and woody debris subsamples were oven dried at 72°C for 48 hr to determine dry mass. Samples were ground using a Thomas-Wiley Intermediate Mill 3383-L10 Series (Swedesboro, NJ, U.S.A.) and analyzed for C and N using a Perkin-Elmer 2400 Series II CHNS/O analyzer (Shelton, CT, U.S.A.).

Soil N Pools and Fluxes. Plant-available soil N pools (NO_3^- and NH_4^+) and net mineralization and nitrification rates were measured on two dates during the post-burn period (June and October 2000). On both dates, two replicate soil samples were removed from each of two plots for both habitats (glade and forest) and treatments (burned and unburned) at all three study sites ($n=48$). Samples of the top 10 cm of mineral soil were collected with a 5-cm diameter corer, transported within a plastic cooler, refrigerated at 4°C , and processed within 48 hr. An initial subsample was extracted with 1M KCl and analyzed for NO_3^- and NH_4^+ by colorimetric spectrophotometry (Bundy & Meisinger 1994). A second subsample was oven dried at 105°C for 24 hr to calculate the gravimetric soil moisture content. Another set of 15-g subsamples was incubated at 26°C for 14 days at field capacity (Binkley & Hart 1989). Field capacity was approximated as the gravimetric water content of a subsample wetted to saturation then allowed to freely drain for 12 hr (gravimetric moisture content of about 50%). Periodically during the incubation, samples were reweighed and wetted with distilled water to maintain a constant mass and moisture content. After 14 days, the incubated subsamples were extracted with 1M KCl and analyzed as previously described. Net mineralization was calculated as the change in NO_3^- plus NH_4^+ and net nitrification as the change in NO_3^- between initial and incubated extracts.

Statistical Analysis

Forest and glade leachate losses were analyzed separately using a three-factor model (ANOVA) to partition variation according to treatment (burn vs. control), time (pre-burn vs.

post-burn), and site (two study sites). In this model, fire effects would be detected through a significant interaction between treatment and time factors (indicative of higher or lower fluxes in burned plots during the post-burn period). Litter and woody debris data (dry mass, C and N content) were collected on a single date during the post-burn period, and a three-factor model was used to assess the effects of treatment (burn vs. control), habitat type (glade vs. forest edge), and site (three study sites). Soil N pools and fluxes were averaged for two dates during the post-burn period, and a three-factor model was used to partition variation according to treatment (burn vs. control), habitat type (glade vs. forest edge), and site (three study sites).

Results

Soil Leachate

For both the forest and the glade habitats, burned and control plots exhibited comparable leaching losses of nitrate (NO₃⁻), total dissolved phosphorus (TDP), chloride (Cl⁻), and base cations throughout the pre- and post-burn monitoring period (Fig. 1). The three-factor statistical models accounted for 23–46% of the variation in NO₃⁻, TDP, Cl⁻, and base cation leaching losses from glade and forest habitats (all models significant; *p* < 0.05). No significant fire effects were detected for any of the solutes in either the forest or the glade habitat. Significant differences among sites were observed in both the forest

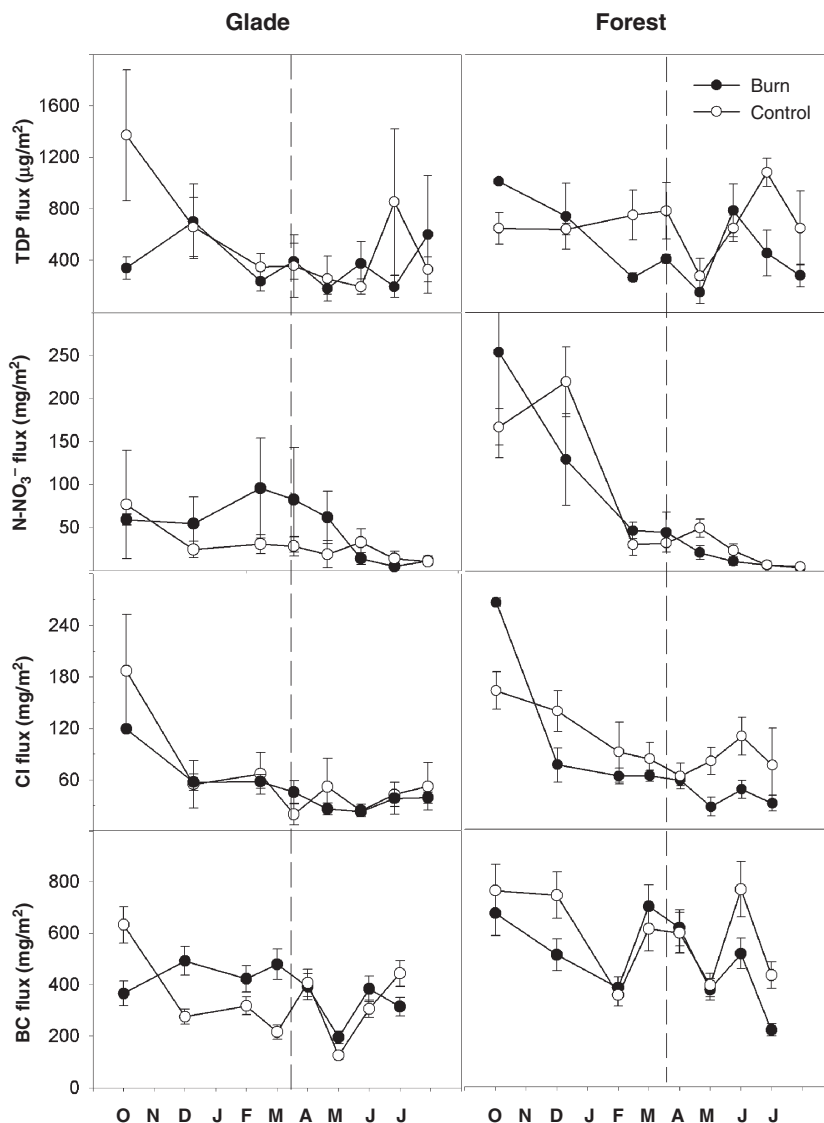


Figure 1. Leaching losses of total dissolved phosphorus (TDP), nitrate (N-NO₃⁻), chloride (Cl⁻), and base cations (BC) from control (unburned) and burned plots located in glade and forest habitats. Dashed line represents burn treatment (29 March 2000). Bars denote standard error of the mean among lysimeters at sites 1 and 2.

(Cl⁻, TDP, and base cations) and the glade (TDP and base cations). No consistent seasonal trends were observed although losses tended to be higher during the first two events (October and December 1999) particularly with respect to NO₃⁻. Higher pre-burn losses from forest plots (217 mg NO₃⁻-N/m²) relative to glade plots (49 mg NO₃⁻-N/m²) were largely a result of higher NO₃⁻ concentrations in leachate (=9.25 and 2.11 mg/L in forest and glade, respectively). Average fluxes of TDP (over the entire 8-month sampling) were similar among glade and forest habitats (465 and 448 μg/m², respectively), whereas base cation fluxes were lower in glade (360 mg/m²) relative to forest plots (542 mg/m²). Calcium was the dominant base cation (54% of total) followed by Mg²⁺ (34%), K⁺ (6%), and Na⁺ (5%).

Litter and Woody Debris

Litter mass was three times higher in forest plots (0.69 kg/m²) than in glade plots (0.23 kg/m², $p=0.001$; Fig. 2). Forest litter also contained a higher nitrogen (N) content (1.9%) compared to glade litter (1.3%). The combined effect of higher mass and N content yielded a 6-fold higher litter N mass in the forest (14.1 g/m²) relative to the glade (2.4 g/m²). Burning resulted in a significant reduction in forest litter ($p=0.024$) from 0.69 to 0.43 kg/m². The 37%

decrease in forest litter was accompanied by a proportional loss of carbon (C) (36%), but greater loss of N (45%). In glade plots, burning had no effect on litter mass, C, or N. There were no significant differences in litter mass, C, or N among the three study plots.

The mass of woody debris in forest plots (0.19 kg/m²) was 2-fold higher than in glade plots (0.10 kg/m², $p < 0.005$) with corresponding differences in C mass. Forest woody debris contained a greater proportion of N such that forest sites had 3-fold higher woody debris N mass than glade sites (0.7 vs. 0.2 g/m², $p < 0.001$). In forest plots, fine (<7.6 cm) and coarse (>7.6 cm diameter) woody debris were approximately equal proportions of the total woody debris mass, whereas in glade plots total woody debris fuel load was entirely comprised of fine woody debris. Burning did not result in a measurable loss of woody debris in either the forest or the glade habitats. There were no significant differences in woody debris mass, C, or N among the three study plots.

Soil N Pools and Fluxes

Soil NO₃⁻ and ammonium (NH₄⁺) pools were significantly higher in forest plots compared to glade plots ($p < 0.001$; Fig. 3). Fire effects on soil N pools were inferred from comparisons of burned and control plots in each habitat type, and they revealed significant differences in NO₃⁻ ($p=0.004$) but not in NH₄⁺ ($p=0.11$). In forest soils, NO₃⁻ pools were higher among burned plots (0.20 g/m²) compared to control plots (0.09 g/m²). Glade NO₃⁻ pools were also higher among burned plots (0.06 g/m²) relative to control plots (0.03 g/m²). Between-site differences were not found to be statistically significant, and the overall model accounted for 56% (NO₃⁻) and 43% (NH₄⁺) of the variation in inorganic soil N pools. Statistically significant differences in net mineralization and nitrification were observed between vegetation types ($p=0.001$ and

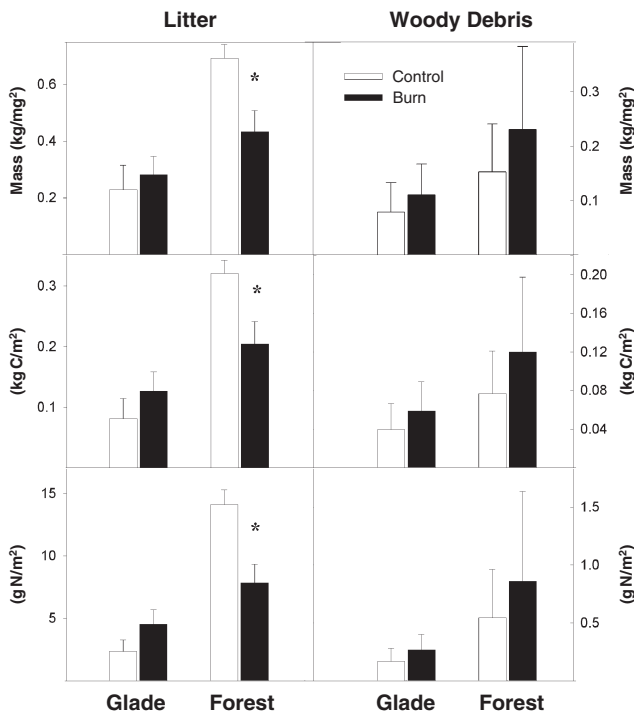


Figure 2. Litter and woody debris dry mass, carbon and nitrogen from control (unburned) and burned plots located in glade and forest habitats (\pm SE). Asterisks denote statistically significant differences between control and burn plots ($p < 0.05$). Note different scales for litter and woody debris.

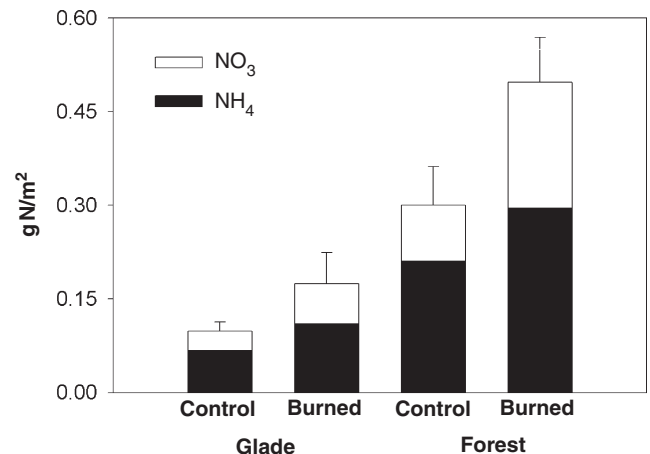


Figure 3. Soil ammonium and nitrate pools from control (unburned) and burned plots located in glade and forest habitats (\pm SE).

0.091, respectively) with higher rates measured in forest plots (Fig. 4). Net mineralization rates in the forest averaged 0.35 g N/m^2 during the 14-day incubation and corresponded to 0.14% of the total N pool ($2,438 \text{ kg N/ha}$, 0–10 cm soil). In the glade, net mineralization rates (0.15 g N/m^2) and the total soil N pool ($1,074 \text{ kg N/ha}$) were correspondingly lower, yielding a comparable estimate of transformation rates (0.14%). No significant differences among sites or between burned and control plots were detected, and the overall model accounted for 39% (net mineralization) and 31% (nitrification) of variation.

Discussion

The prescribed fires conducted in this study resulted in a 37% loss of forest litter mass. Combustion losses were comparable to those reported after prescribed burns in New Jersey pine barrens (30%; Boerner 1983), Kentucky oak-pine forest (32%; Blankenship & Arthur 1999), and Appalachian pine-hardwood forest (34%; Vose et al. 1999). Combustion of forest litter resulted in disproportionately large losses of nitrogen (N) relative to mass (45%). Our estimate of N loss through combustion of forest litter (6.27 g/m^2) was high compared with some other studies (2.53 g/m^2 , Kauffman et al. 1994; 2.44 g/m^2 , Vose et al. 1999) reporting comparable estimates of mass loss. We attribute greater N loss to our higher litter N concentration (1.89%) relative to some previously reported values (0.90–1.17%; Kauffman et al. 1994; Vose et al. 1999). High litter N content is often associated with N_2 -fixing species. The leguminous tree species, *Cercis canadensis* (eastern redbud), accounted for 30% of relative density along the edge of the glade (607 stems/ha ; Rhoades et al. 2004). The abundance of this species could account for elevated N loss through combustion of N-rich litter and suggests that atmospheric sources of N may be important in our system. This species may play a key role in the recovery of soil N capital after fire.

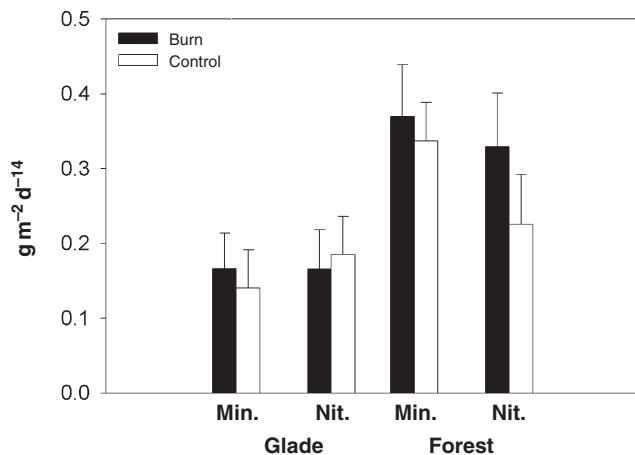


Figure 4. Rates of net mineralization and nitrification in control (unburned) and burned plots located in glade and forest habitats (\pm SE).

We did not observe measurable losses of woody debris. Rain events during the week before the burn (7.0 cm) may have raised the moisture content of woody debris and prevented combustion (Cole et al. 1992). A previous study of spring burns in a central hardwood forest also documented losses from leaf litter but not woody debris at temperatures similar to this burn (Boerner 2000). The lack of burn effects on litter and woody debris in glade plots was likely a result of low fuel loads. The previous year's drought (1999) may have contributed to low standing biomass and sparse grass-clump density resulting in patchy fire coverage.

Prescribed burning significantly increased soil nitrate (NO_3^-) pools in forest plots but had little effect in glade plots. Although studies in other grass-dominated glades have reported higher rates of N mineralization after burns (Rhoades et al. 2002), this was not observed in our study perhaps due to the patchy fire coverage. The prescribed burn did not increase N, phosphorus, or base cation leaching from glade or forest plots. Forest burns associated with land clearing have been shown to increase nutrient leaching losses (Weston & Attiwill 1996), whereas fires occurring within intact forests often do not (Vose et al. 1999). Our prescribed burn was apparently not of sufficient intensity or aerial coverage to bring about detectable increases in nutrient leaching. Maximum temperatures at the soil surface were above 500°C , but the patchiness of the fire resulted in little ash accumulation or loss of living and non-living woody material. The prescribed burn was conducted in late March after a period of wet weather and preceding the start of the growing season. Greater herbaceous plant growth was observed in burned than in control plots (Rhoades et al. 2004), and higher vegetative demand may compensate for modest post-burn increases in soil nutrient availability and prevent leaching losses. We cannot discount the possibility that our limited sampling array (16 lysimeters) may preclude detection of small post-burn changes in leaching, given the spatial variability typically associated with lysimeter data.

We compared the mass of N lost through forest litter combustion with annualized estimates of precipitation inputs and leaching losses to assess fire impacts on N availability. The N lost due to forest litter combustion (6.3 g N/m^2) could be replaced in 4.5 years through atmospheric inputs based on estimates of wet and dry deposition for our region ($1.4 \text{ g N m}^{-2} \text{ year}^{-1}$; EPA 1999). Losses of N were also large in comparison with our estimates of annual N leaching from forest soils ($2.4 \text{ g N m}^{-2} \text{ year}^{-1}$) and suggest that combustion losses were equivalent to 2.6 years of leaching losses. Our annualized estimates were based on collections from eight events that represented 26% of the annual precipitation. We cannot discount the possibility that elevated NO_3^- fluxes observed during the initial one to two collections (October and December 1999) were a result of the relatively recent installation of the lysimeters (August 1999). Exclusion of these data yields a lower estimate of the annual leaching loss ($0.6 \text{ g m}^{-2} \text{ year}^{-1}$)

and a correspondingly higher estimate of the magnitude of combustion losses (10.5 years). Caldwell et al. (2002) also found N losses due to burning greatly exceeded atmospheric deposition and leaching. Our lysimeters were installed at a relatively shallow depth (10 cm) owing to the predominantly rocky substrate in deeper layers. Nitrogen uptake by roots and mycorrhizae in deeper layers (>10 cm) could attenuate leaching losses and further increase the importance of forest litter combustion relative to annual leaching.

Conclusion

Low soil N pools, N production, and N leaching in the glade plots suggest the glade species may be adapted to low-N conditions. The prescribed burn had little effect on soil N pools or fluxes within the glade habitat but resulted in appreciable loss of N capital from the forest-glade margin through litter combustion. Combustion losses may enhance the severity of N limitation in edge habitats along the forest-glade boundary and thereby favor the expansion of glade species into recently burned areas. Additional management practices (stem removal) may be required to achieve canopy reduction because the spring burn resulted in patchy surface fires with little mortality in the surrounding oak-hickory forest. Our analyses suggest that reductions in N capital achieved through prescribed fire will be offset through atmospheric inputs in as little as 5 years, or faster where leguminous tree species (e.g., eastern redbud) are abundant. To maintain or enlarge glades, periodic burns will be required to reverse woody plant encroachment and to favor species with high N-use efficiency characteristic of the N-poor glade soils.

Acknowledgments

This study was sponsored by the Center for Watershed Research and a grant from the Bernheim Arboretum and Research Forest. Thanks to M. Shea, Natural Areas Manager at Bernheim, for encouragement and assistance in the field, and to R. Schultz and M. Hamilton for sample analysis of soil water leachate and base cations.

LITERATURE CITED

- Anderson, R. C., J. S. Fralish, and J. M. Baskin, editors. 1999. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, United Kingdom.
- APHA (American Public Health Association). 1999. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, D.C.
- Binkley, D., and S. C. Hart. 1989. The components of nitrogen availability assessments in forest soils. *Advances in Soil Science* **10**:57–112.
- Blankenship, B. A., and M. A. Arthur. 1999. Soil nutrient and microbial response to prescribed fire in an oak-pine ecosystem in eastern Kentucky. Proceedings, 12th Central Hardwood Forest Conference, 28 February, 1–2 March, Lexington, Kentucky. General Technical Report SRS-24. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina.
- Boerner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. *Bioscience* **32**:187–192.
- Boerner, R. E. J. 1983. Nutrient dynamics of vegetation and detritus following two intensities of fire in the New Jersey pine barrens. *Oecologia* **59**:129–134.
- Boerner, R. E. J. 2000. Effects of fire on the ecology of the forest floor and soil of Central Hardwood Forests. Proceedings, Workshop on Fire, People, and the Central Hardwoods Landscape, 12–14 March, Richmond, Kentucky. General Technical Report NE-274. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania.
- Boerner, R. E. J., T. R. Lord, and J. C. Peterson. 1988. Prescribed burning in the oak-pine forest of the New Jersey pine barrens: effects on growth and nutrient dynamics of two *Quercus* species. *The American Midland Naturalist* **120**:108–119.
- Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* **82**:1024–1030.
- Bundy, L. G., and J. J. Meisinger. 1994. Nitrogen availability indices. Pages 951–984 in R. W. Weaver, J. S. Angle, and P. S. Bottomly, editors. *Methods of soil analysis. Part 2*. Soil Science Society of America, Madison, Wisconsin.
- Caldwell, T. G., D. W. Johnson, W. W. Miller, and R. G. Qualls. 2002. Forest floor carbon and nitrogen losses due to prescription fire. *Soil Science Society of America Journal* **66**:262–267.
- Cole, K. L., K. F. Klick, and N. B. Pavlovic. 1992. Fire temperature monitoring during experimental burns at Indiana Dunes National Lakeshore. *Natural Areas Journal* **12**:177–183.
- Deeming, J. E., R. E. Burgan, and J. D. Cohen. 1978. The national fire danger rating system—1978. General Technical Report INT-39. U.S. Department of Agriculture, Forest Service, Ogden, Utah.
- Delcourt, H. R., and P. A. Delcourt. 1997. Pre-Columbian native American use of fire on southern Appalachian landscapes. *Conservation Biology* **11**:1010–1014.
- Dudley, J. L., and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. *The American Midland Naturalist* **130**:286–298.
- EPA (Environmental Protection Agency). 1999. Clean Air Status and Trends Network (CASTNET). Available from <http://www.epa.gov/castnet/sites.html>.
- Fisher, R. F., and D. Binkley. 2000. Ecology and management of forest soils. 3rd edition. John Wiley & Sons, New York.
- Gill, A. M., and J. E. Williams. 1996. Fire regimes and biodiversity: the effects of fragmentation of southeastern Australian eucalypt forests by urbanization, agriculture and pine plantations. *Forest Ecology and Management* **85**:261–278.
- Homoya, M. A. 1999. Vegetation alliances of Bernheim Forest: map and descriptions. Bernheim Arboretum and Research Forest, Clermont, Kentucky.
- Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1994. Relationships of fire, biomass, and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. *Journal of Ecology* **82**:519–531.
- Mackensen, J., D. Holscher, R. Klinge, and H. Folster. 1996. Nutrient transfer to the atmosphere by burning of debris in eastern Amazonia. *Forest Ecology and Management* **86**:121–128.
- Moore, P. D. 1996. Fire damage soils our forests. *Nature* **384**:312–313.
- Pregitzer, K. S., D. R. Zak, J. Maziasz, J. DeForest, P. S. Curtis, and J. Lussenhop. 2000. Interactive effects of atmospheric CO₂ and soil-N availability on fine roots of *Populus tremuloides*. *Ecological Applications* **10**:18–33.
- Pyne, S. J., P. L. Andrews, and R. D. Laven. 1996. Introduction to wildland fire. 2nd edition. John Wiley & Sons, New York.
- Rhoades, C., T. Barnes, and B. Washburn. 2002. Prescribed fire and herbicide effects on soil processes during barrens restoration. *Restoration Ecology* **10**:656–664.

- Rhoades, C. C., S. P. Miller, and M. M. Shea. 2004. Soil properties and soil nitrogen dynamics of prairie-like forest openings and surrounding forests in Kentucky's Knobs Region. *American Midland Naturalist* **152**:1–11.
- Rhoades, C., and M. Shea. 2003. Forest type influences response of vegetation and soil chemistry to edge clearing in dry glades (Kentucky). *Ecological Restoration* **21**:42–43.
- Soil Conservation Service. 1986. Soil survey of Bullitt and Spencer Counties, Kentucky. U.S. Government Printing Office, Washington, D.C.
- Thomas, A. D., R. P. D. Walsh, and R. A. Shakesby. 2000. Solutes in overland flow following fire in eucalyptus and pine forests, northern Portugal. *Hydrological Processes* **14**:971–985.
- Vose, J. M., W. T. Swank, B. D. Clinton, J. D. Knoepp, and L. W. Swift. 1999. Using stand replacement fires to restore southern Appalachian pine-hardwood ecosystems: effects on mass, carbon, and nutrient pools. *Forest Ecology and Management* **114**:215–226.
- Weston, C. J., and P. M. Attiwill. 1996. Clearfelling and burning effects on nitrogen mineralization and leaching in soils of old-age *Eucalyptus regnans* forests. *Forest Ecology and Management* **89**:13–24.