

REPORT

Tropical pasture carbon cycling: relationships between C source/sink strength, above-ground biomass and grazing

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Abstract

We measured net ecosystem CO₂ exchange (NEE) in Panamá over C₄ pasture plots that varied in grazing intensity. After adjusting for variation in light, there were noticeable effects of grazing-related variables on CO₂ exchange that were largely dependent on the developmental stage of the plant canopy. Above-ground productivity was positively related to grazing intensity ($r^2 = 0.30$). Two experimentally grazed fields had significantly lower standing crop biomass but no significant difference in CO₂ uptake (24.2 $\mu\text{mol}/\text{m}^2/\text{s}$) compared with two ungrazed fields (20.3 $\mu\text{mol}/\text{m}^2/\text{s}$). Grazed fields had significantly lower ecosystem respiration rates (10.3 $\mu\text{mol}/\text{m}^2/\text{s}$) than did ungrazed fields (17.6 $\mu\text{mol}/\text{m}^2/\text{s}$). These results suggest that, although these pastures were possible sources of CO₂ during the time intervals sampled, the size of the sources tended to be dampened by cattle grazing through reductions in ecosystem respiration. Thus, it appears that disturbance caused by cattle grazing will not always result in an increase in CO₂ release from tropical pastures to the atmosphere.

Keywords

C cycle, grasslands, grazing, net ecosystem carbon exchange, Panamá, tropical ecology.

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INTRODUCTION

Identifying the factors that determine the carbon source/sink strength of ecosystems is important for reducing uncertainty in the global carbon cycle (Houghton *et al.* 1992). In temperate, boreal and arctic ecosystems, temperature and moisture (e.g. Oechel *et al.* 1994; Valenti *et al.* 1995; Saleska *et al.* 1999), atmospheric CO₂ concentrations (Oechel *et al.* 1994; Luo *et al.* 1996; Hungate *et al.* 1997), and nutrient availability (Oechel *et al.* 1995; Goulden *et al.* 1996; Alm *et al.* 1999) correlate with changes in carbon exchange. Ruimy *et al.* (1995) reviewed dozens of data sets on net ecosystem CO₂ exchange (NEE) from both agricultural and natural systems. There were fewer data sets from grasslands than from forests, and only one from a tropical system (Leroux & Mordelet 1995). Grace *et al.* (1998) present the only data from tropical pasture. Thus, it is largely unknown which environmental factors are associated with CO₂ exchange in tropical ecosystems (Grace *et al.* 1995; Leroux & Mordelet 1995; Miranda *et al.* 1997; Lin *et al.* 1999), especially in grasslands (Grace *et al.* 1998).

Neotropical regions are undergoing large changes in land-use; forests have been, and are continuing to be cleared and

converted into crops and pastures (Jordan 1986; Soepadmo 1993; Dixon *et al.* 1994; Dale 1997). Much work has been done on how this conversion from forest to pasture affects soil C and nutrients (e.g. Brown & Lugo 1982; Nepstad *et al.* 1994; Bawa & Dayanandan 1997; Neill *et al.* 1996). However, after forests are converted into pasture, further land-use changes such as grazing regimes or land abandonment will affect the carbon balance of an area (Eden *et al.* 1990; Reiners *et al.* 1994). Differing land-use patterns and rates of disturbance within and among land holdings will result in spatially variable exchanges across the landscape at multiple scales. Little is known about how ecosystem carbon exchange varies spatially, especially at small spatial scales within ecosystems (e.g. Waddington & Roulet 1996; Alm *et al.* 1999).

One especially important component of small-scale spatial variability is grazing pressure (McNaughton 1984; Shiyomi *et al.* 1998). In African and North American grasslands, the disturbance caused by ungulate grazing is patchy. As a result, different proportions of the canopy are removed, which leads to grassland patches with differing heights, leaf surface area, and standing crop biomass (McNaughton 1984; Knapp *et al.* 1999). Ungulates have

large indirect effects on nutrient cycling by converting plant materials that would normally cycle through the detritivore food web into more readily available forms of nutrients in urine and dung patches (McNaughton 1985; Day & Detling 1990; Wilsey 1996; Frank *et al.* 1998; Knapp *et al.* 1999). Moderately grazed patches have been found to have increased above-ground productivity and higher leaf nutrient content compared to ungrazed patches (McNaughton 1985; Day & Detling 1990; Frank & McNaughton 1993). Thus, because grazing can so greatly modify canopy structure and nutrient cycling, it could potentially affect pasture carbon uptake and respiration.

Studies of cattle grazing and net ecosystem carbon exchange have been made on a Danish salt marsh (Morris 1998) and North American short-grass prairie (LeCain *et al.* 2000). LeCain *et al.* (2000) found that grazed canopies in the USA had higher ecosystem photosynthesis early in the growing season, presumably due to less litter and better light penetration. There are no studies that we know of for neotropical pasture. Jordan (1986) speculated that grazing by cattle in neo-tropical pastures causes soil compaction, increased run-off and erosion, and reduced long-term productivity in most cases. Reiners *et al.* (1994) found that conversion of forest to pasture in Costa Rica led to an increase in soil bulk density, a decrease in porosity, and an increase in erosion potential. However, there is little direct information on how grazing affects ecosystem processes and especially carbon cycling in the tropics (Kellman & Tackaberry 1997; Grace *et al.* 1998). The objectives of this study were to: (1) determine if relationships exist between NEE, grazing intensity, and net primary productivity, and (2) determine if removal of grazing could lead to changes in NEE variables. We addressed these objectives with the use of chamber techniques, which are the only methods available to measure small-scale spatial variation, and found that grazing actually reduces the amount of CO₂ released to the atmosphere.

MATERIALS AND METHODS

Both studies were carried out in pastures located near Sardinilla, Panamá (9°E19' N, 79°E38' W), which is 55 km north of Panama City. To study spatial variability in NEE, we sampled nine plots located in a 6-ha pasture during parts of 1997 and 1998 (hereafter called the 'sampling study'). In 1998–99, we conducted a separate study comparing NEE of grazed and ungrazed fields in an adjacent pasture (hereafter called the 'grazing experiment').

Study area

The elevation of the site was approximately 70 m a.s.l. Mean annual precipitation at nearby Buena Vista is 2351 mm, with

25–50 mm per month during the dry season (January – March), 120–130 mm per month during the transition period in April and December, and 250 mm per month during the rainy season (May to November). Daily and seasonal temperatures were relatively constant throughout the year: at nearby Barro Colorado Island, daily maximum temperatures (°C) ranged from 32.3 in November to 34.3 in April (annual mean = 33.1) and daily minima 21.1 (January) to 22.4 (May) (mean = 21.7). Underlying geology appears to be Tertiary limestone and other sedimentary rocks with soils of the clayey typic tropudalfs and aquic tropudalfs (Tim Moore, unpublished data).

The study area was logged by the owner in 1952 and 1953 at a rate of 3–4 ha/year. The area was used for agriculture for two years to grow corn, rice, otoi, plantain and yucca. After two years in crops, the site was converted into pasture by seeding it with a C₄ African grass, *Hyparrhenia rufa*, which is no longer found locally. The area has been grazed by cattle since that time, and is now dominated by C₄ grasses, with *Ischaemum indicum* (rotana) being the most important. This grass commonly dominates pastures in Panamá and Costa Rica (Reiners *et al.* 1994).

Sampling study

Nine sampling locations were randomly established in 6 ha of grazed pasture land and sampled for NEE during the late rainy season 1997 (November), the following dry season (February 1998) and early rainy season (May/June 1998). These dates were chosen to provide comparisons among seasons and among different canopy sizes. Within a location, we established three 40 × 40 cm plots that had the same initial height and species composition and visually appeared the same (e.g. correlation coefficients for height among the three were all > 0.9) at the beginning of the study. Each of the three plots was then randomly assigned to be one of either a net ecosystem exchange (NEE), a control (g) or a temporary enclosure plot (ng).

Temporary enclosures (61 × 61 × 61 cm with 2.5 cm plastic mesh) were erected to estimate rates of consumption and grazing intensity (McNaughton 1985; McNaughton *et al.* 1996). Above-ground biomass was clipped to ground level in 40 × 40 cm plots inside (ng) and outside (g) enclosures at the end of each sampling period for the nine sampling locations. (Enclosures were then set-up in a new spot during the following season.) Consumption was then derived by comparing biomass inside and outside: $C = (g - ng)/\text{time}$, with time being the number of days enclosures were in place (McNaughton 1985).

Above-ground productivity (g/day) was estimated for 1997 by dividing peak biomass (g) in November by the length of growing season (Paton 1998) and then adding the estimated amount that was consumed by cattle (C).

Above-ground productivity was estimated for the May/June sampling period by summing positive biomass increments between February and May/June, dividing this by the number of days from the start of the growing season (Paton 1998), and then adding C. Grazing intensity (McNaughton 1985) was calculated as $GI = C/prod.$

Consumption and grazing intensity were not measured during the dry season (February 1998) because there were no cattle in the pasture.

Soils were sampled in the centre of each location during June 1998. Soil bulk density was determined by oven-drying the soils. Soil pH was determined in a water suspension.

Grazing experiment

To test experimentally whether grazing affects ecosystem carbon exchange variables, we had cattle graze two fields from 1998 through the 1999 rainy season and then compared responses to two adjacent fields that received no grazing (fields were approximately 0.21 ha each). Within each grazed and ungrazed field, net ecosystem CO_2 exchange was measured on three subplots during each of two sampling periods (July and August 1999). Thus, we had a total of 12 subplots: 4 fields \times 3 subplots each. In each of the experimentally grazed fields, four cattle grazed for 1 week per month. This was meant to simulate the average grazing intensity in the pasture used for the sampling study, which had 25 cattle on 6.7 ha for 5–6 months per year. Above-ground standing crop biomass and diversity (Simpson's D) was measured in each of the 12 subplots after all NEE measurements were made. Plants were dried and weighed to determine if grazing affected CO_2 exchange variables. No estimate of consumption was made for these plots.

NEE measurements

NEE was measured using a closed enclosure system. A 40-cm \times 40-cm square base \times 100 cm height (160 000 cm³) acrylic chamber was used for the measurements. The chamber fitted into grooves cut into wooden collars that were inserted 5 cm into the soil at the beginning of each field trip, at least 1 week prior to any NEE measurements. The chamber was connected to a portable LCA-4 infra-red gas analyser (ADC Company, Hoddesdon, England) in a closed configuration. Temperature (and indirectly, relative humidity) within the chamber was maintained within 1 °C of ambient by pumping ice water through a small car radiator attached to the inside of the chamber (Waddington & Roulet 1996). A fan blew air over the radiator, and this effectively mixed the air. PPFD (photosynthetic photon flux density) was measured with a Parkinson PAR sensor placed at the top inside of the chamber.

Initial tests determined that the CO_2 concentrations inside the chamber were strongly linear (r^2 near 1) for up to

15 min, so measurements of CO_2 inside the chamber were made at the beginning and after 9–11 min for the sampling study. For the enclosure experiment, we made one measurement of CO_2 each minute for 5 min after placing the chamber onto the collar. The slope of CO_2 concentration over time was then calculated ($\mu\text{mol}/\text{mol}/\text{s}$), and multiplied by the effective size of the chamber (44.6 mol/m²) (Ruimy *et al.* 1995), resulting in an estimate of NEE in $\mu\text{mol}/\text{m}^2/\text{s}$. The LCA-4 corrects CO_2 readings for changes in pressure due to increases in water vapour from transpiration. Errors associated with pressure build-up within the chamber were assumed to be minimal due to the large chamber size, short duration of measurements, and influence of canopy processes (Healy *et al.* 1996). Measurements were made on each of the nine plots once per sampling period (10.00–15.00 on sunny days) during the late rainy season 1997 (November 26 to December 1), the dry season 1998 (March 2 to March 6), and the early rainy season 1998 (May 21 to June 1). Rainfall was 35% below average during the 1997/1998 sampling periods (1703 mm in 1997 vs. 2626 mm during 1929–96, Paton 1998).

Light-response curves were produced by making two measurements of NEE each under ambient light and reduced light (shade screen over chamber), and four measurements under darkness (black shade cloth over chamber) on each plot during each sampling period. The chamber was vented between each measurement. The NEE and PPFD measurements were used to develop regression relationships between PPFD and NEE, and following Ruimy *et al.* (1995), we fitted the following linear and hyperbolic equations:

$$NEE = \alpha \text{PPFD} - R \text{ (linear)}$$

$$NEE = \frac{\alpha \text{PPFD } NEE_{\max} - R}{\alpha \text{PPFD} + NEE_{\max}} \text{ (hyperbolic)}$$

where α is quantum yield (initial slope in the hyperbolic equation), NEE_{\max} is NEE maximum, and R is respiration rate, or NEE at PPFD = 0. A measurement of net ecosystem uptake (NEE_{cap}) was then derived as NEE with PPFD of 1800 $\mu\text{mol}/\text{m}^2/\text{s}$, or at saturating light. Departure from linearity (D) was calculated as r^2 hyperbolic $-r^2$ linear (Frolking *et al.* 1998).

Statistical analyses

Derived variables from these regressions (NEE_{cap} and R) were compared among the three sampling dates (late rainy season 1997, early rainy season 1998, dry season 1998) with repeated measures ANOVA. To determine if relationships existed between variables that are directly or indirectly influenced by grazing (above-ground standing crop biomass and productivity, dominance of *Ischaemum indicum*, grazing intensity; soil bulk density and pH), temperature, and

derived flux variables (NEE_{cap} , R), we conducted step-wise multiple regression. Analyses of seasonal variation were carried out by combining dates and spatial variation among plots within a season was performed on individual data sets. To avoid problems of high collinearity among variables, we combined variables that had significant correlations with $r > 0.6$ before conducting the analysis. Independent variables were allowed to stay in the model if $P < 0.10$. Variables were \ln transformed or arc-sin transformed (grazing intensity, dominance of *Ischaemum indicum*) if they were not normally distributed (Steel & Torrie 1980). We tested if productivity changed with grazing intensity (McNaughton *et al.* 1996) and if consumption increased with productivity, as predicted for native ungulates (McNaughton 1985; Frank & McNaughton 1992) and cattle in India (Pandey & Singh 1992) with regression.

To separate the direct and indirect links between grazing intensity and the derived variables R and NEE_{cap} , we used path analysis (Legendre & Legendre 1998). The first model allowed us to understand the importance of grazing intensity on soil bulk density (indirectly through compaction), above-ground biomass and productivity, and their joint influences on NEE_{cap} . The second model related these same variables to R. The path model was solved by the following set of partial regression equations: (1) $y_2 = \rho_{12}y_1$; (2) $y_3 = \rho_{13}y_1 + \rho_{23}y_2 + \rho_{43}y_4$; (3) $y_4 = \rho_{14}y_1$; (4) $y_5 = \rho_{25}y_2 + \rho_{35}y_3 + \rho_{54}y_4$; where y_1 is grazing intensity, y_2 soil bulk density, y_3 above-ground biomass, y_4 above-ground productivity, and y_5 either NEE_{cap} or R and where ' ρ ' are the associated path coefficients. These analyses were performed independently for November and May/June, resulting in four separate data sets. Soil bulk density from the May sampling was used in both data sets under the assumption that it does not vary among seasons. Variables were standardized, which reduced each set of variables to units with a mean of zero and a standard deviation of one, before analysis. Path analysis was performed using SYSTAT, version 5.2.1. All other statistical analyses were performed with SAS.

For the grazing experiment, response variables R and NEE_{cap} were analysed with a randomized block design ANOVA; with field(graze) as the error term for grazing, and sampling period (July or August) as the blocking term. Above-ground standing crop biomass and Simpson's diversity index were analysed with the same model, but without the block term. Variables were normally distributed ($P > 0.05$) and no transformations were made.

RESULTS

Chamber effects

The chamber slightly modified the environment. The cooling system successfully kept temperatures inside and outside the

chamber similar; they were not significantly different ($P = 0.43$) between inside (mean 33.02 °C, SE = 0.47) and outside (mean 32.53 °C, SE = 0.41) during any month sampled. The chamber reduced PPFD by 6%. Dew point temperature and relative humidity were not monitored during this study, but subsequent measurements on Texas grasslands have found that the cooling system keeps dew point temperatures within 5 °C of ambient. The fan in the chamber mixed air at a constant rate, and thus, there was a much less variable 'wind' inside.

Sampling study

Seasonal differences in NEE

A hyperbolic function between NEE and PPFD fits the data well for the late rainy season (November 1997) and early rainy season (May/June 1998) when data from all nine plots were combined (Fig. 1a,b). However, scatter was introduced by combining all plots, i.e. significant spatial variation was found among plots, especially at low light levels. The relationship between NEE and PPFD during the late rainy season 1997:

$$NEE = \frac{0.109(PPFD)21.787 - 9.94}{0.109(PPFD) + 21.787} \quad (1)$$

with an $r^2 = 0.78$, and departure from linearity (D) of 0.16. NEE saturated fairly rapidly with increasing PPFD, as denoted by the large departure from linearity. The relationship between NEE and PPFD during the early rainy season 1998 also followed a hyperbolic relationship:

$$NEE = \frac{0.073(PPFD)8.598 - 6.602}{0.073(PPFD) + 8.598} \quad (2)$$

with an $r^2 = 0.71$, and a D of 0.22. For the dry season, when the plants were dormant in all but one plot, there was no significant relationship between NEE and PPFD (Fig. 1c).

When NEE/PPFD regressions were analysed for each plot individually, there were significant seasonal differences in mean NEE_{cap} and R. Mean NEE_{cap} was substantially higher during late rainy season 1997 (8.46 $\mu\text{mol}/\text{m}^2/\text{s}$, SE = 1.4) than it was during the early rainy season 1998 (1.11 $\mu\text{mol}/\text{m}^2/\text{s}$, SE = 0.8) (ANOVA, $P < 0.01$). Respiration (R) also varied among dates with the largest R occurring during the late rainy season date (9.40 $\mu\text{mol}/\text{m}^2/\text{s}$, SE = 1.8) and the lowest during the February dry season date (2.38 $\mu\text{mol}/\text{m}^2/\text{s}$, SE = 1.04) (ANOVA, $P < 0.03$). The early rainy season date had intermediate rates of respiration (5.86 $\mu\text{mol}/\text{m}^2/\text{s}$, SE = 1.1).

The step-wise multiple regression also identified several significant predictors of NEE_{cap} and R. In the combined data set, which emphasizes seasonal variation because seasonal data sets are combined, NEE_{cap} was positively related to above-ground biomass ($P = 0.001$, $r^2 = 0.42$) and

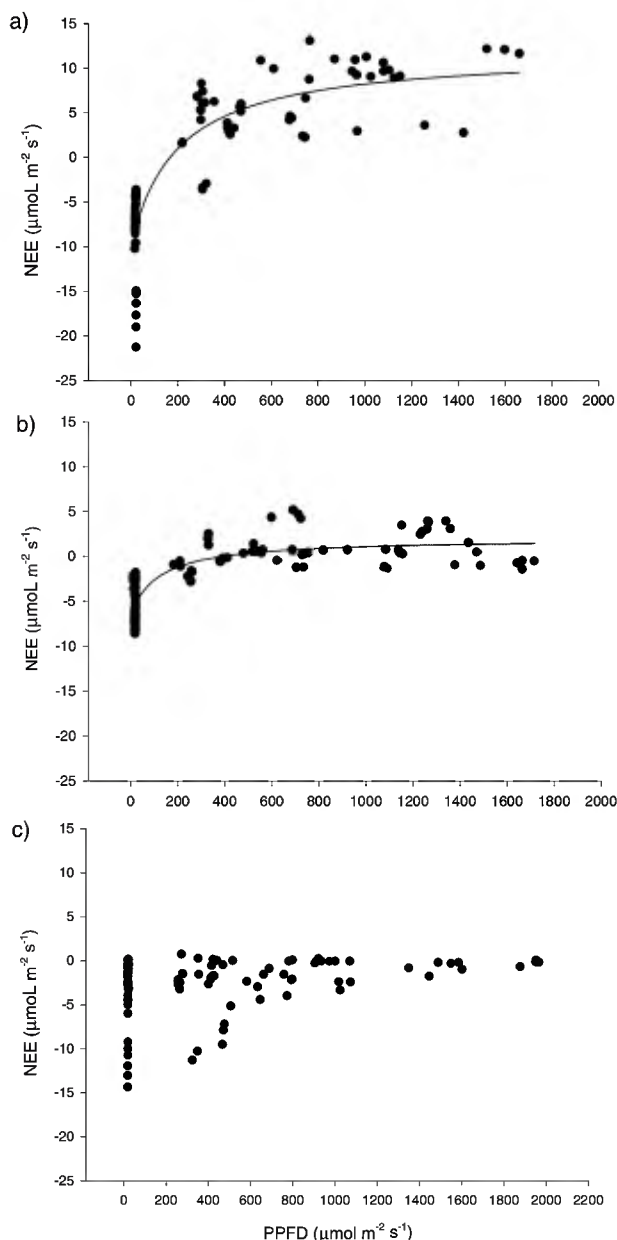


Figure 1 Net ecosystem CO_2 exchange for (a) late rainy season (November) 1997, (b) early rainy season 1998, and (c) dry season 1998 as a function of photosynthetic flux density in a pasture in Panama (all plots combined). Most of the scatter in the data is caused by spatial variation among plots rather than by measurement error.

dominance of *Ischaemum indicum* ($P = 0.011$, $r^2 = 0.38$), and (weakly) negatively related to soil bulk density ($P = 0.037$, $r^2 = 0.06$). Above-ground biomass was much higher in the late rainy season 1997 (biomass: 375 g/m^2 , $\text{SE} = 82$) compared to other dates (biomass: $89[37]$ and $96[30] \text{ g/m}^2$ during dry and early rainy season 1998, respectively). Above-

ground productivity averaged 441 g/m^2 ($\text{SE} = 84$) during the rainy season 1997, and 126 g/m^2 ($\text{SE} = 38$) during the early rainy season 1998.

Within-season spatial variation in NEE

When dates were analysed individually to address spatial variation within a season, different relationships were found. The best predictor during late rainy season 1997 (after a full canopy had developed) was above-ground biomass, which accounted for 55% of the variation in NEE_{cap} ($P = 0.009$). However, as opposed to the combined data set, NEE_{cap} actually decreased with above-ground biomass. (Above-ground biomass was also strongly negatively correlated with dominance of the short-statured *Ischaemum indicum*, so, therefore, NEE_{cap} also increased as the dominance of this grass increased.) During the early rainy season 1998, while the canopy was developing, the best predictor of NEE_{cap} was grazing intensity, which accounted for 75% of the variation ($P = 0.001$). NEE_{cap} declined as grazing intensity increased (and the canopy size decreased). Temperature was only marginally significant as a predictor ($P = 0.06$, $r^2 = 0.12$). During the dry season, when the canopy was largely dormant, there was little uptake and variation among plots (Fig. 1c), so there were no variables that were significantly related to NEE_{cap} .

Dark respiration (R) was much more consistently explained by measured variables. Above-ground biomass (and productivity), grazing intensity, and temperature were the best predictors, although much of the variation was left unexplained. In the combined data set, which emphasizes variation among seasons, respiration increased with above-ground standing crop biomass ($P = 0.003$, $r^2 = 0.26$) and temperature ($P = 0.024$, $r^2 = 0.22$). Within the late rainy season 1997, respiration increased with temperature ($b = 38.2$, $P = 0.087$, $r^2 = 0.37$) and as above-ground biomass increased ($b = 4.8$, $P = 0.087$, $r^2 = 0.26$). During the early rainy season 1998, at the beginning of canopy development, other variables were less important, and respiration decreased solely as grazing intensity increased (and biomass decreased) ($P = 0.083$, $r^2 = 0.37$).

Our path models had a high explanatory power, with 82% and 52% of the variance in R and 64% and 79% of the variance in NEE_{cap} accounted for by the model. Above-ground standing crop biomass, which is a good measure of canopy size, was explained well by grazing intensity, with biomass decreasing as grazing increased (-0.95 November, -0.23 May/June). NEE_{cap} was influenced both through influences on biomass and indirectly through changes in soil bulk density (-0.43 November, -0.71 May/June). However, influences of biomass were inconsistent between sampling dates: NEE_{cap} decreased with biomass during the late rainy season 1997 (-0.95) and increased with biomass during the early rainy season 1998 (0.34). Respiration was much more

influenced by direct changes in biomass (0.52, 0.90) than by indirect changes in soil bulk density (−0.1, −0.2). Respiration consistently decreased with increases in grazing intensity.

Relationships between grazing and above-ground productivity

Consumption increased strongly with increases in above-ground productivity during both the late rainy season 1997 ($n = 9$, $r^2 = 0.919$, $P < 0.01$) and the early rainy season 1998 ($n = 9$, $r^2 = 0.522$, $P < 0.05$), thus, the amount of biomass that entered the grazing pathway was greater in plots with high primary productivity. Consumption ranged from 0 to 12.9 g/m²/day across plots.

There was a significant increase in above-ground productivity with grazing intensity, and this relationship continued even under very high grazing intensities ($r^2 = 0.3$, Fig. 2). An average of 54% (range: 0–91) of above-ground productivity was consumed by cattle during the late rainy season 1997. Grazing intensity averaged 30% (range: 0–76) in the early dry season 1998.

Grazing experiment

Experimentally removing cattle led to a 60% increase in standing crop biomass (Fig. 3a) (1,2 d.f. $F = 373$, $P < 0.01$), and no significant (short-term) change in plant species diversity. Grazed plots had a mean biomass of 216.3 g/m², whereas ungrazed plots had 351.9 g/m². Simpson's diversity index averaged 1.30 for grazed plots and 1.59 for ungrazed (1,2 d.f., $F = 0.5$, $P = 0.54$).

Decreases in biomass caused by grazing resulted in light response curves that were fairly similar at high light levels, but that were noticeably different at low and zero light levels. Grazing significantly reduced R (1,2 d.f., $F = 18$,

$P = 0.05$) and caused smaller and nonsignificant differences in other carbon exchange parameters (Fig. 3b). The reductions in R due to grazing (70%) were roughly similar to the reductions in biomass (60%). The uptake parameter (NEE_{cap}) was not significantly different between grazed (24.1, SE = 3.7) and ungrazed (20.3, SE = 4.0) fields (NEE_{cap} : 1,2 d.f., $F = 0.47$, $P = 0.56$).

Estimates of daily CO₂ source strength

The purpose of this study was to look at relationships between NEE_{cap} , R, and grazing, but, with several assumptions, a rough estimate of daily NEE can be attempted. Based on data from 24-h cycles, we found that night-time estimates of respiration were consistently lower than respiration estimates made during the day with a black shade cloth (paired $t = -4.1$, $P < 0.05$), probably because of lower night-time temperatures. Estimates of R were 61.6% lower at night compared to during the day.

By subtracting estimated night-time respiration from day-time NEE, we obtained an estimate of daily NEE. Based on the analysis of the 24-h cycles, we used 0.616 times our day-time estimate of R for the estimate of night-time NEE. Subtracting this value from day-time measurements of NEE gave us an estimate of daily NEE (Table 1). The only season that had a positive value for daily NEE was the November 1997 estimate. NEE estimates across plots for other sampling periods indicated that the pasture was a net source for CO₂ to the atmosphere (sign convention used: + is uptake and − is loss from the ecosystem) (Table 1). A second set of estimates were made with eqns 1 and 2 using measured NEE (under ambient light) and R, and mean PPFD values (from a tower above the canopy on nearby Barro Colorado Island; Paton 1998). These are better estimates of NEE because they use actual measurements of PPFD rather than values obtained during gas exchange measurements. These estimates were consistently negative, but the standard errors were fairly high, which suggests that they are not significantly different from zero.

DISCUSSION

Studies of temperate and arctic ecosystems have found that ecosystem CO₂ uptake and respiration are functions of PPFD (Ruimy *et al.* 1995), temperature (Oechel *et al.* 1994), water table depth, and plant standing crop biomass (Bellisario *et al.* 1998; Morris 1998). The variation that we measured among seasons suggests that water availability was also important in our system. Respiration and especially C uptake were lower in the dry season, when plants were largely dormant and soils were dry (personal observation), than during the two wet seasons. Relationships between NEE and light were similar to temperate systems (Ruimy

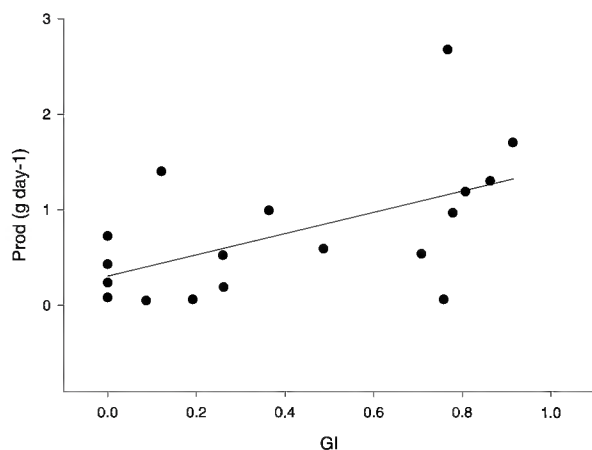


Figure 2 Relationship between above-ground productivity (ln g day^{−1}) and grazing intensity for rainy season dates ($n = 18$, $r^2 = 0.304$, $P < 0.01$).

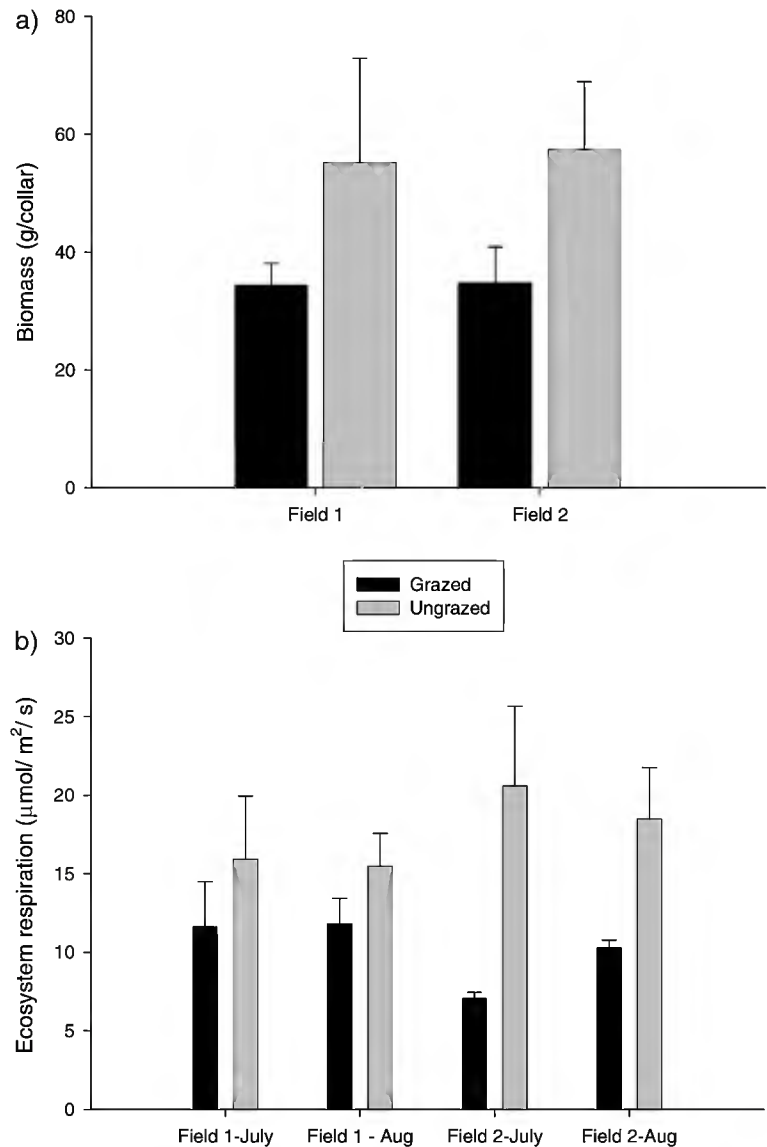


Figure 3 (a) Above-ground standing crop biomass and (b) ecosystem respiration in fields that were grazed and ungrazed after 1 year. Each bar represents the mean and one SE of three subplots per field.

et al. 1995), except that the departure from linearity tended to be higher (the relationship was more curved). This result suggests that NEE became rapidly light saturated in this tropical pasture. This was somewhat surprising since the pastures were dominated by C_4 grasses, which are expected to have a more linear relationship (Grace *et al.* 1998).

Effects of grazing

In contrast to among-season comparisons, which tend to emphasize water availability and phenological differences, within-season comparisons of NEE variables emphasized spatial variation in plant standing crop biomass and grazing. During the early rainy season, when the plant canopy was developing, NEE_{cap} was positively related to biomass, as

expected. However, during the late rainy season, when a full and partially senescent canopy was present, plots with high biomass (lightly grazed) had smaller NEE_{cap} compared to plots with lower standing crop biomass. Thus, the large canopy in lightly grazed areas was not taking up as much carbon as smaller, green canopies in the grazed areas. Leaf level studies have found that older leaves in ungrazed canopies sometimes photosynthesize at a significantly lower level than younger regrowing leaves in grazed canopies (Detling *et al.* 1979; Gold & Caldwell 1990; Wallace 1990). With R, we found that relationships with grazing were much more consistent, with respiration being negatively correlated with grazing intensity in both sampling periods. This reduction in R with grazing largely balanced the loss in uptake during the early rainy season, and added to the

Table 1 Estimates of daily net ecosystem CO₂ exchange (NEE) in a tropical pasture in Panama during the 1997 rainy season (November), the 1998 dry season (February), early in the 1998 rainy season (May and June), and the middle of the 1999 rainy season. Negative values denote movement of CO₂ from the ground surface to the atmosphere (net source)

Season	PPFD ¹ (μmol/m ² /s)	NEE ² day	NEE ³ night	NEE ⁴ total	NEE ⁵ day	NEE ⁶ total
Late Rainy	479.2	7.16 (1.3)	-5.79 (1.1)	1.37 (2.0)	5.43	-0.36
Dry	898.1	-1.98 (0.7)	-1.47 (0.6)	-3.45 (1.3)		
Early Rainy	659.7	1.11 (0.6)	-3.60 (0.7)	-2.49 (0.61)	1.23	-2.37
Mid Rainy						
July						
Grazed		4.63 (1.2)	-5.76 (1.0)	-1.13 (0.9)		
Ungrazed		5.70 (3.2)	-9.68 (1.24)	-3.98 (2.7)		
August						
Grazed		7.96 (1.0)	-6.90 (0.6)	1.07 (1.16)		
Ungrazed		8.86 (3.0)	-12.04 (1.69)	-3.17 (2.00)		
Mean		6.79 (1.1)	8.59 (0.8)	-1.80 (0.95)		

¹PPFD was measured on the top of a Lutz tower above the plant canopy on Barro Colorado Island (Paton 1998).

²Estimates of NEE during day-time based on ambient light measurements.

³Estimates of night-time NEE, based on the relationship $0.616(R)$, where R is day-time respiration (NEE at 0 PPFD) derived from light-response curves, and 0.616 is the estimated proportion of night-time respiration to day-time respiration from 24-h cycles.

⁴Estimates of NEE, subtracting night-time NEE from day-time NEE, using actual measurements under ambient light and with the assumptions of 12 h daylight and 12 h darkness, and that night-time $R = 0.616(\text{day-time } R)$.

⁵Estimates of NEE during day-time from entering in mean PPFD for the months in question into eqns 1 and 2.

⁶Estimates of NEE for the months under consideration, with the assumption of 12 h daylight and 12 h darkness, and that night-time $R = 0.616(\text{day-time } R)$.

increased uptake effect in grazed plots during the late rainy season. Thus, we found that NEE was largely dependent on the developmental state of the canopy.

The experimental removal of grazing further supported the suggestion that grazing caused a reduction in CO₂ loss by significantly lowering R with no change in NEE_{cap} . The reduction in R due to grazing was very similar to the reduction in biomass, which suggests that this effect might have been caused by lower maintenance respiration in grazed plants. Morris (1998) also found that cattle grazing caused a reduction in canopy size and ecosystem respiration in a Danish salt marsh. However, it is important to remember that NEE has soil and plant respiration components, and differences could have also been caused by changes in soil respiration. Determining the relative roles of plant and soil respiration to grazing effects remains an important area for future research (Bremer *et al.* 1998).

In Africa and North America, there is often a strong positive relationship between primary productivity and grazing intensity. This has been found through the use of temporary exclosures (e.g. McNaughton 1985; Hik & Jefferies 1990; Frank & McNaughton 1993), in field clipping studies (e.g. Wilsey 2002) and in growth chamber and greenhouse experiments (e.g. McNaughton *et al.* 1983; Wilsey 1996). This study, which is the first to look at the relationships between grazing intensity and net primary productivity in a neotropical pasture, also found a strong

positive correlation between these variables. However, this relationship was correlative: it could be that either cattle sought out productive areas, i.e. productive areas received a proportionally greater amount of grazing, or, grazing caused productivity to increase. It is unfortunate that we were not able to test this by measuring consumption in the grazing study. Nevertheless, we did not find that grazing led to a reduction in productivity as suggested earlier (Jordan 1986).

Estimating daily NEE

We estimated daily NEE using (1) direct measurements of gas exchange and PPFD, and (2) with values calculated from eqns 1 and 2 and with mean measurements of PPFD (Table 1). This second estimate was developed because NEE measurements were made on sunny days, which overestimated the PPFD available to the vegetation. Although our estimates were relatively crude and were highly variable, they were usually negative, suggesting that pastures may have been a net source of CO₂ during the periods sampled.

These estimates of NEE, however, should be interpreted with caution, as they were made on only a few weeks out of the year and were not done continuously during the sampling intervals. Furthermore, the high standard errors suggest that differences between our estimates and positive

estimates (small sink) were not significant. It is also important to note that the 1997 and 1998 sampling periods were influenced by the El Niño Southern Oscillation. The year 1997 was the driest on record (at nearby Barro Colorado Island). However, our 1997 estimates were similar to estimates made during 1999, which was a higher than average rainfall year. We also did not measure cattle respiration, and these source estimates are again underestimated when one considers that cattle were respiring at an unknown rate and were converting carbon into methane. Although cattle respiration rates are usually assumed to be minor (Schlesinger 1997), measurements are rare and need to be incorporated into grassland C cycle models in the future. The only other data set that we know of from tropical pastures is that of Grace *et al.* (1998), who found that uptake by the ecosystem exceeded release in a Brazilian pasture, with a net flux of $0.16 \text{ mol/m}^2/\text{day}$. Additional data sets, which make frequent measurements at multiple locations, are required to determine if tropical pastures are acting as a source or sink for CO_2 .

In conclusion, we found that the estimated strength of the CO_2 source from these pastures was smaller with moderate grazing by cattle. This occurred because the smaller canopies (and associated soil organisms) with grazing respired at a slower rate than did ungrazed canopies without having consistently reduced net CO_2 uptake. Thus, it appears that disturbance caused by cattle grazing will not always result in increased CO_2 release from tropical pastures.

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