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Canopy interception of nitrogen in bulk precipitation by annually burned and unburned tallgrass prairie

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Summary. Nitrogen content of bulk precipitation and throughfall (canopy leachates) was measured on annually burned and unburned tallgrass prairie during a 20 month period. Throughfall amounts averaged 58% of precipitation on unburned prairie while throughfall on annually burned sites averaged 76% of precipitation inputs. Stemflow was measured in late summer and autumn. Volumes were correlated with stem density; maximum stemflow volumes measured in this study averaged about 50% of throughfall volumes.

Bulk precipitation averaged 530, 456, and 420 μg/l of nitrate, ammonium and organic nitrogen, respectively. Throughfall on burned sites averaged 345, 344 and 980 μg/l of nitrate, ammonium and organic nitrogen, and throughfall on unburned sites averaged 258, 196 and 1701 μg/l of nitrate, ammonium and organic nitrogen. Microbes on standing dead vegetation and litter of the unburned sites were estimated to remove more inorganic nitrogen from bulk precipitation than did foliage on burned sites. Only a portion of the inorganic nitrogen in bulk precipitation is immediately available for plant use, and this availability is influenced by the amount of detritus present on the prairie.

The importance of energy, nitrogen and water to the productivity of grasslands has been emphasized by many investigators (McNaughton et al. 1983, Knapp 1984 and references therein). Any of these variables, alone or in combination with the others, may limit plant productivity during a particular portion of the growing season. However, the amount and structure of the vegetation can also influence the availability of energy, water or nitrogen (Conant and Risser 1974; Knapp 1984). Tallgrass prairie that is unburned and ungrazed for several years develops a large amount of standing dead vegetation and litter (Weaver and Rowland 1952). The presence of this detritus in a vegetative canopy usually reduces net primary productivity of tallgrass prairie (Hadley and Kieckhafter 1963; Kucera et al. 1967; Hulbert 1969; Old 1969). Standing dead and litter can reduce the amount of photosynthetically active radiation reaching young grass shoots by over 50% during the first 30 days of the growing season (Knapp 1984).

Another feature of the tallgrass prairie that may indirectly contribute to the decreased productivity of unburned areas is the relatively low nitrogen content of senescent and dead grasses. Grasses retranslocate, volatilize and/or leach large quantities of nitrogen in autumn (Risser and Parton 1982). Nitrogen concentrations in recently dead foliage drop to below 0.5% nitrogen and to below 0.2% nitrogen for flowering stem tissues (Koelling and Kucera 1965). Such substrates will exhibit slow decomposition, and microbes on these substrates will immobilize nitrogen during initial stages of decay. Koelling and Kucera (1965) presented data showing that decaying foliage and stem tissues exhibited absolute increases in nitrogen amounts during much of the first two years of decomposition.

The present study measured nitrogen concentrations and amounts in bulk precipitation and throughfall of annually burned and unburned tallgrass prairie. The objective of the study was to test the hypothesis that standing dead vegetation and litter function as a nitrogen filter, i.e., microbes on detritus scavage a significant portion of the nitrogen in bulk precipitation. The average nitrogen content of bulk precipitation to tallgrass prairies has been assumed to be about 1 $g/m^2/y$, or about 25% to 50% of the maximum amount of nitrogen observed in tallgrass prairie foliage (Risser et al. 1981). Hence, immobilization of this input by microbes on detritus could significantly influence nitrogen dynamics on unburned sites.

Study site and methods

Research was conducted at the Konza Prairie Research Natural Area, a 3,487 ha site located 10–20 km south of Manhattan Kansas. Vegetation of this area is typical of tallgrass prairie and is dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), Indiangrass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*) as described by Bragg and Hulbert (1976). Rainfall for this area averages 83 cm/y, of which 75% occurs during the 6 month growing season, April through September.

Throughfall collectors were constructed using 5 cm × 100 cm stainless steel v-notch troughs connected by a short length of plastic tubing to 4 l collecting jugs. A second set of troughs was constructed using 5.6 cm × 100 cm of split PVC pipe. Two sites that had not been burned or grazed for at least 5 years and two sites that had been burned annually for the last 4–5 years were selected as study sites. Eight troughs (4 stainless steel, 4 PVC pipe) were placed on each site in April 1982. One end of the troughs was elevated approximately 5 cm above the soil surface to provide sufficient slope for gravity collection of leachates. No visable disturbance of the canopy was evident from the installation or maintenance of the troughs (see photos in

Clarke 1940). Nylon cloth was attached to the ends of the tubing so that the leachates were filtered prior to entering collecting jugs. This cloth had approximately 0.05 mm^2 openings, and particulates smaller than this size did not significantly increase or decrease nitrogen concentrations of the leachates (paired t-test on 16 samples analysed for NO_3, NH_4 and total Kjeldahl nitrogen both before and after filtration through a 0.45 micron fiberglass filter, $P >$ 0.10 for all tests).

A rain guage and a bulk precipitation collector were installed at each of the four sites. Whenever possible, collections of bulk precipitation and throughfall were made following each rainfall event. Volumes were measured, and subsamples from each collector were refrigerated for nitrogen analyses. A major problem confronting this study was periodic contamination or destruction of the throughfall troughs. Problems included: 1) frequent contamination by dirt and feces of arthropods, earthworms, small mammals and birds, 2) plugging of the tubing of troughs by litter debris, and 3) physical damage to collectors by small mammals. Approximately 15% of all samples were affected. Collectors were cleaned of debris and repaired at two-week intervals; however, the probability that any single collector could produce uncontaminated samples for an extended period was not high. Thus, the usual procedure of compositing samples for a single monthly analysis was of dubious value, and nutrient analyses were therefore conducted on samples following each precipitation event. Any sample visably contaminated was not analyzed for nitrogen. Samples producing nitrogen values more than three standard deviations away from the mean (calculated without that sample) were assumed to be contaminated and discarded. Nitrogen amounts for each precipitation event were calculated by multiplying nitrogen concentrations times volume per unit area Monthly inputs were calculated from the sums of these values.

Microbial activity in the collecting jugs was inhibited in 1982 by adding 1 ml of 2 N sulfuric acid to the containers prior to placing these in the field. This procedure necessitated additional titrations in the laboratory; therefore, samples obtained in 1983 were preserved with 1 ml of 1 mg/g phenylmercuric acetate. Clean, acid-washed collecting jugs and bulk precipitation collectors were placed in the field following each collection.

The annually burned sites were burned in mid April of each year. Throughfall equipment was removed prior to burning and not replaced until a sufficient grass canopy justified its presence. During this period (4–6 weeks) canopy interception was assumed to be zero and the chemistry of throughfall was assumed to equal that of bulk precipitation.

Preliminary analysis of results obtained in summer and autumn of 1982 suggested that duplication of sites was unnecessary. In November 1982 the number of sites was reduced from four to two, representing one unburned and one burned site. Unfortunately, woodrats (*Neotoma floridana*) repeatedly destroyed the collectors on the remaining unburned site, and no throughfall data were collected on the unburned site for Nov. and Dec. of 1982. In January 1983 and thereafter, collections consisted of samples from 6 stainless steel troughs on each annually burned and unburned site.

Samples were analysed for ammonium within 1–3 days after the actual precipitation event using the phenolhypochlorite procedure. Nitrate (and whatever traces of nitrite were present) were measured with the cadium reduction – sulfanilamide procedure, and organic nitrogen was measured with a micro-Kjeldahl procedure (Strickland and Parsons 1972). Organic nitrogen was assumed to equal the Kjeldahl nitrogen value minus the ammonium value for that sample. Contamination problems with the micro-Kjeldahl procedure resulted in the loss of several months' data on organic nitrogen concentrations. In mid-1983 the Kjeldahl procedure was replaced with the total persulfate nitrogen procedure (D'Elia et al. 1977, as modified by R.T. Edwards, University of Georgia, pers. comm.). The persulfate procedure was more precise than the Kjeldahl procedure, and a paired t-test indicated no significant differences in the results of the two methods. The persulfate method measured total nitrogen, and organic nitrogen content of the sample was assumed to equal total nitrogen minus nitrate and ammonia concentrations.

The amount of water moving directly down the tillers or stems of the grasses (i.e. stemflow) of the prairie was unknown. Clarke (1940) reported that stemflow in an eastern Nebraska tallgrass prairie was insignificant compared to throughfall amounts. Corbett and Crouse (1968), however, cited studies and presented data suggesting that stemflow was very significant in other grasslands. The importance of stemflow to the hydrologic budget of the Konza Prairie in 1982 was measured by placing 6–9 tillers of big bluestem in 3 troughs at each site. Volumes of rainfall collected in the throughfall plus stemflow collectors versus those receiving only throughfall were compared. In 1983 two replicates of 2, 4, 8 or 16 stems were placed in throughfall troughs at an annually burned site, and volumes of 9 rain events were recorded. As these stems were cut and held in troughs with modeling clay, no nitrogen analyses were made on those samples. Canopy structure appeared unaltered by the addition of these stems (e.g., see photos in Clarke 1940).

Estimates of plant biomass and necromass located above the troughs on burned and unburned sites were obtained twice in 1982. Samples were obtained by placing 0.1 m^2 quadrats (0.5×0.2 m) approximately 1 m away from each throughfall trough. Two additional samples were obtained by sampling 1 m from the sides of the first and last troughs. Samples were clipped at 5 cm above the soil, sorted into living vegetation (produced during the year of study) or dead vegetation (produced in previous years), dried at 60° C and weighed.

Results

Rainfall, throughfall and stemflow amounts

Precipitation during the study period averaged 7.6 cm/mo, somewhat higher than the long-term average of 6.9 cm/mo for this area. Throughfall amounts from unburned sites averaged 4.4 cm/mo, or 58% of the precipitation input during this interval (Fig. 1). Throughfall amounts on annually burned sites averaged 5.7 cm/mo, or 76% of inputs. Removal of the canopy by burning obviously reduced canopy interception of precipitation to zero. However, the grasses on the burned sites quickly formed a new canopy (Table 1), and throughfall amounts between burned and unburned treatments were similar in August through late autumn of both years. Regardless of treatment, canopy interception was maximized in autumn, when the mass and surface area

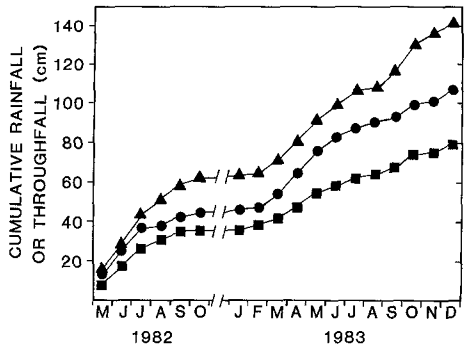

Fig. 1. Cumulative rainfall (▲) and throughfall on unburned (■) and burned (●) sites

Table 1. Estimates of living and dead vegetation on annually burned and unburned tallgrass prairie. Samples were clipped 5 cm above the soil surface

Material	g/m² (std. dev.)			
	29 July 1982		15 Sept. 1982	
	Unburned ($n=20$)	Burned ($n=20$)	Unburned ($n=10$)	Burned ($n=10$)
Living Vegetation	239 (113)	444 (59)	364 (114)	481 (87)
Dead Vegetation[a]	457 (113)	0	525 (177)	0
Total	696 (195)	444 (59)	889 (222)	481 (87)

[a] Vegetation produced in previous growing seasons

of living and dead vegetation were also maximized (Table 1 and Conant and Risser 1974). The similarity in throughfall volumes between treatments is somewhat surprising given the large differences in living and dead mass on the unburned and burned sites. Canopy interception was minimized in winter when some or all of the monthly precipitation occurred as snow.

Stemflow appeared to be an important component of the hydrologic budget of the tallgrass prairie. Throughfall in late summer and early autumn of 1982 averaged 49% of rainfall in troughs not containing stems, while troughs with stems averaged 75% of rainfall amounts (n = 75 and 38, respectively, $P<0.001$). No statistically significant differences in volumes were found between treatments; hence the amount of water moving down equal numbers of stems was similar between sites. Results from the 1983 experiments were similar and showed increased volumes of leachates with increased stem densities in collectors. Throughfall averaged about 49% of rainfall in troughs without stems, and 49%, 54%, 59% and 71% of rainfall for 2, 4, 8 and 16 stems per trough, respectively.

Nitrogen content of bulk precipitation and throughfall

Nitrate and ammonium amounts of throughfall on unburned sites were consistently below that of bulk precipitation, while organic N amounts were consistently higher than those of bulk precipitation (Fig. 2). Annually burned prairie exhibited characteristics intermediate between unburned prairie and bulk precipitation. Immediately following burning, the vegetation had little ability to modify either the amounts of water or chemical content of the bulk precipitation. By August, however, the canopy of the burned site exhibited characteristics of unburned prairie. Burned sites were seldom observed to reduce the concentrations of inorganic nitrogen to levels observed on unburned sites during

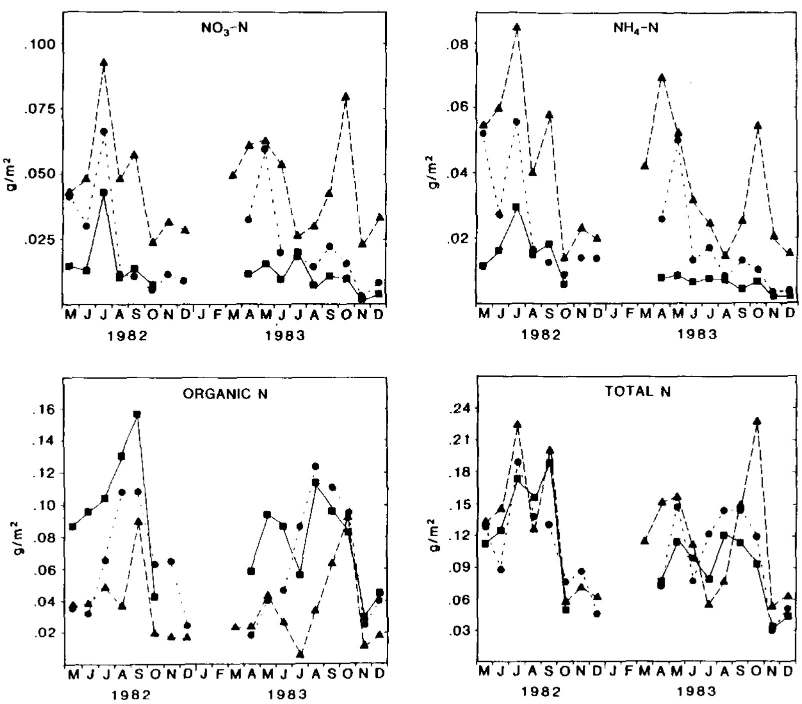

Fig. 2. Nitrate, ammonium, organic nitrogen and total nitrogen amounts for bulk precipitation (▲) and throughfall from unburned (■) and burned (●) sites

Table 2. Nitrogen concentrations and amounts in bulk precipitation and throughfall[a]

Variable	Bulk Precipitation	Throughfall	
		Unburned	Burned
NO_3–N (μg/l)	530	258	345
NO_3–N (g/m^2/mo)	0.058	0.013	0.022
NH_4–N (μg/l)	456	196	344
NH_4–N (g/m^2/mo)	0.042	0.010	0.020
Organic N (μg/l)	420	1,701	980
Organic N (g/m^2/mo)	0.039	0.085	0.063
Total N (μg/l)	1,406	2,155	1,669
Total N (g/m^2/mo)	0.138	0.108	0.105

[a] 15 month volume-weighted average

spring or summer, nor did burned sites leach as much organic nitrogen. While a continuous 12 month record of inorganic and organic nitrogen in bulk precipitation and throughfall was not obtained in this study, an average monthly estimate was constructed from the available data based on 15 months of records (Table 2). From these monthly averages, the yearly input of nitrogen in bulk precipitation would be 0.70, 0.50, and 0.46 g/m^2 of nitrate, ammonium and organic nitrogen, respectively, or 1.66 g/m^2/y of nitrogen. All values were somewhat high due to the relatively wet conditions, and the value for organic nitrogen may have resulted from redeposition of materials produced locally. Throughfall on the unburned watersheds would contain 0.15, 0.12 and 1.02 g/m^2/y of nitrate, ammonium and organic nitrogen, respectively, for a total of 1.29 g/m^2/y. Throughfall on annually burned sites would contain 0.26, 0.24 and 0.76 g/m^2/y of nitrate, ammonium and organic nitrogen, respectively, for a total of 1.26 g/m^2/y of nitrogen.

Discussion

Standing dead vegetation and litter have a significant effect on the hydrologic and inorganic nitrogen budgets of the tallgrass prairie. Results of Clarke (1940) and those presented here (Fig. 1) indicate that throughfall amounts, as expressed as a percentage of rainfall, are lower than values reported for most forests (e.g. Parker 1983). Unlike Clarke's (1940) results, however, this study found that stemflow during late summer and early autumn accounted for a large percentage of water reaching the soil surface. Thus, the percentage of rainfall as throughfall and stemflow in tallgrass prairie is believed to be more comparable to values for forests than those reported by Clarke (1940). Moreover, stem densities used in this study may have been insufficient to reflect the true importance of stemflow in prairies. Hulbert (1969) reported densities of 911 and 342 stems/m^2 in burned and unburned plots, respectively, sampled in midsummer. Those densities would be equivalent to about 46 and 15 stems in the throughfall troughs used in this study. Results presented here cannot be extrapolated to estimate stemflow from burned sites, but those findings certainly suggest higher stemflow values for areas with higher stem densities as usually occur in burned areas. This interpretation would explain why burned areas, with less vegetative mass than unburned areas (Table 2), would have throughfall volumes similar to those of unburned sites in autumn (Fig. 1).

The vegetation of both the burned and unburned sites appeared to act as a sink for nitrogen in bulk precipitation (Fig. 2 and Table 2). More inorganic nitrogen was absorbed by foliage or microbes than was leached in either organic or inorganic form from living and dead tissues. Accurate measurements of nitrogen gains and losses from the vegetation could not be calculated without information on stemflow volumes. Nonetheless, the general patterns of inorganic nitrogen uptake and organic nitrogen leaching from the burned and unburned prairie are evident (e.g. Table 2). Inorganic nitrogen concentrations were reduced 54% by passing through the vegetation of unburned prairie, while inorganic nitrogen concentrations were reduced by only 30% on burned areas. Assuming 1) that the volume of leachates are somewhat less on unburned areas, (Fig. 1) and 2) that the litter horizons below the throughfall collectors (0–5 cm above the soil) also remove inorganic nitrogen, then the conclusion that unburned vegetation removes about twice as much inorganic nitrogen as does burned prairie is justified. If stemflow volumes are in function of tiller density, and tillers are more numerous on burned areas (Hulbert 1969), then this difference in inorganic nitrogen inputs to burned and unburned prairie is enhanced. The conversion of inorganic nitrogen in bulk precipitation to an organic form by microbes on unburned watersheds may represent a delay in nitrogen cycling, with mineralization proceeding at some subsequent time, or this nitrogen may accumulate as soil organic nitrogen (Woodmansee 1978) or may be lost from the system because of increased groundwater export of nitrogen from unburned prairie (Seastedt, unpublished).

To summarize, standing dead and litter of tallgrass prairie reduce the amount of water reaching the soil surface and alter the relative amounts of inorganic and organic nitrogen in these leachates. Combined with the changes in the energy environment of the prairie (e.g. Knapp 1984), the potential impacts of detritus in tallgrass prairie on net primary productivity are considerable. Detritus functions as an energy, water and inorganic nitrogen filter, and, in most years, this filter has a negative effect on the productivity of the prairie.

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