

GRASS RESPONSE TO CLIPPING IN AN AFRICAN SAVANNA: TESTING THE GRAZING OPTIMIZATION HYPOTHESIS

H. LERICHE,^{1,3} X. LE ROUX,^{2,4} F. DESNOYERS,¹ D. BENEST,¹ G. SIMIONI,¹ AND L. ABBADIE,¹

¹Laboratoire d'Ecologie ENS, UMR 7625 CNRS, 46 rue d'Ulm, 75005 Paris, France

²UMR-PIAF (INRA-Université Blaise Pascal), 234 avenue du Brézé, 63039 Clermont-Ferrand cedex 02, France

Abstract. It has been suggested that grazing could stimulate the aboveground dry mass and/or nitrogen yields available to grazers (i.e., the grazing optimization hypothesis, GOH), but the actual importance of this effect is still controversial. The GOH has only been tested for a few grasslands and one savanna ecosystem, but not for the moistest and warmest grasslands and savannas of the world. The objectives of this study were to test the GOH in the humid savanna of Lamto (West Africa) by analyzing the growth of grasses in response to a field trial with three levels of clipping $\times$ two levels of fertilization. We quantified the effects of clipping and fertilization on the dry matter and nitrogen yields to grazers (i.e., mass or nitrogen amount in clipped-off tissues during the experiment) and on the remaining yield (i.e., mass or nitrogen amount in residual phytomass at the end of the experiment) over a three-month period. Total phytomass yield, the sum of yield to grazers, and the remaining yield was maintained under moderate clipping frequency and fertilization as compared to control conditions. Both clipping frequencies decreased the remaining phytomass yield as compared to control plots. Clipping frequency significantly increased nitrogen concentrations in the total yield, in the remaining yield, and in the yield to grazers. Total nitrogen yield and nitrogen yield to grazers were 65% and 91% higher on the plots experiencing moderate clipping frequency with fertilization as compared to control plots. The study shows that grazers in this humid savanna system could potentially modify ecosystem processes in such a way as to partly alleviate nutritional deficiencies, but only in the presence of increased nitrogen availability.

Key words: *Andropogoneae savanna; experimental test; grass response; grazing optimization hypothesis; herbivory; Lamto, West Africa; nitrogen; yield.*

INTRODUCTION

Herbivores have major effects on ecosystem structure and function (e.g., McNaughton et al. 1988), and strongly influence plant growth and development (McNaughton 1983a, Gautier et al. 1999). Herbivory was originally considered always detrimental to plants (e.g., Crawley 1983), and negative impacts of grazing on plant growth have often been reported (Polley and Detling 1989, Hicks and Turkington 2000). However, during the last 25 years, evolutionary (Owen and Wiegert 1976, Paige and Whitham 1987) and functional (Caldwell et al. 1981, Doescher et al. 1997) studies suggested that grazing may not always be detrimental to plants. It has been suggested that, under moderate plant removal levels, net primary production (NPP) should be maintained (compensatory growth) or stimulated (overcompensatory growth) (McNaughton 1979, Hilbert et al. 1981, Hik and Jefferies 1990). In particular, dry mass and nitrogen yields to grazers (i.e., mass and ni-

trogen amounts available for grazers) should be improved on grazed stands as compared to protected stands. Such improvement of dry matter and/or nitrogen yields to grazers is called the grazing optimization hypothesis (GOH). Note that this hypothesis can be tested with respect to either dry matter or nitrogen.

Several studies (McNaughton 1979, 1983b, Cargill and Jefferies 1984, Hik and Jefferies 1990) and model simulations (Hilbert et al. 1981, Coughenour et al. 1984, Dyer et al. 1986, de Mazancourt et al. 1998) support the existence of overcompensatory growth in response to grazing. In particular, overcompensatory growth has been reported for potted grasses subjected to clipping (Detling et al. 1979, McNaughton et al. 1983, Georgiadis et al. 1989), in a salt marsh (Hik and Jefferies 1990), in a mixed prairie (Alward and Joern 1993), and for the savannas of Serengeti (McNaughton 1983a, c, Chapin and McNaughton 1989). However, the GOH was not supported in other ecosystems, where only compensatory growth was observed at best: a constant herbaceous production at moderate grazing or clipping levels has been reported in an *Ipomopsis* dominated canopy of Arizona (Maschinski and Whitham 1989), in a tallgrass prairie of Kansas (Turner et al. 1993), and in mixed prairies of North America (Biondini et al. 1998, Green and Detling 2000). More generally, critical appraisals questioned the ecological sig-

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³ E-mail: hleriche@biologie.ens.fr

⁴ Present address: Laboratoire d'Ecologie Microbienne (UMR 5557 CNRS-Université Lyon I, USC INRA), bat 741, 43 bd du 11 novembre 1918, 69622 Villeurbanne, France.

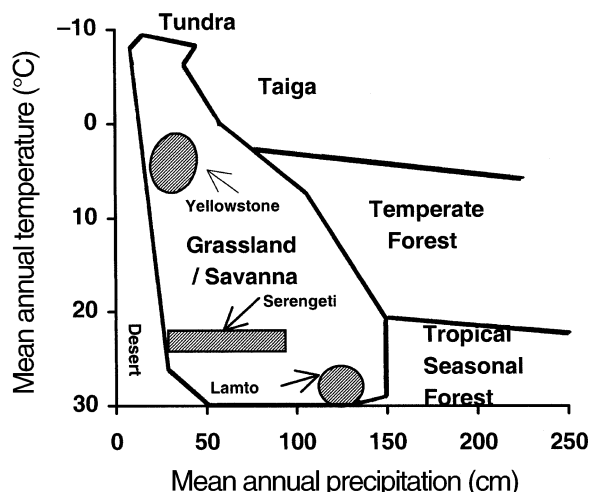


FIG. 1. Approximate placement of Lamto savannas and two other savannas widely studied for the effect of grazing (the Yellowstone National Park, North America, and the Serengeti National Park, East Africa) in Whittaker's (1975) climate-biome diagram (after Frank et al. 1998).

nificance and generality of GOH (Belsky 1986, 1987, Belsky et al. 1993). A review based on a worldwide 236-site data set (Milchunas and Lauenroth 1993) found that most of the effects of grazing on primary production were negative or neutral, but concluded that grazing can increase production in some cases.

The impact of grazing on plant production involves many functional processes controlling the availability of the water, light, and nitrogen resources (see McNaughton 1983b, c, Noy-Meir 1993, Leriche et al. 2001). In particular, nutrient availability is a major determinant of plant response to grazing (McNaughton 1979, Coughenour et al. 1985, Chapin and McNaughton 1989). Several studies reported compensatory growth when the soil was fertilized whereas no compensation was observed in nonfertilized plots (Bryant et al. 1983, Ruess and McNaughton 1984, Georgiadis et al. 1989, Maschinski and Whitham 1989, Holland and Detling 1990). Modeling approaches have also underlined the importance of nutrient cycling and nutrient availability to plants in the growth response to grazing (Holland et al. 1992, de Mazancourt et al. 1999, Leriche et al. 2001).

To our knowledge, the GOH has been tested in only one tropical savanna system, namely the savannas of the Serengeti, East Africa. This ecosystem is characterized by high soil fertility (Chapin and McNaughton 1989). No data are available for other savannas, and particularly the nutrient poor humid savannas dominated by *Andropogoneae*, which cover 3×10^6 km² in West Africa (Menaut et al. 1991). Previous studies using a theoretical (de Mazancourt et al. 1998) or process-based (Leriche et al. 2001) modeling approach suggested that the GOH was feasible in the nutrient poor humid savanna of Lamto (West Africa) depending on

nitrogen cycling and availability to plants. The objectives of this study were (1) to test the GOH in the Lamto humid savanna by analyzing the growth of grasses in response to a clipping $\times$ fertilization trial in the field, and (2) to distinguish the effects of clipping and fertilization on the dry matter and nitrogen yields to producers (i.e., mass or nitrogen amount of residual phytomass at the end of the experiment) and to grazers (i.e., mass or nitrogen amount of clipped-off tissues during the experiment).

METHODS

Study site

The Lamto reserve (5°02' W, 6°13' N, Ivory Coast) lies in the Guinea zone (precipitation $\sim$ 1250 mm/yr) just north of the West African moist forest zone (Menaut and César 1979). Lamto savannas thus correspond to the moistest and warmest grassland types of the world (Fig. 1). Most of the Lamto savannas overlie granite geology that produces tropical ferruginous soils (Menaut and César 1979). Total soil nitrogen concentration is 0.5 g N/kg. The herbaceous cover mainly consists of grasses ($>90\%$ of the total biomass) (Menaut and César 1979) and is dominated by the C₄ bunch grass species *Hyparrhenia diplandra*, *H. smisthiana*, *Andropogon canaliculatus*, and *A. schirensis* (see Plate 1). Annual nitrogen uptake by the herbaceous cover is ~ 7 g N·m⁻²·yr⁻¹ (Abbadie et al. 1992). In Lamto, the density of mammalian herbivores (3 kob/km², *Kobus kob* and 2.4 buffalo/km², *Syncerus caffer nanus*) is typical of densities reported for other West African savannas (Fritz 1997). Given a mean live mass of 80 kg per kob and 450 kg per buffalo this corresponds to a total live mass of 1320 kg/km².

The reserve is burned in mid-January every year, consuming most of the aboveground grass mass. In 2000, the area was burned on 14 January. The experiment lasted for 18 weeks following the fire, until late May, i.e., during the vegetative growth period (flowering stage is attained in July or August at Lamto). Soil water availability was not considered to have limited plant growth, except in March (Fig. 2).

Clipping and N fertilization trials

Four replicate exclosures with 2 m high fences to exclude mammalian herbivores were set up within a 1-ha savanna area (see Plate 1). A factorial design with two levels of nitrogen fertilization (fertilization or not) and three levels of clipping frequency (zero, once a month, and every two weeks) was applied in each exclosure. In other words, each exclosure contained six plots, each 2 $\times$ 2 m in size. The clipping treatment consisted in removing all the vegetation above 10 cm (Wallace et al. 1984, Coughenour et al. 1985). Moderate-frequency clipped plots were clipped on weeks 6, 10, 14, and 18 after the fire; the high-frequency clipped plots were clipped on weeks 6, 8, 10, 12, 14,



PLATE 1. (Left) View of the exclosures at the Lamto reserve study site. (Right) Bunch grass species in one of the experimental plots. Photos by H. Leriche.

16, and 18. N fertilization was applied on weeks 6, 10, 14, and 18 for all the fertilized plots. N fertilization consisted in hand scattering granules of 0.13 g N/m^2 at each fertilization date. The cumulative nitrogen input was thus 0.52 g N/m^2 at the end of the experiment. Treatments were applied to the entire 4-m^2 extent of the plots, but only the vegetation inside the central $1.5 \times 1.5 \text{ m}$ area was collected for analysis, to avoid edge effects.

Aboveground phytomasses and nitrogen concentration

All plant parts removed during the clipping treatments were collected, and sorted into green vs. dead material. At the end of week 18, all aboveground vegetation was removed from each $1.5 \times 1.5 \text{ m}$ subplot, distinguishing plant parts above and below 10 cm, and again sorting into green vs. dead matter. All vegetation samples were oven dried to constant weight at 60°C .

Dry samples of aboveground green and dead grass were milled in a Fritsch rotor mill (Retsch, Haan, Germany). Nitrogen concentration was measured with an elemental analyzer (NA 1500 series 2, Fisons, Milan, Italy).

Computations and statistical analyses

The dry matter-remaining yield was defined as the mass of the residual phytomass $<10 \text{ cm}$ at the end of the experiment (McNaughton 1985). The nitrogen-remaining yield was computed from nitrogen concentration and phytomass values as the nitrogen amount in the residual phytomass at the end of the experiment. The dry matter yield to grazers was computed as the sum of the masses of clipped-off tissues plus the mass of plant parts collected $>10 \text{ cm}$ at the end of the experiment. The dry matter yield to grazers with zero frequency of clipping was the final harvest $>10 \text{ cm}$ at the end of the experiment. Aboveground production was defined as the sum of the dry matter yield to grazers

and the dry matter remaining yield. The nitrogen yield to grazers was computed from the nitrogen concentration and phytomass values of clipped-off tissues during the experiment and those of plant parts collected $>10 \text{ cm}$ at the end of week 18. The aboveground nitrogen yield was defined as the sum of the nitrogen-remaining yield and the nitrogen yield to grazers.

Block effect was tested by an analysis of variance and corrected to account for mean values observed per block when it was significant. Analyses of variance were performed with two-way ANOVA (GLM procedure, SAS Institute 1990) for testing the clipping, fertilization, and clipping $\times$ fertilization effects. Differences between means were tested using Tukey's tests at the $P = 0.05$ level.

RESULTS

Dry matter yields

Both clipping frequency and fertilization significantly influenced ($P \leq 0.0001$ and 0.0002 , respectively) total phytomass yield. No clipping $\times$ fertilization interaction effect was detected ($P = 0.15$). Total phytomass yield was significantly lower for the moderate

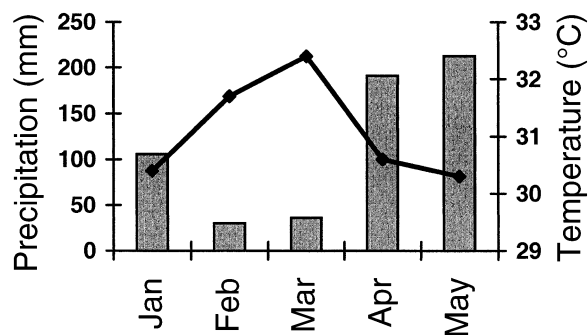


FIG. 2. Seasonal course of monthly precipitation and monthly mean air temperature during the study.

clipping frequency without fertilization, and for the high clipping frequency with or without fertilization as compared to the control plots (Fig. 3). In contrast, total phytomass yield was maintained on the plots experiencing moderate clipping frequency with fertilization as compared to control plots.

The yield to grazers was significantly influenced by both clipping frequency and fertilization ($P = 0.013$ and 0.0006 , respectively), and no clipping $\times$ fertilization interaction effect was detected ($P = 0.17$). Phytomass yield to grazers tended to be higher on the plots experiencing moderate clipping frequency with fertilization, and lower on the clipped plots without fertilization as compared to control plots, although these differences were not significant (Fig. 3).

The remaining yield was significantly influenced by the clipping frequency ($P \leq 0.0001$), whereas no fertilization and clipping $\times$ fertilization effects were observed ($P = 0.74$ and 0.35 , respectively). Both clipping frequencies decreased total phytomass remaining yield as compared to control plots (Fig. 3).

When considering dead parts only, which can be assessed on the figures by the difference between yield and green yield, there was no fertilization effect ($P > 0.6$) on dead matter yields to producers, grazers, or total dead matter yield, but these yields were reduced by clipping ($P \leq 0.0001$).

Nitrogen concentrations

No fertilization and clipping $\times$ fertilization effects were observed on the nitrogen concentrations in the total yield, in the remaining yield, and in the yield to grazers ($0.37 < P < 0.95$) (Fig. 4). Clipping frequency significantly increased nitrogen concentrations in the total yield, in the remaining yield, and in the yield to grazers ($P \leq 0.0001$ in each case).

Nitrogen yields

Both clipping frequency and fertilization significantly influenced ($P = 0.0022$ and 0.0009 , respectively) total nitrogen yield. No clipping $\times$ fertilization interaction effect was detected ($P = 0.17$). Total nitrogen yield was 65% higher on the plots experiencing moderate clipping frequency with fertilization as compared to control plots (Fig. 5).

The nitrogen yield to grazers was significantly influenced by both clipping frequency and fertilization ($P = 0.0047$ and 0.0011 , respectively), and no clipping $\times$ fertilization interaction effect was detected ($P = 0.22$). In particular, nitrogen yield to grazers was 91% higher on the plots experiencing moderate clipping frequency with fertilization than control plots (Fig. 5).

No clipping frequency, fertilization, and clipping $\times$ fertilization effects were observed on the nitrogen remaining yield ($P = 0.067$, 0.25 , and 0.12 , respectively). Nitrogen remaining yield was indeed always ~ 0.55 g N/m² on all the plots (Fig. 5).

DISCUSSION

Effects of clipping and fertilization on aboveground phytomass and nitrogen yields

In our study, the growth response of the grass layer depended on clipping frequency. The detrimental effect of clipping frequency on phytomass yield is consistent with results obtained in other ecosystems. In mixed-grass prairie of south Dakota, usually grazed by bison, aboveground primary production was maintained under moderate clipping frequency (once a month), but decreased under higher clipping frequency (twice a month) (Green and Detling 2000). Similarly, production of the African grass *Sporobolus kentrophyllus* was stimulated only at moderate clipping frequency (Georgiadis et al. 1989).

Our results showed that aboveground phytomass yield decreased with increasing clipping frequency on unfertilized plots, whereas moderate clipping frequency under fertilization allowed maintenance of phytomass yield as compared to control plots. These results were consistent with conclusions derived from a modeling study of Lamto grassland (Leriche et al. 2001). We actually showed that conservation of NPP can occur under moderate grazing, but that the simulation results strongly depended on nitrogen availability to plants. Compensatory and over-compensatory growth has already been observed under moderate clipping frequency and fertilization for other ecosystems. For instance, an increase in aboveground phytomass yield has been observed for fertilized and clipped plots of mountain grasslands as compared to control plots (Fahnestock and Detling 1999). Improved production was also observed for potted individuals of the African grass *Sporobolus kentrophyllus* when defoliation was coupled to fertilization (Georgiadis et al. 1989). The positive effect of N fertilization in the growth response of grassland to grazing suggests that N return to the soil insured by animal excreta probably plays a key role (Ruess and McNaughton 1984, 1987).

Concurrently to the maintenance of phytomass yield, an increase in total N yield was observed under moderate clipping and fertilization as compared to control plots. Increased N yields were also observed for defoliated and fertilized individuals of the African grass *Sporobolus kentrophyllus* (Georgiadis et al. 1989), and for fertilized and clipped plots of mountain grasslands as compared to control plots (Fahnestock and Detling 1999). Furthermore, N yield of Lamto savanna was maintained under high clipping frequency (C2N+). Our results thus suggest that (1) enhancement of N yield by grazing occurs more often than enhancement of phytomass yield, and (2) the maintenance of N yield occurs at higher clipping frequency than for phytomass yield, as already observed in a mixed-grass prairie under moderate clipping frequency (Green and Detling 2000). This is due to the increase in plant nitrogen concentration induced by

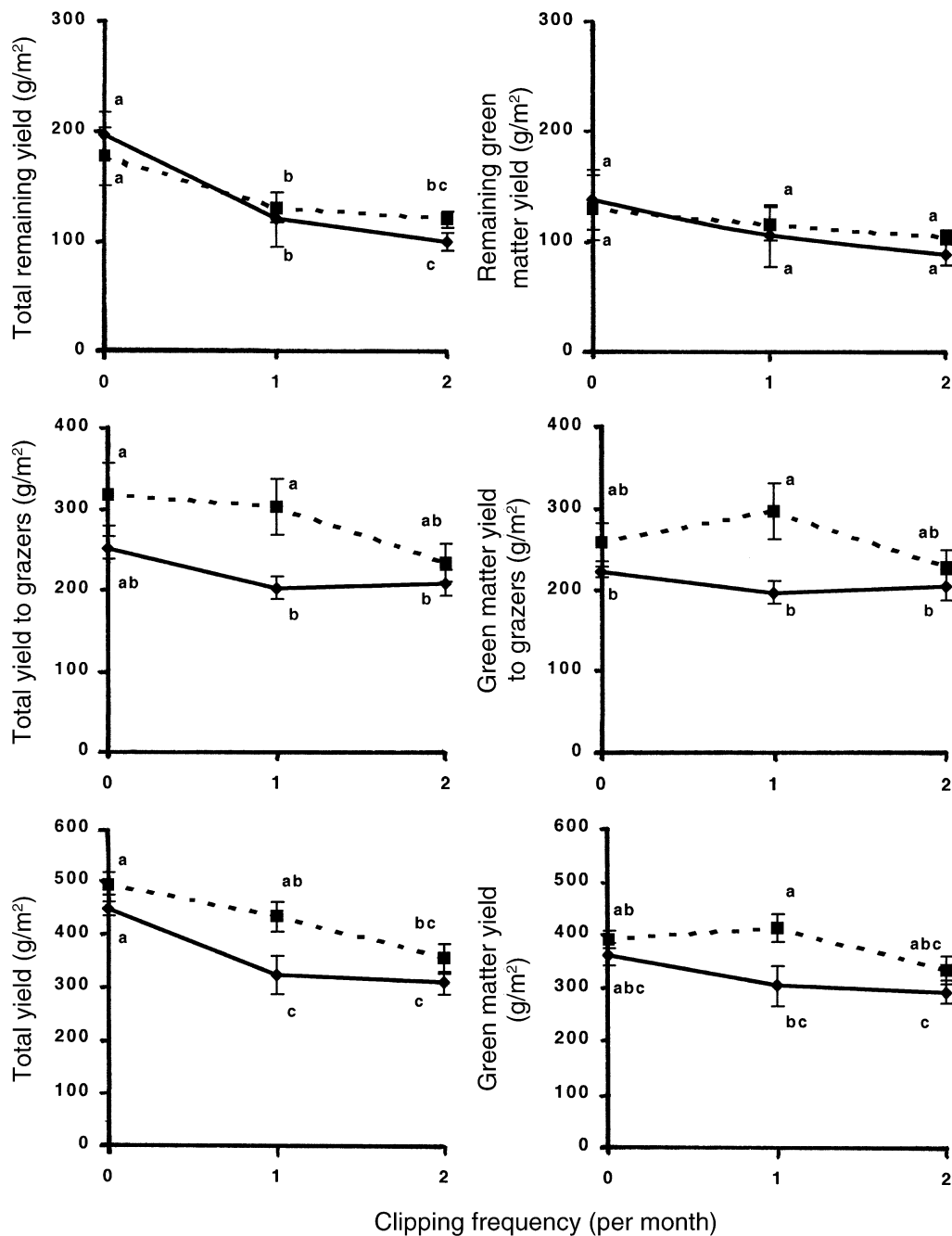


FIG. 3. Remaining dry matter yield (top, left) and green matter yield (top, right) (0–10 cm height), dry matter yield (top, left) and green matter yield (middle, right) to grazers (up to 10 cm height), and total yields (bottom panels) as a function of clipping frequency (per month) with (dashed line) and without (solid line) fertilization. Error bars indicate ± 1 SE.

grazing, as already observed in a mixed-grass prairie (Green and Detling 2000), and a tallgrass prairie (Turner et al. 1993). Such an increase in N concentration is probably due to the dilution of a relatively fixed amount of plant nitrogen in a total phytomass much lower than in control plots. More particularly, this could be partly due to a decrease in the necromass-

to-biomass ratio (Hamilton et al. 1998), and also to a decrease in the mean leaf age of the plant cover. Given the strong dependency of photosynthetic capacity on leaf nitrogen reported in *Hyparrhenia* sp. (Le Roux and Mordellet 1995), such increase in N concentration clearly enhances the growth potential per unit leaf area or mass of plants after clipping.

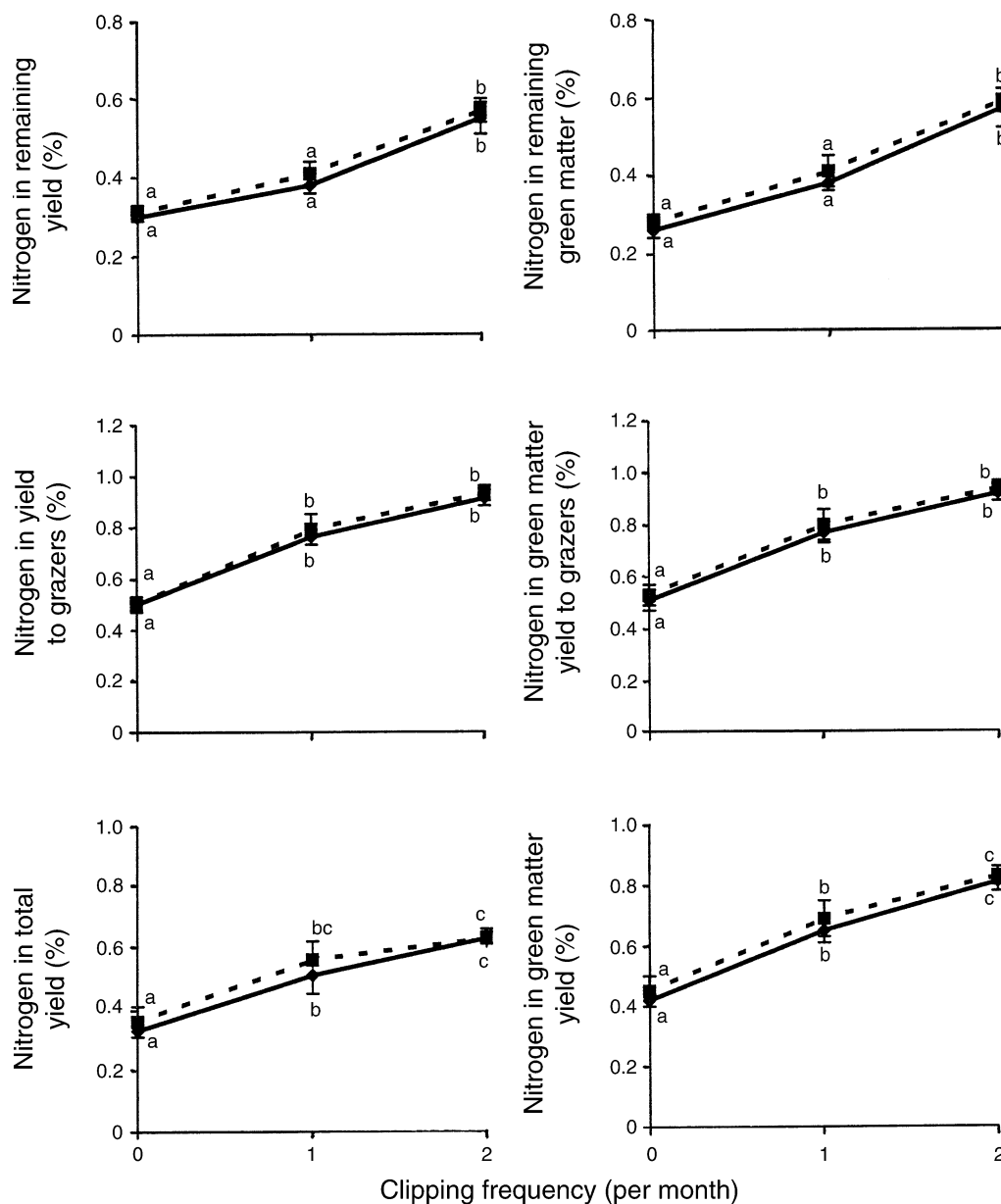


FIG. 4. Nitrogen concentration in remaining dry matter yield (top, left) and in green matter yield (top, right) (0–10 cm height), dry matter yield (middle, left) and in green matter yield (middle, right) to grazers (up to 10 cm height), and total yield (bottom panels) as a function of clipping frequency (per month) with (dashed line) and without (solid line) fertilization. Error bars indicate ± 1 SE.

Effects of clipping and fertilization on phytomass and nitrogen yields to grazers

Our results provide evidence that the GOH (i.e., increase in yield to grazers in response to moderate grazing, McNaughton et al. 1983) is not sustained from a dry matter perspective (compensatory growth was observed for moderately frequent clipping), but is sustained from a nitrogen perspective for Lamto grassland, namely in the moistest and warmest domain of the world where grassland ecosystems can be encountered. An increase in the nitrogen yield to grazers was ob-

served under moderate simulated grazing when fertilizer was added. Similarly, in mixed-grass prairie, nitrogen yield to grazers was increased under moderate defoliation, whereas phytomass yield to grazers was maintained (Green and Detling 2000).

Concurrently with constant yield to grazers, decreased remaining yield was observed for clipped plots as compared to control plots. This is consistent with the decrease of the ratio remaining yield/total yield observed in clipped as compared to unclipped individuals of *Kyllinga nervosa* (McNaughton et al. 1983).

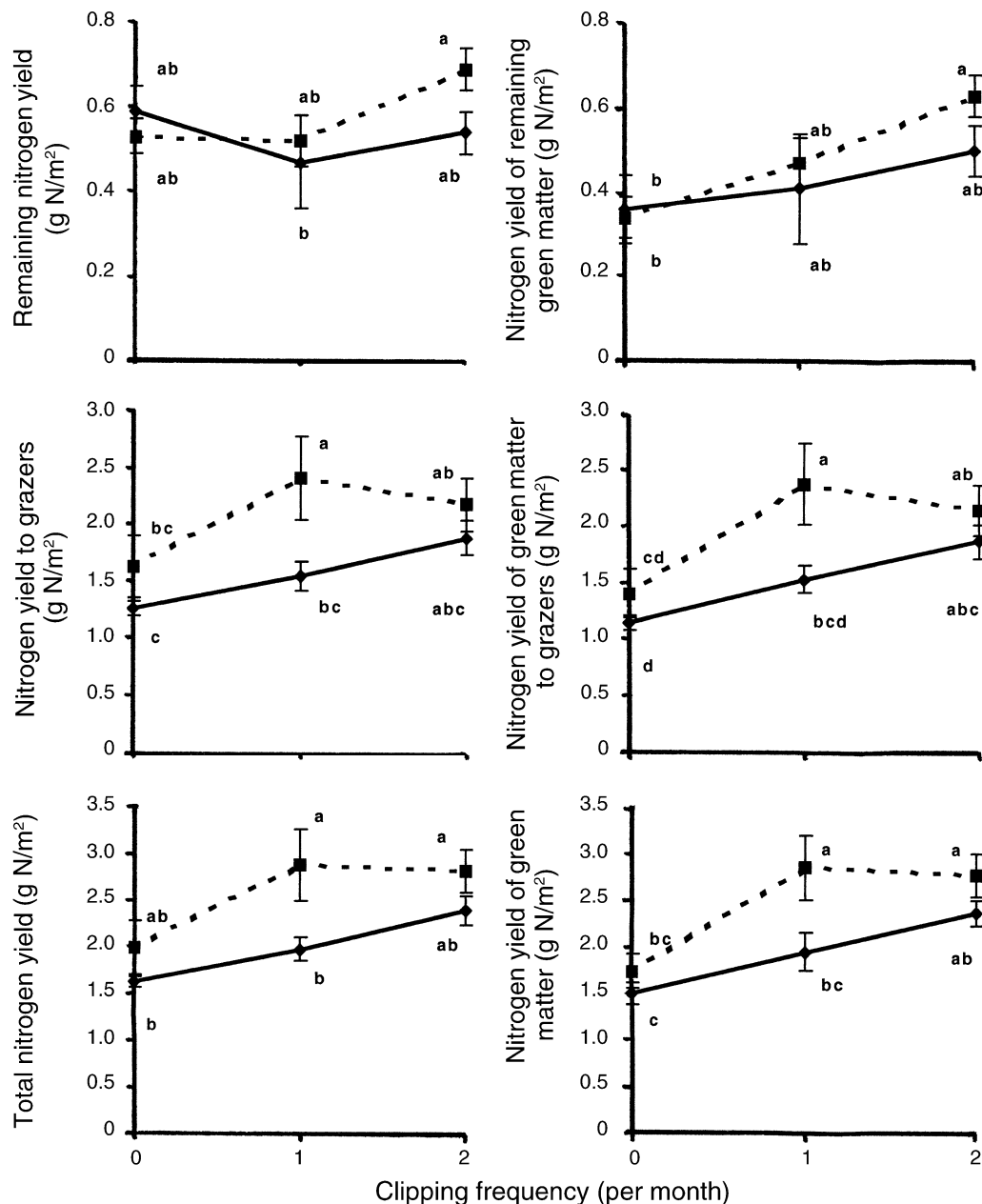


FIG. 5. Nitrogen remaining yield (0–10 cm height; top panels), to grazers (up to 10 cm height; middle panels), and total yield (bottom panels) provided as total dry matter (left) or green matter (right) as a function of clipping frequency (per month) with (dashed line) and without (solid line) fertilization. Error bars indicate ± 1 SE.

Such changes in the pattern of yield distribution concurrently to improved grass quality (i.e., higher nitrogen concentration of the biomass available for grazers) show that in the presence of adequate nitrogen supply, grazers can modify ecosystem processes, and particularly N allocation, in a way that helps to alleviate nutritional deficiencies of the ecosystem to grazers (McNaughton et al. 1997). The extent to which N return by urine and dung deposits can directly or indirectly

enhance N availability to plants is thus of major importance in this context.

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