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Simulated effects of precipitation and nitrogen on Serengeti grassland productivity

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Abstract. In the Serengeti National Park, Tanzania, precipitation and soil nitrogen vary greatly between northwestern tallgrass areas and southeastern shortgrass areas, with the tallgrass having higher total precipitation and lower soil fertility. We used a model of grassland productivity, carbon/nitrogen cycling, and abiotic factors to test the hypothesis that tallgrass productivity is limited primarily by nitrogen availability while shortgrass productivity is limited by water. Under observed grazing intensities and ungrazed conditions, precipitation exerted primary control over grassland productivity for both regions, with differences in soil texture mediating soil water availability to the grasses. Mineral nitrogen availability interacted with water availability to influence productivity at precipitation levels ⩾ 130% of the mean. Nitrogen mineralization and precipitation were positively related for each grassland type, however, nitrification varied both between grassland types and between grazed and ungrazed conditions. Combined mineralization and nitrification could not maintain soil mineral nitrogen levels in the face of plant nitrogen uptake stimulated by increased precipitation, thus providing the mechanism by which nitrogen becomes a secondary limiting factor for both grasslands. Model experiments indicated that the pattern of primary limitation by precipitation and secondary limitation by nitrogen was robust to model assumptions concerning ungulate deposition of urine and dung nitrogen to the soil.

Introduction

Separate studies have indicated that African savanna productivity is limited by precipitation (Coe et al. 1976; Deshmukh 1984; McNaughton 1985) and, independently, by nitrogen (Keya 1973; Penning de Vries et al. 1980). The dichotomy of these studies is heightened by the fact that infertile African savanna soils generally occur in high rainfall areas, while eutrophic soils are found in more arid areas (Bell 1982; Cole 1986). Although this spatial correlation in soil fertility and precipitation may explain how independent studies find each of these factors important in controlling savanna grassland productivity, the simple dichotomy is complicated by several other factors. First, correlated with differences in soil fertility are differences in soil structure. Soil texture strongly affects runoff, percolation of soil water derived from precipitation, and soil moisture available to growing grasses (Noy-Meir 1973; McCown et al. 1974; Dye & Spear 1982). Secondly, soil mineralization processes are dependent on physical factors such as soil temperature and moisture (Haynes 1986; Paul & Clark 1989). In particular, African savannas are subject to convective rainstorms leading to alternate wetting and drying of soils which results in pulses of mineralization (Birch & Friend 1956; Birch 1958, 1960). Such pulses are further complicated by large variations in soil microbial biomass which are often correlated with soil texture (Ruess & McNaughton 1987; Ruess & Seagle, in press). Finally, most African grasslands evolved under grazing by native ungulates. Grazing is known to influence productivity of grasses (McNaughton 1985), plant water balance (Coughenour et al. 1985; Toft et al. 1987), nutrient uptake (Ruess et al. 1983; Ruess 1984; Ruess & McNaughton 1984), nutrient availability (Ruess & McNaughton 1987; Holland et al. 1992), and loss of volatile nutrients from ecosystems (Ruess & McNaughton 1988). Thus, within a whole-system context that includes abiotic driving variables, edaphic conditions, and biotic factors, it is difficult to predict the relative importance of simple rainfall amount and gross soil fertility in driving savanna grassland productivity.

The Serengeti region of Tanzania, East Africa, has been recognized for the migratory movements of large ungulate herds (Pennycuick 1975; Maddock 1979). As with most migratory animals, these herds have evolved to capitalize on spatial variation in limiting or potentially limiting resources (McNaughton 1990). Community (McNaughton 1983), ecosystem (Coughenour 1984a, b; Ruess 1984; McNaughton 1985; Ruess & McNaughton 1987), and landscape (Seagle & McNaughton 1992) studies of the Serengeti have all identified great diversity in biotic composition and in ecological processes that are strongly influenced by broad southeast to northwest gradients of precipitation, soil fertility, and grazing intensity by the migratory animals.

The northwest extreme of the Serengeti is characterized by tallgrass communities on sandy soils with a mean annual rainfall often > 120 cm; in the southeast, shortgrass communities occur on soils with a much higher clay content and a mean annual precipitation of 40—60 cm (McNaughton 1985). General soil fertility is lower in the tall grasslands of the northwest (Ruess & McNaughton 1987, McNaughton 1990), as are forage nutrient concentrations (McNaughton 1990). Migratory herds, composed primarily of wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and Thomson's gazelle (*Gazella thomsonii*), graze intensively on the southeastern plains during the wet season, and most of the wildebeest and zebra migrate to the tallgrass where they remain through the dry season (Maddock 1979).

Principal questions that we address here are: What are the roles of precipitation and soil nitrogen fertility in governing savanna ecosystem productivity and nutrient cycling? How do precipitation or nitrogen interact with biotic regulators such as grazing, and abiotic factors such as edaphic characteristics?

Methods

Model structure and simulated processes

We used a simulation modeling approach to examine the interactions of grass production, grazing and nitrogen cycling processes with the abiotic parameters of precipitation, soil structure and soil fertility. Model algorithms for grass production and morphology, carbon allocation, light interception, nutrient use, and grazing are described in Coughenour (1984) and Coughenour et al. (1984a, b). The submodel for decomposition of dung and litter, belowground nitrogen and carbon flows, and microbial population dynamics is described in Seagle et al. (1992). Here we focus on the salient points of the model, and emphasize model improvements and processes of special interest to this study.

The model algorithms for photosynthesis, carbon allocation, and nitrogen uptake functioned on a 2-day timestep over the growing (wet) season, with these growing seasons being 232 days and 328 days for the shortgrass and tallgrass regions, respectively. Photosynthesis was governed by leaf area and leaf nitrogen concentration (Coughenour et al. 1984a), and the resulting photosynthate was allocated among shoot growth, root growth, crown growth and respiration from a pool of mobilizable plant carbon. Aboveground shoot morphology and number was a function of existing shoot number, crown biomass and mobilizable stored carbon. Root biomass was stratified by soil layer, with newly produced root biomass allocated to layers based on measured vertical root biomass distributions.

Grazing was simulated by removal of aboveground biomass to a user-specified height and defoliation frequency (Coughenour et al. 1984b). Carbon and nitrogen removed from the simulated sward by grazing may be (1) removed from the system without replenishment, (2) returned to the soil in either depleted (grazer retention) or enhanced (grazer concentration) amounts as urine and dung, or (3) returned to the soil as urine or dung in equivalent amounts with each defoliation (Seagle et al. 1992). Seagle et al. (1992) simulated these replacement strategies and found major impacts on nitrogen cycling processes and sward productivity. In the field all three strategies can occur and create patchy soil-plant processes.

Hydrological, temperature/heat and radiant energy balance submodels (Coughenour 1984) interfaced with the plant productivity and decomposition submodels, allowing interaction of biotic processes with abiotic driving variables. Baseline precipitation was based on 20-yr growing season means for two specific, well-studied sites in the shortgrass and tallgrass regions of the Serengeti (McNaughton 1985). These means were 61.2 cm and 79.8 cm, respectively. Interception of precipitation by the plant canopy was simulated using the methods of Corbet & Crouse (1968) and Parton (1978). Precipitation reaching the soil surface successively filled each soil layer to field capacity with excess water passing to deeper soil layers (Coughenour 1984). Water flow between soil layers was modeled as a function of hydraulic conductivities, which were dependent on soil water potentials and soil texture (Gardner 1960; Coughenour 1984). Heat flow among soil layers was proportional to thermal conductivity, distance between layers, and the existing temperature gradient (Coughenour 1984). Thermal conductivity of any soil layer was related to its water content (Munn 1966). Soil temperatures were determined by layer from heat contents that were updated by heat fluxes.

Although the biotic aspects of the model functioned on a 2-day timestep, soil water and temperature were calculated hourly. The plant canopy energy budget was a function of total radiation flux to leaves (global, longwave sky, and longwave radiation emitted by soil surface and other plant tissues) and heat loss by leaves using individual leaf and atmospheric boundary layer resistances, stomatal resistance (as a function of light, plant water potential, leaf age, leaf temperature, and leaf nitrogen content), and transpiration (Coughenour 1984). Soil surface energy balance and evaporation were based on absorbed radiation minus reflected radiation, using soil surface temperature, subsoil temperature, soil surface boundary layer resistance, soil thermal conductivity, diffusion resistance to evaporation, and distance between soil surface and subsurface layers (Coughenour 1984).

Decomposition algorithms were derived from McGill et al. (1981). All belowground state variables (such as root and microbial biomass), plant and microbial uptake/decomposition processes and nitrogen transformations were stratified by soil layer, with soil moisture and temperature exerting influence on each. Substrates entering the decomposition submodel (Seagle et al. 1992) included litter, dung, and urine. Field observations indicated little litter buildup in any region of the Serengeti, especially under grazed conditions. However, in the model the small amount of litter accumulating from leaf fall was collected into a soil-surface litter compartment and subjected to leaching as a function of precipitation. Assimilation of this litter into the upper soil layer was modeled as an exponential decay function. Due to dung beetles, dung was incorporated directly into the top two soil layers where it decomposed. Urine nitrogen was subjected to volatilization loses and entered the soil nitrogen pool as ammonium, with 25% remaining in the top soil layer and the remainder entering the second soil layer. Both litter and dung were divided into a readily decomposable fraction and a more recalcitrant structural fraction (McGill et al. 1981). Dead microbial and root biomass were similarly divided and remained stratified by soil layer while decomposing. Although two classes of soil organic matter, passive and active, were included in the model, the lengths of their turnover times (approximately 500 and 25 yr, respectively) sharply limited their importance to soil properties in a single growing season. Microbial biomass estimates for shortgrass and tallgrass sites were derived from Ruess & McNaughton (1987) and Ruess & Seagle (in press), respectively, with microbial death and respiration adjusted to maintain microbial biomass within +/− 10% of these estimates (Seagle et al. 1992). Microbial decomposition of the labile metabolic substrate was modeled as a Michaelis-Menton expression; decomposition of structural substrates depended on microbial C/N ratio and microbial density (McGill et al. 1981). Microbial ammonification and uptake also depended on microbial C/N, total microbial N, and soil temperature and moisture. Uptake of both nitrate and ammonium was modeled as a Michaelis-Menton function (Seagle et al. 1992) with maximum uptake rates and half-saturation constants from McGill et al. (1981). If soil nitrogen was limiting, plants and microbes competed for mineral nitrogen by allocation of available nitrogen based on relative magnitudes of calculated uptake demands (Seagle et al. 1992).

Modifications of model structure

In savanna ecosystems the timing of rainfall is an important determinant of ecosystem productivity. Thus, to standardize model runs and examine the effects of rainfall amount and its potential interaction with other abiotic factors, the same monthly pattern of precipitation was used for each simulation. In order to manipulate precipitation effects in the model, growing season rainfall was controlled by increasing or decreasing each rainfall event by a user-specified proportion while retaining monthly and daily patterns. Thus

$$\mathrm{RAIN} = \mathrm{RAINB} \times \mathrm{PROP} \tag{1}$$

where RAIN was simulated daily rainfall, RAINB was baseline daily rainfall calculated from 20-yr monthly means and distributed over the days of each month, and PROP was the multiplier by which rainfall was manipulated in a given simulation.

Mineral nitrogen in the plant-soil system was manipulated to simulate changes in soil fertility. Baseline values for ammonium and nitrate-nitrogen were for specific Serengeti locations corresponding to the rainfall data. Because of the pulsing effect that would be elicited by injecting nitrogen into the system periodically throughout the simulation (Seagle et al. 1992), we multiplied the baseline ammonium and nitrate concentrations by a factor to systematically increase or decrease the amount of mineral nitrogen as each simulation began. This procedure resulted in no increased loss of nitrate nitrogen from the system by leaching, and also produced no major standing pools of either ammonium or nitrate nitrogen because of rapid assimilation by the plants and microbes. In this study, we assumed that grazer activities resulted in a balance of carbon and nitrogen input and removal from a simulated sward; 85% of excreted nitrogen was assumed to be urinary nitrogen (Ruess & McNaughton 1987) with the remainder found in dung.

Microbial biomass was simulated as

$$\mathrm{MB} = \mathrm{DCMP} - \mathrm{MICD} - \mathrm{MRSP} \tag{2}$$

with

$$\mathrm{MICD} = \mathrm{T_S} \times \mathrm{W_S} \times \mathrm{MD_{MAX}} \times [\mathrm{MB} \times (1.0 - (\mathrm{MB_{MIN}}/\mathrm{MB}))] \times \mathrm{DT} \tag{3}$$

and

$$\mathrm{MRSP} = [((1.0 - \mathrm{YLD_{MAX}}) \times \mathrm{DCMP}) + (\mathrm{T_S} \times \mathrm{MB_{MTN}} \times \mathrm{MB})] \times \mathrm{DT} \tag{4}$$

In equation 2, MB was microbial biomass (g C), DCMP was carbon (g $\mathrm{DT^{-1}}$) gained by the MB per model time step (DT) by decomposition of metabolic and structural substrates, and MRSP was microbial respiration (g C $\mathrm{DT^{-1}}$) which represented assimilation plus maintenance costs. $\mathrm{T_S}$ and $\mathrm{W_S}$ were the effects of soil temperature and soil moisture on microbial activity (McGill et al. 1981), respectively. In addition, $\mathrm{MD_{MAX}}$ was the maximum microbial death rate, MB_{MIN} was the minimal microbial biomass (g C), YLD_{MAX} (in %) was the maximum yield of carbon to microbes from decomposing substrates, and MB_{MTN} was the microbial maintenance cost expressed as a proportion of MB.

Initial tallgrass microbial biomass reflected more recently measured values (Ruess & Seagle, in press) than for previous simulations (Seagle et al. 1992). The magnitude for most of the rate parameters and constants were derived from McGill et al. (1981). However, respiration/maintenance costs and microbial biomass yields were adjusted to maintain microbial biomass levels within 5% of initial values rather than the 10% used previously; this narrow range for microbial biomass reflected our increased confidence in microbial levels over that used previously. These model adjustments resulted in more stable microbial populations, particularly in the tallgrass region, and some process rate and state variable differences from those published previously (Seagle et al. 1992).

Experimental simulations

Our primary goal was to examine the effects of varying precipitation and soil mineral nitrogen availabilities on grassland productivity and system water and nitrogen dynamics. Our preliminary simulations were aimed at establishing a range over which each factor could be varied independently and elicit a system response. This was accomplished by varying precipitation and initial soil mineral nitrogen (both ammonium and nitrate) independently both above and below measured values for both shortgrass and tallgrass systems. Decreasing either factor generally led to a monotonic decrease in productivity; thus, we used a lower limit of 10—20% of field levels for each. Increasing either factor independently resulted in primary production increasing to a plateau. The percentage of that factor at which a plateauing effect was observed varied considerably between precipitation and mineral nitrogen, as well as between regions. Thus to standardize contour plots of precipitation-nitrogen interactions while encompassing the full range of grassland responses, upper limits of 360% for precipitation and 250% for mineral nitrogen were chosen for use with both tallgrass and shortgrass simulations. In examining system response to precipitation alone, the full range of production response to precipitation (shortgrass: 500%; tallgrass: 450%) was used.

Our first analysis examined the interaction of precipitation and mineral nitrogen. These factors were co-varied over the above mentioned ranges, and aboveground productivity (g C growing season^{-1}) and total productivity (above- plus belowground, g C growing season^{-1}) were used as response variables. Contour plots of the response variables were developed using a kriging technique (Anonymous 1990). A replicate set of simulations and analyses was performed in which all grazed nitrogen was removed from the plot without replacement. This second set of simulations represented the worst case field scenario for nitrogen loss from the model systems.

The apparent importance of precipitation to system productivity led us to focus on the fate of precipitation and the impact of precipitation on nitrogen-cycling processes. Composite plots of the fate of precipitation reaching the soil surface were created for both shortgrass and tallgrass under grazed and ungrazed conditions. For this purpose, precipitation was partitioned into four broad categories: (1) uptake by grasses for storage or transpiration, (2) evaporation, (3) runoff from the simulated plot surface, and (4) deep soil drainage out of the grass rooting zone. These simulations were carried out over the entire response range for precipitation. In addition, net microbial nitrogen mineralization, nitrification, nitrate levels, and ammonium levels were plotted in response to precipitation for grazed and ungrazed tallgrass and shortgrass. A balance of nitrogen removal and return by grazers was assumed for these simulations.

Results

Precipitation — nitrogen interactions

Under grazed conditions and the range of precipitation-nitrogen interactions simulated, total productivity (above- plus belowground) of shortgrass (Fig. 1a) ranged from 100 g C m^{-2} to 1000 g C m^{-2} over the 232-d growing season. Lack of interaction between precipitation and nitrogen and a steep productivity gradient indicated that precipitation exerted a strong control over shortgrass productivity up to approximately 130% of the mean precipitation levels, regardless of initial mineral nitrogen levels. Once total productivity was stimulated above 500 g C m^{-2} by increasing precipitation, productivity co-varied with precipitation and mineral nitrogen levels, as indicated by the diagonal orientation of the productivity contours in Fig. 1a. Aboveground productivity (Fig. 1b) showed a similar response to total productivity, ranging from 50 g C m^{-2} to 750 g C m^{-2}. Precipitation was thus the primary limiting factor for shortgrass total productivity under naturally occurring grazing regimes and over a broad range of precipitation levels. Allocation of photosynthate to above- and belowground growth was also affected by the interaction of precipitation and nitrogen, with aboveground productivity ranging from 50% of total

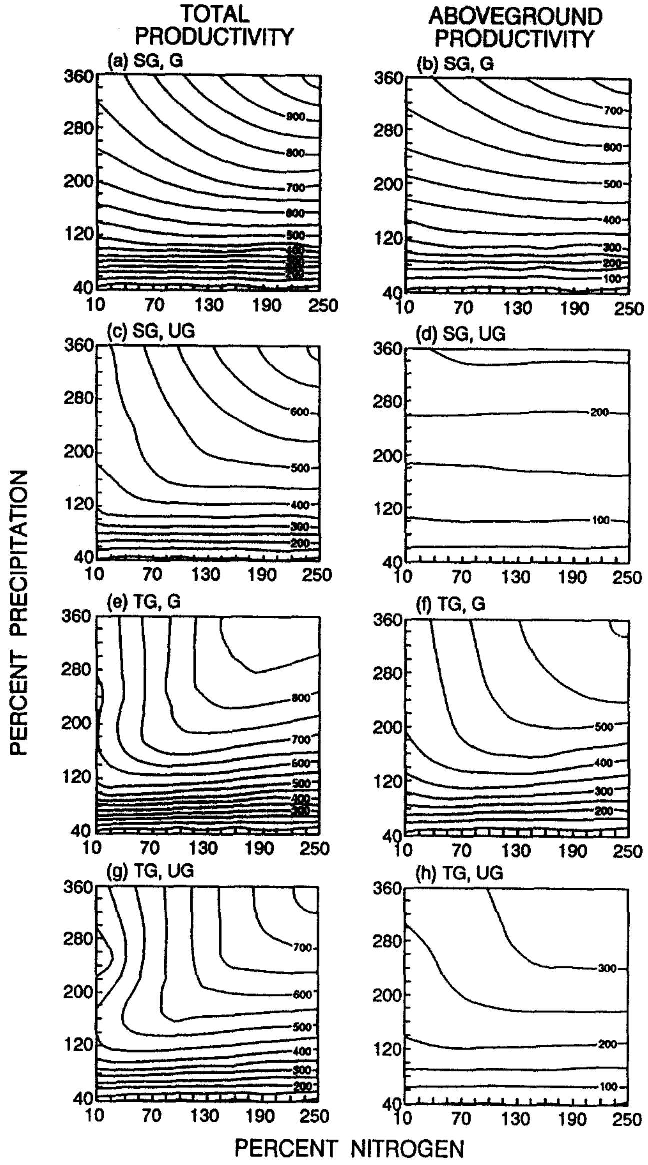

Fig. 1. Simulated total and aboveground primary productivity (g C m^{-2}) for shortgrass (SG) and tallgrass (TG) regions under grazed (G) and ungrazed (UG) conditions as a function of precipitation and nitrogen. Precipitation is presented as the percentage of mean annual precipitation, and nitrogen as the percentage of total soil mineral nitrogen (ammonium plus nitrate) measured for representative shortgrass and tallgrass sites. The ranges of precipitation and mineral nitrogen simulated approximate the range over which each elicited a response in plant production independently. These simulations assumed a balance between carbon and nitrogen removed from the sward by grazers and that returned to the soil in dung and urine.

productivity at low precipitation and any nitrogen level to 75% at high precipitation and high nitrogen levels.

In simulations without grazing (Fig. 1c), total shortgrass productivity was lower. This decline was due to the lack of feedback to the soil system from grazer inputs of dung and urine nitrogen. Total productivity ranged from less than 100 g C m^{-2} at low precipitation levels to 700 g C m^{-2} at the highest levels of precipitation and nitrogen simulated. Despite the lack of grazing-induced nitrogen recycling, precipitation maintained control over production up to 120% of its mean level. Nitrogen control of total productivity was much stronger for ungrazed shortgrass above 150% of mean precipitation than for the grazed condition. In addition, aboveground productivity (Fig. 1d) showed a disproportionally large decline as a percentage of total productivity in comparison to the grazed simulations, reaching maximal levels of only 36% of ungrazed productivity and 33% of grazed aboveground productivity.

Comparisons of total and aboveground productivity for ungrazed shortgrass (Fig. 1c, d) showed that only precipitation exerted control over aboveground productivity. This control resulted in broad horizontal productivity contours with no thresholds for the precipitation effect. Under ungrazed conditions, alleviation of precipitation and nitrogen stress resulted in greater allocation of growth to belowground tissues. In simulations of grazing without nitrogen recycling (i.e. removal of grazed carbon and nitrogen from the simulated system) precipitation still retained control over total productivity and aboveground productivity below 120% of mean precipitation (Fig. 2a, b). In addition both total and aboveground productivity showed nitrogen limitation above 120% precipitation. Although water limitation was apparent, the impact of nitrogen removal from the system forced productivity to levels lower than the ungrazed simulations.

Tallgrass simulations of precipitation-nitrogen interactions indicated that under grazed conditions total productivity was limited by precipitation until 120—130% of the mean precipitation level (Fig. 1e). Above 130%, joint limitation of production by precipitation and nitrogen was shown. This synergistic interaction was apparent for grazed tallgrass aboveground productivity as well (Fig. 1f). Unlike the shortgrass simulations, carbon allocation shifted little between precipitation control (<130% precipitation), where aboveground production was 64—67% of total production, and joint precipitation-nitrogen limitation (upper right corner of the plot), where aboveground was 71% of total productivity. Simulations of ungrazed tallgrass (Fig. 1g, h) were similar to the results of the grazing simulations; however, there was the expected decrease in overall productivity. Tallgrass grazed simulations without nitrogen recycl-

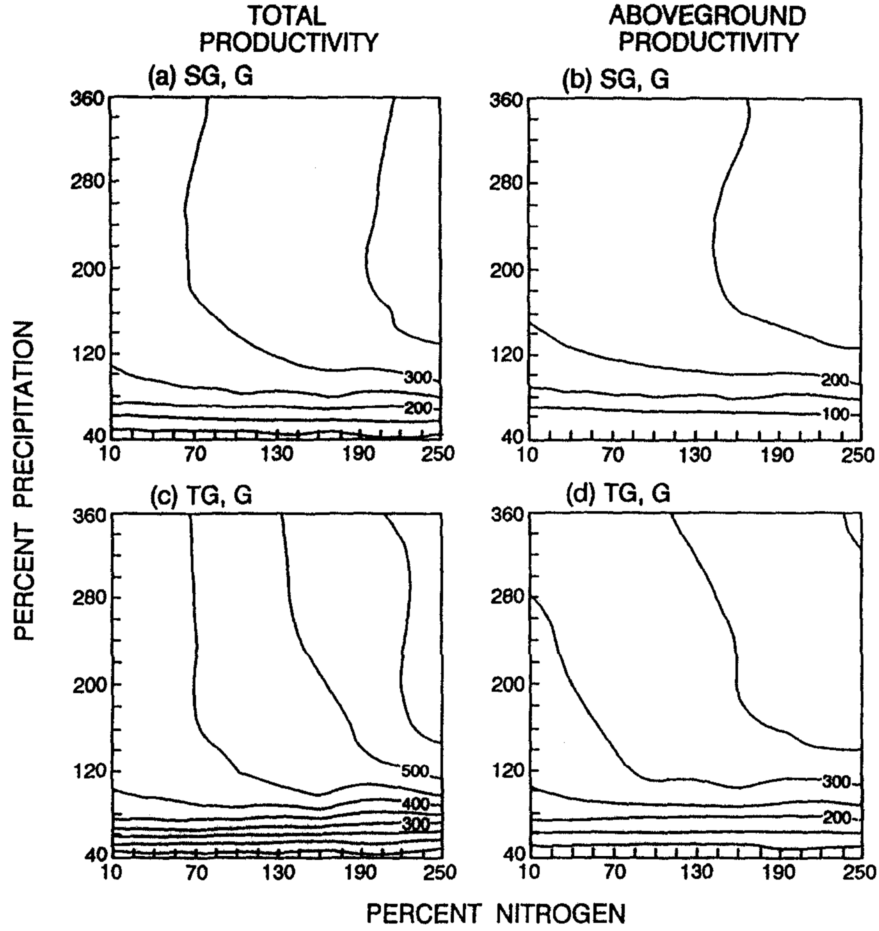

Fig. 2. Simulated total and aboveground primary productivity (g C m^{-2}) under grazed (G) conditions for shortgrass (SG) and tallgrass (TG) regions as a function of percentages of mean annual precipitation and soil mineral nitrogen. In these simulations, grazed carbon and nitrogen was totally removed from the simulated sward, i.e. there is no dung or urine input, to simulate the most extreme condition of nitrogen depletion by grazer activity.

ing (Fig. 2c, d) showed water limitation at < 120% of mean precipitation and the important influence of nitrogen removal from the system which lowered overall production below ungrazed levels.

Hydrologic budgets

Given the importance of precipitation in controlling both shortgrass and tallgrass productivity near and below mean precipitation values and the difference in total precipitation between the two regions we compared the hydrologic budgets for each region (Fig. 3). For the shortgrass region, both grazed and ungrazed simulations at 100% of mean precipitation indicated that the bulk of precipitation was removed from the soil by grasses or evaporation (Fig. 3a, b). Without grazing, the relative amount of precipitation available to plants increased to 56%, compared to 50% when grazed. This increase resulted from the ungrazed plant canopy lowering soil temperatures and decreasing evaporation. Only a small amount of precipitation was lost to runoff and there was no deep soil drainage. Below the mean precipitation level (100%), the proportion of evaporation

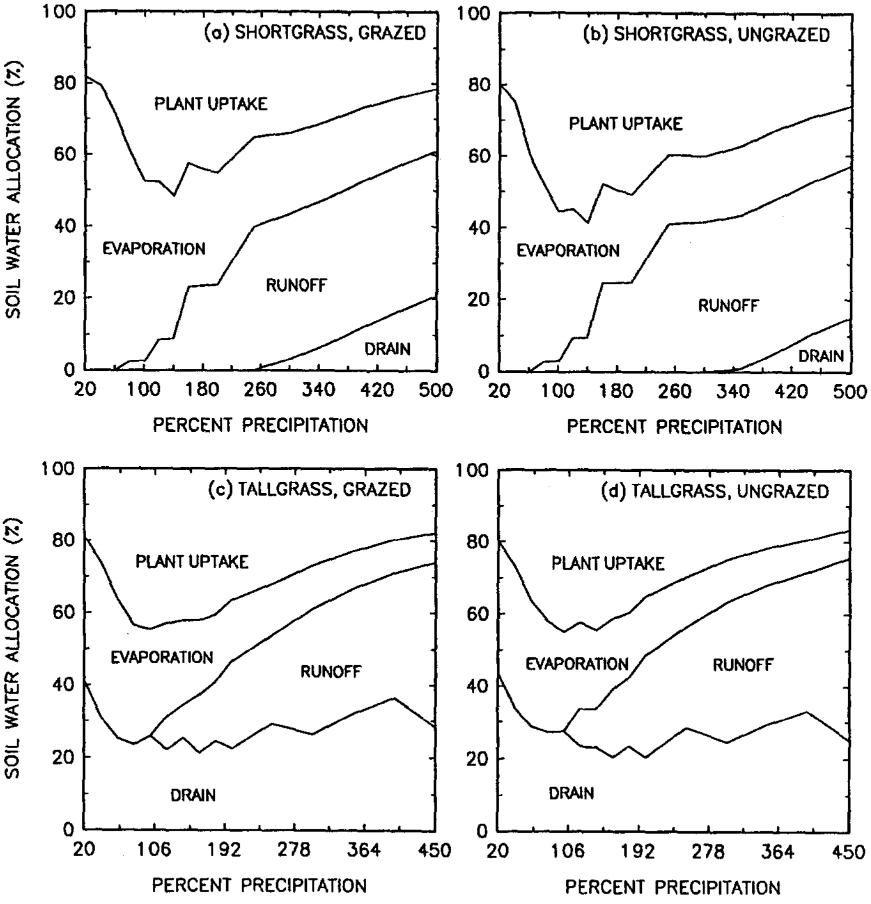

Fig. 3. Allocation of precipitation reaching the soil surface for shortgrass and tallgrass regions under grazed and ungrazed conditions as a function of the percentage of mean annual precipitation. The breadth of precipitation levels simulated represents the range over which major changes in allocation patterns occurred.

sharply increased. Above the mean precipitation level, runoff from the clayey shortgrass soils became important, and, if precipitation was high enough, deep soil drainage became important especially when the simulated sward was grazed. The proportion of soil water going to plant water uptake increased sharply over the precipitation range $\leqslant$ 130% of the mean value (Fig. 3a, b). When grass growth was limited by decreased rainfall, root uptake and transpiration declined. Being a physical property, soil capillary action, leading to soil surface evaporation, should remain active even below rainfall levels that limit grass growth. Thus below 130% of mean precipitation, plant uptake and evaporation may be viewed as competing processes.

In contrast to the shortgrass, grazed and ungrazed tallgrass hydrologic budgets reflected the effect of sandier soils that resulted in deep soil drainage (Fig. 3c, d). Evaporation was also a major component of the budget, although less so than deep drainage. The mean precipitation of the tallgrass was greater than the shortgrass mean, but approximately the same percentage (45%) of soil water was available for plant uptake under mean rainfall and grazed conditions. Low grazing intensity in the tallgrass region resulted in similar sward canopies and thus similar transpiration and water uptake rates as ungrazed swards. As in the shortgrass simulations, increasing water uptake occurred in response to 120—130% of mean precipitation and correlated with precipitation control over productivity (Fig. 1e—h) without any nitrogen effects.

Precipitation interaction with nitrogen dynamics

Although water appeared to control productivity for both shortgrass and tallgrass, water can have both direct physiological effects on plant growth and indirect effects on plant growth through mediation of nutrient cycling processes. Plant water potential (PWP) is an inverse measure of plant water status and, over the range of precipitation levels simulated for the shortgrass under grazed conditions, mean (averaged over all timesteps for each simulation) PWP was negatively correlated with precipitation (r = 0.94, P = 0.0001). In addition, both net microbial mineralization and nitrification responded positively to increasing precipitation (Fig. 4a). Increased nitrification occurred over the range of 10—120% of mean precipitation, making greater amounts of nitrate nitrogen available for plant growth. Nonetheless, increased nitrogen uptake by actively growing grasses resulted in a net decline in the soil nitrate level (Fig. 4a) with increasing precipitation.

Shortgrass soil ammonium responded little to changing precipitation under the grazing scenario (Fig. 4a). In these simulations net mineraliza-

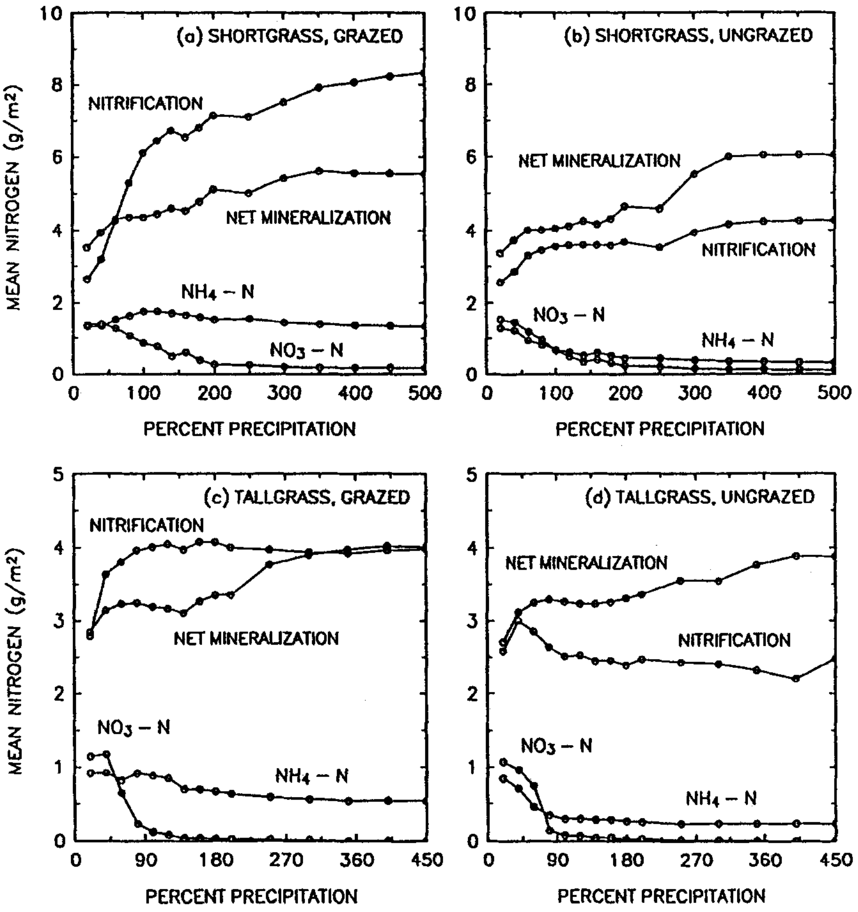

Fig. 4. Soil mineral nitrogen dynamics for shortgrass and tallgrass regions under grazed and ungrazed conditions as a function of the percentage of mean annual precipitation. Each plotted point is a single simulation run. Plotted values for ammonium and nitrate are means calculated from values at each model timestep; nitrification and net mineralization values are sums over each simulation run.

tion was calculated only from microbial decomposition of active and passive soil organic matter components. Hydrolyzed urea entering the ammonium pool contributed to an abundant substrate for nitrification but it was not used in tallying nitrogen mineralized. Thus nitrification rates were high relative to net mineralization in grazing simulations. Without grazing, shortgrass nitrification showed less increase because of lower levels of ammonium as a substrate for nitrifying bacteria (Fig. 4b), and net mineralization (Fig. 4b) was only slightly increased relative to the grazed scenario. Greater nitrification and/or net mineralization resulted in greater plant nitrogen uptake.

Over the 10—130% range of simulated precipitation, regressions of total photosynthesis (g C m^{-2}) vs. mean shoot C/N (CN) and mean plant water potential (PWP) were significant ($P < 0.001$, $R^2 >= 0.97$) for both grazed and ungrazed shortgrass scenarios:

Shortgrass, Grazed: $$\text{PHOTO} = -739.1 + 58.1\,(\text{CN}) \tag{5}$$

$$\text{PHOTO} = 2427.7 - 70.6\,(\text{PWP}) \tag{6}$$

Shortgrass, Ungrazed: $$\text{PHOTO} = -745.6 + 47.5\,(\text{CN}) \tag{7}$$

$$\text{PHOTO} = 3058.2 - 82.4\,(\text{PWP}). \tag{8}$$

Thus over the range of precipitation that controlled shortgrass productivity (Fig. 1a—d), grass sward photosynthesis was positively correlated with shoot C/N and negatively correlated with plant water potential. Although the indirect effect of increasing precipitation did increase available mineral nitrogen and plant nitrogen uptake, shoot C/N did not decrease. Thus, the direct effect of increasing precipitation and improving plant water status accounted for increased photosynthesis rather than indirect nitrogen effects.

Very similar results for soil nitrogen dynamics occurred for the grazed and ungrazed tallgrass (Fig. 4c, d) over the range of simulated precipitation levels. However, nitrification declined because of a very low ammonium substrate level. Regressions relating tallgrass PHOTO to CN and PWP were significant ($P < 0.001$, $R^2 \geqslant 0.94$) for both grazed and ungrazed scenarios:

Tallgrass, Grazed: $$\text{PHOTO} = -44.3 + 49.9\,(\text{CN}) \tag{9}$$

$$\text{PHOTO} = 3394.9 - 99.9\,(\text{PWP}) \tag{10}$$

Tallgrass, Ungrazed: $$\text{PHOTO} = -301.2 + 37.8\,(\text{CN}) \tag{11}$$

$$\text{PHOTO} = 3218.4 - 88.9\,(\text{PWP}) \tag{12}$$

As in the shortgrass simulations, the stimulation of productivity by precipitation was apparently due to direct effects on plant water status and not the result of indirect effects of increased soil nitrogen availability for plant uptake.

Discussion

O'Connor (1985) reviewed a large body of literature from southern Africa which indicated that fertilization can stimulate primary production in savanna ecosystems. In contrast, our simulations clearly indicated that precipitation, and subsequent soil water availability, dominates primary production in grassland ecosystems (Coupland 1958) such as the Serengeti. Our simulation results, by virtue of their focus on biotic-abiotic interactions, help explain the diversity of field results concerning water and nutrient control of grassland primary productivity. We focus our discussion on (1) comparison with regional analyses of grassland productivity, (2) mechanistic explanation of our results for Serengeti grazing ecosystems, and (3) spatial and temporal scales of water and nitrogen impacts on savanna productivity.

Sims et al. (1978) summarized the characteristics and abiotic correlates of primary production for ten western North American grasslands, concluding that the dynamics of above-ground components were most highly correlated with precipitation and water-use variables. Sala et al. (1988) confirmed the paramount importance of water availability in controlling annual primary production in an extensive statistical study of 9500 sites from the central grasslands region of the United States. In their analysis, aboveground productivity for individual sites was best predicted by annual precipitation plus the water-holding capacity or texture of the soil (Sala et al. 1988). Our simulations concurred with these results. Despite having lower soil fertility and greater rainfall than the shortgrass region, Serengeti tallgrass primary production was normally controlled by water availability. Coarse-textured tallgrass soils allowed deep drainage (25%) of soil water below the rooting zone and negated runoff due to rapid infiltration. Another 35% of soil water was lost to evaporation. Thus only 40—45% of soil water was available for plant uptake. Low intensity grazing during the growing season resulted in well-developed canopies for both grazed and ungrazed tallgrass and decreased evaporation from the soil, but also resulted in high transpirational water loss. Thus tallgrass canopy biomass and the lack of intensive grazing resulted in water conservation at the system level, but high water requirements for plant physiological performance.

As we hypothesized, primary production in the shortgrass region was water limited. In addition to lower annual rainfall, fine-textured soils resulted in high evaporation because of slow percolation and strong capillary action. In addition, lack of shading from a heavily grazed grass canopy exacerbated evaporation; without grazing evaporation deceased and resulted in greater soil water available for plant use. At mean precipitation, runoff was minimal (3%). The net result of these factors was the uptake of 50 and 55% of soil water by shortgrass under grazed and ungrazed conditions, respectively.

The inverse-texture hypothesis (Noy-Meir 1973) states that the same vegetation may occur on coarse-textured soils below 300—500 mm annual precipitation as on fine-textured soils with greater than 300—500 mm rainfall. This difference results from the water-holding capacity of different soil textures as described previously. Sala et al. (1988) extended this hypothesis and suggested that below 370 mm of precipitation North American grasslands display greater productivity on coarse soils, and above 370 mm a greater productivity on fine-textured soils. We found similar basic relations among soil structure, soil water, and plant productivity for Serengeti grasslands. Tallgrass savanna, on coarse soil, increased production under simulated precipitation increases because of greater volumes of water percolating through the rooting zone. Plant uptake alleviated water stress, stimulated productivity, and created a positive feedback to water uptake that decreased the percentage of soil water lost to deep drainage. Our shortgrass simulations also indicated a positive response of productivity on fine-textured soils to increased precipitation, reflecting (1) alleviation of 'competition' for soil water between water-stimulated grass growth and the physical process of evaporation, and (2) the simple paucity of precipitation in the shortgrass region. These observations for Serengeti grassland productivity are explanatory of plant-water relations in many African savannas where, unlike temperate regions, high rainfall savannas are often found on heavily leached soils derived from basement rocks and low rainfall savannas are associated with volcanic, fine-textured soils (Bell 1982; Cole 1986).

Long-term studies of savanna fertilization (O'Connor 1985) have indicated changes in species composition (Donaldson et al. 1984) and increased yield (Penning de Vries et al. 1980) under high levels of nitrogen application (up to 200 kg ha^{-1} yr^{-1}). This increase can be both immediate and long-lasting (Penning de Vries et al. 1980). Our short-term simulations also projected a positive effect of nitrogen fertilization on primary productivity — once precipitation limitation was alleviated. We are not surprised that over several years fertilization can increase savanna grassland productivity. Even if primary control is exerted by rainfall, plant growth is stimulated by either opportunistic utilization of fertilizer nitrogen during higher rainfall years or 'luxury' uptake of mineral nitrogen by fertilized perennial grasses, with subsequent storage and utilization during higher rainfall years. Our simulations suggested the latter mechanism because, even though there was no increase of primary production with fertilization under average rainfall conditions, plant C/N ratios dropped as much as 33% for both shortgrass and tallgrass savannas. In addition, Lauenroth & Sala (1992) demonstrated that annual variation in precipitation can have long-term impacts on temperate grassland production. Nitrogen fertilization can interact closely with precipitation to affect patterns of grassland production because perennial grasses integrate environment fluxes over several growing seasons.

At the physiological level, simulated nitrogen fertilization increased total photosynthesis by increasing leaf nitrogen concentrations. Over the growing season this increased photosynthate production was offset by increased shoot maintenance respiration associated with nitrogen storage, resulting in no net gain in primary production. This respiration cost was more acute for the tallgrass species because of their greater shoot biomass in comparison to the shortgrass. Respiration costs from fertilization were alleviated during high rainfall simulations when photosynthate production greatly exceeded respiration costs. Thus our simulations showed the physiological mechanisms behind the lack of response to fertilization under ambient rainfall and the synergistic effects of increased rainfall plus supplemental mineral nitrogen. In simulations with increased rainfall and no fertilization, favorable soil moisture conditions increased net mineralization and nitrification (Fig. 4). These processes increased mineral nitrogen uptake by grasses but failed to provide enough nitrogen to increase leaf nitrogen concentrations in rapidly growing grasses released from water stress. As indicated by our regression analyses, these conditions resulted in no nitrogen stimulation of photosynthesis.

Increased rainfall carries multiple interactive ramifications for ecosystem processes such as nutrient cycling. By stimulating nitrogen mineralization and nitrification (Fig. 4), increased precipitation in our simulations resulted in redistribution of system nitrogen, with more nitrogen available for plant growth. Stimulated photosynthesis and uptake of this additional mineral nitrogen was largely responsible for declining ammonium and nitrate in both tallgrass and shortgrass under grazed and ungrazed conditions (Fig. 4). Grazing returns urea nitrogen to the soil, where it is rapidly hydrolyzed to ammonium (Ruess & McNaughton 1988) and maintains higher soil ammonium levels under grazed conditions despite the stimulation of nitrification from increasing precipitation. In the model, this resulted largely from the faster uptake kinetics of nitrate and lower mobility of ammonium. In shortgrass and tallgrass grazed simulations, nitrification exceeded net N mineralized because of greater ammonium substrate levels from urine deposition. Without grazing, total nitrification in both shortgrass and tallgrass was lower than under grazed conditions, and nitrification is lower than net mineralization for all ungrazed simulations, no matter the precipitation level.

Our simulations of precipitation-fertilization interactions without return of grazed nitrogen to the simulated sward, showed the importance of precipitation in controlling primary production even under the worst conditions of nitrogen depletion in the field. Such field conditions are very plausible, especially for grasslands that receive short-term grazing by migrating herds in the Serengeti. This nitrogen depletion also increased the degree of control nitrogen exerts over primary production under high rainfall scenarios (Fig. 3).

Grazing can stimulate primary production and influence carbon allocation in plants (Coughenour et al. 1984b; McNaughton 1985; Holland et al. 1992; Seagle et al. 1992), as well as alter mineral nitrogen availability to plants (Holland et al. 1992; Seagle et al. 1992). With grazing, shortgrass productivity patterns in response to precipitation and nitrogen suggested that both above- and belowground carbon allocation were affected similarly (Fig. 1a, b). Without grazing, however, nitrogen exerted no control on aboveground production over the ranges of precipitation and mineral nitrogen simulated (Fig. 1c, d). Thus, precipitation alone controlled aboveground production while precipitation and nitrogen together controlled belowground production after initial water deficits were met. Tallgrass simulations (Fig. 1e—h) suggested this phenomenon, but not clearly so. The physiological explanation for this difference lies in the photosynthate investment required by tallgrasses for shoot structural growth and leaf photosynthesis (Coughenour 1984b). Less plant carbon is allocated to root growth under conditions of high nutrient availability (Chapin et al. 1987). Thus it was not surprising that nitrogen availability influenced shortgrass root production when lack of grazing slowed nutrient cycling; tallgrasses, on more nutrient poor soils, may exhibit this phenomenon but the necessity to invest in shoot growth obscured it in our simulations. Our simulations thus demonstrate the potential direct and indirect impacts that grazing has on photosynthate allocation under varying combinations of precipitation and nitrogen fertilization.

Savanna ecosystems reflect complex interactions of several driving variables that operate on different time and space scales (Walker 1987). We have addressed several of these variables — rainfall, nitrogen availability, and grazing. Rainfall patterns *per se* are functionally independent of both general soil nitrogen levels and grazing. Annual Serengeti rainfall conforms to a rather regular pattern that determines growing seasons for each region. Nonetheless, the amount of precipitation differs among regions (McNaughton 1985) and the localized convective rainstorms common to African savannas (Tinely 1982) result in spatial variation of soil moisture within regions. Thus, over the entire Serengeti, rainfall remains the primary driving variable for all regional grasslands, while within region stochasticity of rainfall presents a spatial mosaic of opportunity for grasses to respond to nitrogen as a secondary driving variable. Soil mineral nitrogen itself differs between regions (McNaughton 1985; Ruess & McNaughton 1987), but is strongly influenced within regions by ungulate grazing which tempers both the local distribution of nitrogen and local rates of nitrogen recycling (McNaughton et al. 1988, Seagle et al. 1992). With the ability of grazing herds to track localized convective rainfall and the influence grazing has on plant physiology, sward structure, and nutrient recycling, it is indeed difficult to address primary productivity patterns of the Serengeti without considering these interactive variables.

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