Biogeosciences Discussions

Differences in plant cover and species composition of semiarid grassland communities of Central Mexico and its effects on net ecosystem exchange

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Abstract

Changes in land use across the semiarid grasslands of Northern Mexico have driven a decline of plant cover and alteration of plant species composition. A number of different plant communities have resulted from these changes, however, their implications on the carbon cycle and regional carbon balance are still poorly understood. Here, we examined the effects of plant cover loss and changes in species composition on net ecosystem CO_2 exchange (NEE) and their biotic and abiotic controls. Five typical plant community types were examined in the semiarid grassland by encasing the entire above-ground ecosystem using the geodesic dome method. Sites included an oat crop (crop), a moderately grazed grassland (moderate grazing), a 28 yr-old grazing exclosure (exclosure), an overgrazed site with low perennial grass cover (overgrazed), and an overgrazed site presenting shrub encroachment (shrub encroachment). For natural vegetation, rates of daytime NEE for sites with a high plant cover (exclosure and moderate grazing) were similar ($P > 0.05$) as compared to sites with low plant cover (overgrazed and shrub encroachment). However, night time NEE (carbon loss) was more than double ($P < 0.05$) for sites with high plant cover compared to sites with low cover, resulting into slight C sinks for the low plant cover sites and neutral or sources for the high plant cover sites on an annual basis. Differences in plant cover and its associated biomass defined the sensitivity to environmental controls. Thus, daytime NEE in low plant cover sites reached light compensation points at lower PPFD values than those from high plant cover sites. Differences in species composition did not influence NEE rates even though there were transient or permanent changes in C3 vs. C4 functional groups.

1 Introduction

Semiarid grasslands cover $\sim 17.7\%$ of global lands (Lal, 2004), with a large fraction being either overgrazed or converted to cropland (Hart, 2008). Conversion of natural grasslands to other land uses primarily causes a loss in plant cover and changes in species composition (Chapin et al., 2008), resulting in alterations of both community structure and ecosystem functions (Belsky, 1992; Noy-Meir, 1995; Houghton and Goodale, 2004), that may turn grasslands into potential sources of carbon to the atmosphere (DeFries et al., 1999).

Grazing by domestic livestock can vary in intensity and frequency, often exceeding the functional capability of grasslands to recover from overuse, leading to a number of changes including; a loss in perennial grass cover and root biomass (Medina-Roldán et al., 2008), an increase in subordinate and non-palatable species (Milchunas and Lauenroth, 1993; Aguado-Santacruz and García-Moya, 1998), and a reduction of fuel and therefore the incidence of natural fires. Collectively, these changes lead to shrub encroachment (Brown and Archer, 1999; Knapp et al., 1999).

Conversion of grasslands to crop fields on the other hand, contributes to the loss of soil organic matter and seasonal loss of plant cover (inter-cropping periods) and an enhancement of soil respiration through common tillage practices (Huggins et al., 1998; Alluvione et al., 2009). Land use change (ex. land conversion and overgrazing) contributes directly to the observed grassland patchy landscapes that result from changes in plant communities and also contributes towards large uncertainties in carbon exchange from these heterogeneous landscapes (Levy et al., 2004).

Net ecosystem exchange for CO_2 (NEE) is the sum of gross ecosystem exchange and total ecosystem respiration (Loescher et al., 2006) and is controlled by biotic (e.g. leaf area index, LAI) and abiotic factors (e.g. photosynthetic photon flux density, temperature, precipitation) (Chapin et al., 2002). These biotic and abiotic controls can influence NEE rates non-linearly and incorporate complex feedbacks that differ depending

on ecosystem type (Chapin et al., 2008; Lindroth et al., 2008) and disturbance regime (rf. Starr et al., 2012).

Current knowledge on the biotic controls on NEE contributed by the different plant communities from grassland landscapes, suggests that the overall carbon uptake capacity of landscapes may decrease as a result of reduced LAI or the substitution of key plant species by less suited ones (ex. substitution of key C_4 by C_3 species). Losses in vegetation cover may also alter the energy balance of ecosystems through an increase in albedo and associated changes in the hydrological cycle (Chapin et al., 2008; Medina-Roldan et al., 2007). Exposed bare soil contributes to carbon losses through increased soil respiration and wind and water erosion. At large spatial scales, changes in ecosystem function across a landscape can influence local and regional climate through complex biosphere-atmosphere feedback mechanisms including; (i) emission of greenhouse gases, (ii) modifications in energy budgets related to alterations in latent and sensible heat fluxes, (iii) changes in emitted long-wave radiation, (iv) changes in aerosol emissions, and (v) changes in surface roughness (Chapin et al., 2008).

In the southernmost part of the grassland biome in Mexico, the geographic sub-province Llanos de Ojuelos, overgrazing, natural fire suppression and conversion to rainfed agriculture have contributed to conform a patchy grassland landscape in 70 % of its 12 000 km^2 (Huber-Sannwald, 2002; Velázquez et al., 2002). Reported ranges of natural plant cover in these grasslands varied from a maximum of 35–38 % to a low of ~ 5 % (Aguado-Santacruz and García-Moya, 1998), with equivalent aboveground biomass accumulation variability ranging from 1500 to 180 kg ha^{-1}, respectively. Because overgrazing causes the key native species *Bouteloua gracilis*, to be replaced by subordinate grass species, the capacity of soil water recharge is reduced (Medina-Roldán et al., 2007). Overgrazing has also been shown to result in a 20 % loss in soil organic carbon content due to 25 % loss in plant cover (Medina-Roldán et al., 2008). Also, the replacement of *Bouteloua gracilis* by perennial shrubs (e.g. *Isocoma veneta*) and non-native herbs (e.g. *Asphodelus fistulosus*), contribute to decreased plant productivity (Aguado-Santacruz and García-Moya, 1998; Medina-Roldán et al., 2007). Changes

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in species composition on the other hand, could also potentially enhance carbon uptake with the establishment of perennial woody species that may display higher annual carbon uptake rates (Scott et al., 2006). These studies suggest complex interactions among community composition, community structure, hydrological processes, and regional carbon dynamics, all related to landscape patch composition.

For the patchy semiarid grassland landscapes of Llanos de Ojuelos, we hypothesized that reductions in plant cover will cause an overall decline in net carbon uptake as a result of less perennial vegetation and lower production of LAI and aboveground biomass (H_1). To examine the influence of environmental controls on NEE for each land-use type, we hypothesize that a decreased plant cover (and related reduction of aboveground biomass) will increase the sensitivity of key ecosystem processes governing productivity (i.e. photosynthesis and respiration) to environmental factors; air temperature (T_a), photosynthetic photon flux density (PPFD) and soil water content (SWC). Therefore, NEE should reach maximum rates faster and sooner at sites with low plant cover relative to sites with high plant cover (H_2). Finally, we hypothesize that NEE rates will not differ among plant communities with similar amounts of plant cover but distinctive species composition (H_3). To test these hypotheses, NEE fluxes of the most common plant communities found in a patchy landscape of semiarid grassland were examined in responses to site-specific biotic (LAI) and abiotic (T_a, PPFD, and SWC) controls.

2 Materials and methods

2.1 Site description

The semiarid grasslands in Mexico (North American graminetum, Aguado-Santacruz and García-Moya, 1998) belong to the shortgrass steppe ecosystem extending from the North American Midwest in the North to the sub-province Llanos de Ojuelos, in Northeast Jalisco in the South. This landscape follows a narrow strip along the

Sierra Madre Occidental within the Chihuahua Desert. The vegetation is dominated by grasses, with *Bouteloua gracilis* H.B.K. Lag ex Steud. (blue grama) forming near mono-specific stands. Native grasslands are one of the most threatened ecosystems in Mexico, because intensive grazing by domestic livestock and land conversion to rainfed
agriculture (Velázquez et al., 2002; Rzedowski, 2006) have created a patchy landscape that exhibits large diversity in plant cover and species composition (Riojas-Lopez and Mellink, 2005). This region has a semiarid climate with mean annual precipitation of 424 mm (last 30 yr) distributed mainly between June and September, followed by 6 to 9 dry months. Winter rains account for only < 5 % of total annual precipitation (García,
2003). Mean annual temperatures are $17.5 \pm 0.5\,°C$ (m, ±1 SE), with mean monthly temperatures ranging between $1.6\,°C$ for the coldest and $> 18.0\,°C$ for the warmest months (dataset from Sitio Experimental Vaquerias, INIFAP). The topography is characterized by valleys and gentle rolling hills. The two dominant soils are haplic xerosols (associated with lithosols and eutric planosols), and haplic phaeozems (associated with
lithosols) (Aguado, 1993). Soils are silty clay and sandy loams, shallow with average depth ranging between 0.3 to 0.5 m with a cemented layer of tepetate (Aguado, 1993; COTECOCA, 1979).

We selected the five most common and contrasting plant communities that have resulted from grazing and agriculture disturbance. All sites had similar soil type, topography and landscape position (Fig. 1). The plant cover was classified as either high (maximum reported for the region 35–38 % of soil covered by vegetation; Table 1, Aguado-Santacruz and García-Moya, 1998), or low plant cover (< 8 % of ground covered by vegetation; Table 1). Sites also represented two conditions in terms of species composition; one in which the key native species, *B. gracilis*, was still dominant (independent of plant cover), while the other presented either subordinate grasses, subshrubs or exotic species as the dominant species. The five site types examined were; (i) a moderate grazing site that was a recovered grassland (∼ 60-yr) to tillage and overgrazing, currently under moderate grazing and prescribed burning (4-yr previous to the study). Even though this site has high plant cover, the native grass species *B. gracilis* has been

largely replaced by subordinate native grass species (30–40 % of total abundance) including; *Muhlenbergia rigida* (Kunth) Trin., *B. scorpioides* Lag., *B. hirsuta* Lag., *Aristida* spp.; (ii) the exclosure site is a 30 yr-old cattle exclosure characterized by a high plant cover dominated by *B. gracilis* (> 80 % abundance); (iii) the overgrazing site (Table 1) had a low plant cover (< 8 %) with *B. gracilis* as the most abundant species; (iv) the shrub encroachment site is also an overgrazed site with low plant cover (< 8 %) having co-dominance with a native shrub *Isocoma veneta* (Kunth) Greene and an exotic Mediterranean perennial herb *Asphodelus fistulosus* L.; and (v) the crop site, a short-grass steppe field converted to rainfed agriculture to produce oat (*Avena sativa* L), that is covering the soil for around 4 months during summer. Biomass removal from grazing or additions from dung were not quantified. Site characteristics can be found in Table 1.

2.2   Measurement of NEE

A large static chamber method (Arnone and Obrist, 2003) was used to directly and non-destructively quantify NEE from these five study sites. The chamber had a 4.2 m base diameter (Shelter Systems Inc., Menlo Park CA, USA) with an internal volume of 16.4 m^3 covering a ground area of 12.25 m^2. When measurements were made, this chamber was sealed to permanent iron bases that were knifed 3 cm into the ground. Iron bases were installed and allowed to equilibrate with the ground for 2 months prior to the beginning of this study. Iron bases protruded an additional 3 cm above the ground for attachment purposes, defining the area of measurement. At each of the 5 sites, six plots (replicates) were randomly established for a total of 30 plots used in this study. Prior to each measurement, two air fans were positioned ~ 0.5 m a.g.l. on opposite sides of the plot to mix air inside the dome (model 3306, Mytek International Inc., Bonita CA). One fan was oriented horizontally, while the other was vertically oriented, both had a flow rate of 54.3 m^3 h^{-1} CO_2 and H_2O concentrations and atmospheric pressure inside the dome were measured using an open-path infrared CO_2/H_2O gas analyzer (IRGA; Li-7500, Li-Cor Inc., Lincoln NE) located in the center of the plot and also mounted 0.5 m a.g.l.

Even though there are several methods that can be used to measure NEE (Livingston and Hutchinson, 1995), this chamber incorporates enough area to measure both the representative plant communities and their physical structure allowing us to directly and consistently measure NEE from these five plant communities with minimal disturbance. Moreover, this approach has been shown to estimate similar fluxes as those obtained through the eddy-covariance method (Wohlfahrt et al., 2008), validating this methodology.

Meteorological sensors were used inside and outside the chamber during each measurement; PPFD, (PARLITE, Kipp and Zonen, Delft, Holland), T_a, (PRT type, RTD-810, Omega Engineering Inc., Stamford CT) with a linearizer (OM5-IP4-N100-C, Omega Engineering Inc., Stamford CT), and SWC (Mini Trase, SoilMoisture Equipment Corp., Santa Barbara CA). Data from all sensors were acquired with a datalogger (CR1000, Campbell Scientific Inc. Logan, UT, USA) at a frequency of 1 Hz, providing the temporal resolution to record the rate of change in CO_2 concentration. These meteorological measurements were used to determine functional relationships between NEE and abiotic environment, and to examine for potential chamber effects.

At each site, NEE measurements were made monthly from October 2008 to September 2009. Each monthly measurement included 4 sampling periods throughout the day: at 08:00, 12:00, 16:00 and 20:00 solar time, allowing us to determine diurnal NEE time series. Because of the length of each sampling period, the distance between sites, and the need for one full day sampling a single site – each monthly campaign consisted of five consecutive days of measurements. The duration for each chamber on the iron base, defining the sampling period was $\sim$ 120 s during daytime and $\sim$ 180 s during night time. Data were recorded immediately after the geodesic dome was sealed to the iron base, data for NEE calculations however, were only used after the first 20 s, i.e. once a constant rate of $[CO_2]$ change inside the dome was observed. Beginning on March 2009, parallel and following daytime measurements, the chamber was covered with a dark "coat" to block light (PPFD was dropped to $< 30 \, \mu mol \, photons \, m^2 \, s^{-1}$). In

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this way, it was possible to measure ecosystem respiration (Re) on a wider range of temperatures.

Calculations of chamber NEE are based on the rate of change of $[CO_2]$ for day and night conditions. The dry mole fraction of CO_2 (C') from the IRGA was estimated by,

$$C' = \frac{C}{1 - \dfrac{W}{10^3\,\mu mol}} \tag{1}$$

where, C and W refer to the measured mole fraction of CO_2 ($\mu mol\,mol^{-1}$) and H_2O ($mmol\,mol^{-1}$), respectively. Then, the measured CO_2 was scaled to the chamber ground area, and the rate of concentration change to estimate NEE according to,

$$NEE = -\frac{V\overline{P}\left(1000 - \overline{W}\right)}{RS\left(\overline{T_a} + 273.15\right)} \cdot \frac{\partial C'}{\partial t} \tag{2}$$

where, NEE refers to the CO_2 flux ($mol\,m^{-2}\,s^{-1}$), V is the chamber volume (m^3), P is the average chamber pressure (kPa), R is the ideal gas constant ($8.314\,J\,mol^{-1}\,K^{-1}$), S is the surface area covered by the chamber (m^2), the analytic solution for $\partial C'/\partial t$ is the slope of least square linear regression of C' for each measurement period per plot and time of day, and the overbar is the time average during the measurement period, i.e. either 100 or 160 s of constant rate of $[CO_2]$ change (Jasoni et al., 2005). Here, we use the micrometeorological convention where negative values indicate uptake of carbon by the ecosystem.

Linear and non linear models were fitted to describe the relationship between NEE and biotic and abiotic drivers. Daytime and nighttime NEE were analyzed separately because they differ in their controls and the way they were influenced.

The functional relationship of daytime NEE fluxes to PPFD was estimated by fitting a rectangular hyperbola function (Ruimy et al., 1995),

$$NEE_{daytime} = \frac{\alpha \cdot PPFD \cdot A_{max}}{\alpha \cdot PPFD + A_{max}} + R_d \qquad (3)$$

where, α is the apparent quantum yield ($\mu mol\, CO_2\, m^{-2}\, s^{-1}\, \mu mol^{-1}$ photons), PPFD ($\mu mol\, photons\, m^{-2}\, s^{-1}$), A_{max} is maximum assimilation rate at light saturation conditions ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$), and R_d represents daytime respiration ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$). Equation (3) is typically calculated assuming infinite PPFD values, which often returns unrealistic values of A_{max}. Hence, we also estimated Eq. (3) by constraining the maximum PPFD value to $2000\, \mu mol\, m^2\, s^{-1}$ to estimate a new, more realistic A_{max} value = A_{2000}.

For the period from March to May, an exponential function was used to describe the relationship between $NEE_{daytime}$ and air temperatures. In this period, since vegetation was senescent there was not active grass leaves (LAI ~ 0) in all sites, thus no C acquisition at daytime occurred and therefore NEE did not respond to PPFD but only to temperature since the predominant flux corresponded to R_e.

$$NEE_{daytime} = r_0 \cdot exp(k_T \cdot T_a) \qquad (4a)$$

$$Q_{10} = exp(10 * k_T) \qquad (4b)$$

where, r_0 and k_T are empirical coefficients; r_0 is the ecosystem respiration rate at $T_a = 0$ ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$), and k_T is the coefficient of temperature response ($^{\circ}C^{-1}$). Equation (4b) is a Q_{10} approach (the increase in respiration rate with a $10\,^{\circ}C$ increase in T_a) to estimate the $NEE_{daytime}$ response to temperature.

Two linear, first-order regressions were used to determine the effect of SWC and LAI on $NEE_{daytime}$, such that,

$$NEE_{daytime} = y_0 + a * SWC \qquad (5a)$$

$$NEE_{daytime} = y_1 + b * LAI \qquad (5b)$$

where, y_i, (i = 0, 1, or 2) are statistical y-axis intercepts, and a, b are empirical coefficients, whereas; NEE$_{nighttime}$, SWC and T_a were fitted to an exponential-power function,

$$NEE_{nighttime} = a e^{(b*T_a)} * SWC^c \qquad (6)$$

where, a, b, and c are empirical coefficients, T_a is air temperature, and SWC is soil water content.

2.3 Calculation of daily NEE

Daytime CO$_2$ fluxes: to calculate the continuous fluxes for each daylight measurement period (hereafter integrated daytime NEE), the rectangular hyperbolic model (Eq. 3) for each site/month under the diurnal cycle was applied. Continuous PPFD data for each month were estimated online in the "clear sky calculator" for quantum sensors website (http://clearskycalculator.com/quantumsensor.htm). Same latitude (21.7° N) and longitude (−101.6°), relative humidity (30 %), and altitude (2200 m a.s.l.) were assumed in the model for the five sites. As the model calculates PPFD at ideal clear sky conditions, daytime NEE was also calculated as ideal NEE rates with no clouds for each site.

Nighttime CO$_2$ fluxes: integrated NEE at night was calculated by the exponential-power model (Eq. 7). NEE data of both the 20:00 to 23:00 sampling periods and daytime on dark conditions were used to model the cycle of NEE at night. Continuous air temperature data (as an average per month) was obtained from a weather station near Moderate grazing site, while for soil water content we used averages measured at each site and time. Modeling nighttime NEE was carried out only for nighttime hours (no daylight, PPFD = 0).

Annual NEE rates were calculated as follows: (i) integrating NEE$_{daytime}$ under the diurnal cycle(NEE$_{daytime}$ in response to PPFD), (ii) integrating NEE$_{nighttime}$ for nighttime cycles (NEE$_{nighttime}$ in response to Ta and SWC), (iii) adding NEE$_{nighttime}$ to NEE$_{daytime}$ to estimate monthly NEE rate (g C m^{-2} d^{-1}), and (iv) averaging monthly balances to

estimate an annual NEE rate. Additionally, annual cumulative NEE was also calculated by integrating the monthly daily NEE rate (NEE$_{daytime}$ – NEE$_{nighttime}$) over each respective month, and adding afterwards monthly totals together for an annual NEE estimate. NEE rates and climate was assumed to be representative for the entire month with this approach.

For each site and sampling period, plant cover, aboveground biomass and LAI were estimated with six $0.25\,m^2$ quadrants, positioned next to- and outside the chamber bases. The only exception was at the shrub encroachment site where the size of the quadrant was increased to $1\,m^2$ to include all vegetation and structural elements. Live aboveground biomass was completely removed from the quadrants and stored in sealed plastic bags containing humidity pads to maintain the leaves at saturated condition until analysis. Collected live leaves where passed through a leaf area meter (Li-3000C, Li-Cor Inc., Lincoln NE) to estimate LAI.

2.4 Statistical analyses

All NEE data were normally distributed on a diurnal time series. Classification variables included site (exclosure, moderate grazing, overgrazing, shrub encroachment, crop). A one-way ANOVA was used to compare integrated daytime and nighttime NEE means among sites ($n = 10$, sites = 5, $\alpha = 0.05$). Analyses were run separated into daytime and nighttime fluxes (NEE$_{daytime}$, and NEE$_{nighttime}$), because both fluxes were subjected to different environmental drivers. The bootstrapping method (Efron and Tibshirani, 1993) was used to estimate the 95 % bias corrected confidence intervals of integrated daytime and nighttime NEE. Resamplings of observed PPFD × NEE, and Ta × SWC × NEE dataset (of equal size to the observed dataset) for each site/month were constructed by randomly sampling with replacement from the original dataset. A new light response curve (Eq. 3) was fitted, and then NEE was integrated for each resampled dataset. This was done with 2000 iterations to obtain 2000 integrated NEE values, from which a mean and confidence interval (95 %) of NEE were computed.

The same method was used to calculated means and confidence intervals of nighttime NEE, but using Eq. (7) as the regression model for each bootstrapped resampling.

For bootstrapping, PPFD and Ta used in regressions were modeled data, while SWC was measured data. This allows us to homogenize environmental conditions (PPFD and Ta) which were independent of the characteristics of plant communities, however SWC was maintained as a site-specific variable, because we assumed that the effects were dependent on plant cover, root systems, and soil characteristics.

Confidence intervals (C. I., 95 %) were used to compare the integrated daytime and nighttime NEE by month, examining C.I. overlapping among adjusted $NEE_{daytime}$, and $NEE_{nighttime}$ curves of the five sites. These C. I. were also used as an estimation of uncertainty which was propagated according to the law of propagation of uncertainty (ISO, 2008) for cumulative NEE. In this case, an uncertainty coverage of 95 % was assumed.

Relationships between the response variable (NEE) and environmental factors (PPFD, T_{av}, SWC, and LAI) were examined with linear and non-linear regression analysis. To determine the amount of variability in $NEE_{daytime}$ and $NEE_{nighttime}$ explained by seasonal abiotic drivers, daily fluxes (integrated $NEE_{daytime}$ and $NEE_{nighttime}$) were used as dependent variable. All regressions, ANOVA, and bootstrapping analyses were performed using SAS 8.0 for windows (SAS Institute Inc., Cary, NC. USA).

3   Results

3.1   Abiotic environment

Annual cumulative precipitation during the study period was representative of the past 30-yr regional average (Fig. 2a), with $\sim 442\,mm\,yr^{-1}$ recorded in both 2008 and 2009. For the long term average, July had the highest monthly precipitation amounts annually, however 2008 and 2009 deviated from this overall pattern. For 2008, August received $\sim 230\,mm$, which was twice as much as the long term average for that month,

and represented 52 % of the total annual precipitation. For 2009, September received ~ 206 mm; the wettest month of this year, representing 47 % of the total annual precipitation (Fig. 2a).

Average PPFD values among sites were recorded with larger divergences among sites during the rainy season as a consequence of cloud scattering (Fig. 2b). Winter and spring (November to May) had the lowest SWC (< 9 %) for all sites coinciding with the long term trends in precipitation (Fig. 2c). In the wet months, the exclosure site had the highest SWC in October 2008, and July and August 2009 (19.0 ± 0.66 %, 29.3 ± 1.07 %, and 35.9 ± 0.66 %, respectively; Fig. 2c), followed by moderate grazing site (16.28 ± 0.66 %, and 26.3 ± 0.66 % for October 2008 and June 2009, respectively). The overgrazed, shrub encroachment and crop sites had the overall lowest SWC (10–15 %) suggesting limitations to recharge and retain soil water after rain events. Peaks of 30 °C of T_a inside the chambers were recorded from February to May (Fig. 2d).

3.2 LAI dynamics

Seasonal changes in LAI were recorded at all sites, with maximum values occurring between June and October (Fig. 2e). Differences in LAI were observed among sites. Thus, the two sites with the highest plant cover, the exclosure and moderate grazing sites also had significantly higher LAI during maximum leaf-out than found at overgrazed and shrub encroachment sites ($P < 0.05$, Fig. 2e). Although their overall phenological development coincided both in time and in magnitude, LAI in the moderate grazing site was 0.15 m^2 m^{-2} larger than LAI in the exclosure site (Fig. 2e). Equally, the shrub encroachment and overgrazed sites maximum LAI $= 0.23 \pm 0.008$ m^2 m^{-2}, were 80, 75 and 65 % less than those recorded for the crop, moderate grazing and exclosure sites, respectively. In contrast, the crop site had the highest LAI of 0.94 ± 0.23 and 1.24 ± 0.30, for August and September, respectively. Because the crop site underwent tillage, seeding, and harvest following typical agronomic management practices, its LAI was close to zero during fallow months from November to May.

3.3 Net ecosystem CO$_2$ exchange

Overall, no significant differences in daytime flux were detected with ANOVA among the ten months ($p > 0.05$, Figs. 3a and 4, Table 2). Still, negative fluxes (carbon uptake) were recorded for most sites during the growing season (October–November 2008,
5 and June–September 2009, Fig. 3a), while neutral or positive NEE (carbon release) was observed during the drought period (December to May). The crop was the only site showing positive NEE flux for November, when exhibited no plant cover. Still, in July the crop cover showed a positive C flux, but in August it changed to the largest NEE$_{\text{daytime}}$ capture (6.08, asymmetric s.e. +4.82, −0.94, g C m^{-2} d^{-1}) coinciding with
10 maximum leaf out and grain-filling stages. These fluxes were 2× larger compare to grassland sites with highest plant cover. In both the exclosure and the moderate grazing sites, NEE$_{\text{daytime}}$ was negative in six of ten recorded months. Sites with lowest plant cover (overgrazing and shrub encroachment) showed three months lower C uptake than those found from the other sites.
15   Maximum NEE$_{\text{nighttime}}$ was observed in the growing season and was almost zero during the dry season. However, NEE$_{\text{nighttime}}$ rates from overgrazed and shrub encroachment sites were much lower than fluxes from moderate grazing and exclosure sites, particularly during the wet months. NEE$_{\text{nighttime}}$ fluxes in the overgrazed site were the smallest throughout the year (< 0.45 g C m^{-2} d^{-1}), resulting in significant lower annual
20 instantaneous NEE$_{\text{nighttime}}$ rates at the end of ten months ($P < 0.05$, Figs. 3b and 4, Table 2). Whereas NEE$_{\text{nighttime}}$ fluxes in exclosure and moderate grazing sites were more than double than sites with low plant cover. The Oat crop site maintained intermediate NEE$_{\text{nighttime}}$ rates that were significantly higher than the overgrazed site fluxes.
    We estimated annual rates of productivity, however, data for both December and April
25 were not included due to sampling logistic problems. Day and nighttime NEE rates were > -0.34 and < 0.43 g C m^{-2} d^{-1}, respectively, for winter months (November to March), with net diurnal rates around 0 µmol m^{-2} s^{-1}. Based on the similar conditions,

we assumed that monthly NEE rates for the two missing months were also carbon neutral.

Interpreting the annual average of CO_2 fluxes ($\overline{NEE_{daytime}} + \overline{NEE_{nighttime}}$, overbar denotes annual average) for the crop, overgrazed, and shrub encroachment sites, the C balance suggest that these sites functioned as carbon sinks (net CO_2 uptake of 0.47, 0.26 and 0.08 $g\,C\,m^{-2}\,d^{-1}$, respectively, Fig. 4a, b, or 145, 77, and 25 $g\,C\,m^{-2}\,yr^{-1}$, respectively, Fig. 4a, b). In contrast, the exclosure behaved as a source (net CO_2 loss of 0.085 $g\,C\,m^{-2}\,d^{-1}$, or 25 $g\,C\,m^{-2}\,yr^{-1}$, Fig. 4a, b) whereas the moderate grazing site was carbon neutral (0.003 $\mu mol\,m^{-2}\,s^{-1}$, or 0.26 $g\,C\,m^{-2}\,yr^{-1}$, Fig. 4a, b).

3.4 Daily and seasonal drivers of CO_2 fluxes

Both abiotic and biotic controls on NEE changed across seasons and phenological stages. Thus, there were five dominant patterns that emerged from this study, including: (i) PPFD control of CO_2 uptake acting on a daily timescale, (ii) T_a also controlled R_e on a daily bases, (iii) SWC and LAI exerted seasonal control on uptake and efflux, strongly suggesting the phenological feedback between leaf activity and SWC as main controls of the annual C balance in this biome, (iv) legacy effects impacting on the carbon balance (i.e. exclosure, agriculture), and (v) rates of uptake and efflux were highest at the more intensely managed site (i.e. crop), were the time of crop cover dictates the annual carbon balance.

For all sites, PPFD was the main factor explaining $NEE_{daytime}$ at daily timescales, with plant communities displaying two principal responses; (i) $NEE_{daytime}$ reached an asymptote with PPFD saturation, and (ii) $NEE_{daytime}$ responding almost linearly to increases in PPFD. For instance, in October 2008, the $NEE_{daytime}$ light response of exclosure and moderate grazing sites was linear and increased well beyond PPFD values of 1000 $\mu mol\,m^2\,s^{-1}$ (Fig. 5a), whereas for June and July 2009, $NEE_{daytime}$ light response curves were hyperbolic (Fig. 5c, d). In general, sites with higher plant cover reached $NEE_{daytime}$ saturation at higher PPFD than those with lower plant cover (Fig. 5a, c, d, e).

For all sites except the crop, T_a, was a better predictor for NEE$_{daytime}$ fluxes during the dry season (March to May, Eq. 5, Figs. 6a, b) compared to the wet season, where no T_a relationship was detected. In general, sites showed relatively small changes in NEE$_{daytime}$ in responses to increases in T_a (k_T coefficients from exponential function <

5 0.1) when $T_a < 30$°C but NEE$_{daytime}$ rates increased above this temperature threshold. In particular, the shrub encroachment site stood out from the other sites with the highest k_T (> 0.14) during the three dry months (Fig. 6). This result was further supported by Q_{10} values for the same site, of 4.2, 4.3 and 4.4 for February, March and May, respectively (no crop present), compared to Q_{10} rates of 2.5 observed from the other

10 sites (data not shown). With more plant cover, NEE$_{daytime}$ rates increased with higher T_a, with no significant difference ($p > 0.05$) due to species composition.

Over the course of the year, the main abiotic control on NEE$_{daytime}$ was SWC and LAI, explaining > 47% and > 67% of NEE$_{daytime}$ variation, respectively (Eq. 5a, b, Table 3). Sites of contrasting plant cover differed respect to what was the main

15 NEE$_{daytime}$ driver. Thus, while both SWC and LAI explained > 56% (linear relationship) of NEE$_{daytime}$ variation in sites with good cover, the overgrazed and crop sites in contrast showed only a relationship to LAI, but through a quadratic and linear relationship, respectively. On the other hand, seasonal NEE$_{daytime}$ variation in shrub encroachment site was explained by SWC, whereas, the crop, NEE was better explained

20 by LAI (Eq. 5, Table 3). Although data did not allow to perform an homogeneity of slopes test, moderate grazing site showed almost doubled the assimilation rate per unit water stored in soil ($0.1 \pm 0.02 \, \mathrm{g\,C\,m^{-2}\,d^{-1}\,\%\,SWC^{-1}}$) than exclosure and shrub encroachment sites (0.0636 ± 0.017, and $0.062 \pm 0.025 \, \mathrm{g\,C\,m^{-2}\,d^{-1}\,\%\,SWC^{-1}}$, respectively). Overall, NEE$_{nighttime}$ was controlled by SWC and Ta, but in this case it was fitted

25 to an exponential-power model (Eq. 6) that explained > 44% of its variation (Table 3). Although, temperature was a main driver for daily NEE$_{nighttime}$, its relationship was seasonally modified by SWC.

Sites were also grouped regarding the proportion of plant cover by empirical parameters of the exponential part of Eq. (6). Thus, sites with low plant cover showed smaller *a* parameter than high cover sites, but in contrast they showed bigger *b* parameters. This values for *a* and *b* indicates that low plant cover sites produced the smallest nighttime fluxes at the end of the ten months in the annual balance.

3.5 Differences due to species composition

We did not measure productivity from individual species within a site. Instead, we assumed that the suite of plant species at a particular site acted collectively for an integrated ecosystem response. However, because we showed that plant cover (amount and phenology) is a key control on productivity, we tested for any species control (H_3) using sites with similar plant cover but differing in species composition. One group included the exclosure and the moderate grazing sites, in which the key species *B. gracilis* for the last site has been replaced by other subordinate native grasses. The second group (i.e. low plant cover) included overgrazed and shrub encroachment sites in which subordinate grasses, subshrubs or non-native grasses and herbs were also abundant. Comparison of shrub encroachment and overgrazed sites revealed no differences in $NEE_{daytime}$, neither there were differences in $NEE_{nighttime}$ ($P > 0.05$, Fig. 4). Similar patterns for $NEE_{daytime}$ and $NEE_{nighttime}$ were estimated between the two high plant cover sites. Thus, there was no clear effect of vegetation species composition on fluxes.

4 Discussion

4.1 Effects of plant cover on NEE

In this study, differences in plant cover from different sites arising from historic changes in land use showed no contrasting rates of NEE. Testing H_1 (reductions in plant cover will cause a decline in net carbon uptake), sites with high plant cover (moderate grazing,

exclosure) did not show larger rates for carbon uptake ($NEE_{daytime}$ Figs. 3, 4) than sites with less plant cover (overgrazed and shrub encroachment). Moderate grazing and exclosure also had proportionally larger biomass and consequently greater ecosystem respiration rates e.g. maintenance costs, than the low plant cover sites. For instance, the larger proportion of R_e observed for the exclosure and moderate grazing sites relative to daytime uptake was the main factor contributing to the exclosure having a net positive annual carbon balance (net loss of CO_2, $R_e > NEE_{daytime}$, Fig. 4). In contrast, the overgrazed and shrub encroachment sites displayed a relatively smaller $NEE_{daytime}$, but an even smaller relative R_e rates making these sites net carbon sinks ($R_e \ll NEE_{daytime}$, Fig. 4). Even though both the overgrazed and shrub encroachment sites had 20 % less plant cover and $< 1/2$ LAI than the moderate grazing and exclosure sites, they displayed similar or even increased annual net carbon uptake rates, thus rejecting H_1.

In these systems, there are several respiring pools (above and below-ground biomass, deposited litter, and soil microbial biomass) that contributed collectively to R_e. Here, we estimated the largest R_e fluxes in the exclosure and moderate grazing sites (Fig. 4), and both also exhibited the largest year-round LAI. If we assume below-ground mass similar to that found aboveground, there would be 2- to 10-fold greater root biomass of these two sites compared to the sites with low plant cover, and this could account for the observed 3 to 5× higher R_e rates. Support for this statement comes from the study by Medina-Roldán et al. (2007) that reported in the same region, 2 to 4× more root biomass in well preserved grasslands, compared to more open and degraded ones, along a long-term grazing gradient.

Examination of disturbance frequency in the high plant cover sites offer interesting insights in terms of mechanisms affecting R_e rates. Both sites exhibited more than 30 % basal plant cover, differentiated by the dominance of *B. gracilis* in the exclosure site (28-yr of protection from the natural disturbances of grazing and fire) in comparison to a mixed species dominance in the moderate grazing site. Moderate grazing site on the other hand is maintained under a grazing and fire management scheme still

allowing aboveground biomass recovery but at a lower extent than in the exclosure site. Thus both high cover sites exhibited a large accumulation of standing litter, which in turn, affect both processes of dead (increased respiration) and alive (decreased photosynthesis) above-ground biomass resulting in overall reduced uptake rates. Thus,
it is likely that microbial standing litter decomposition was one mechanism contributing to R_e. Yet, recent studies also show that photochemical induced CO_2 efflux (by UV radiation) could also trigger higher R_e rates (Brandt et al., 2009) with photodegradation of standing litter as another decompositional pathway in arid environments (Vivanco and Austin, 2006; Martínez-Yrízar et al., 2007; Parton et al., 2007; Henry et al., 2008).
Our data strongly suggests that standing litter attenuates the radiative transfer. Evidence for this included: positive NEE fluxes at the late afternoon (data not presented), lower daytime NEE rates at similar PPFD (Fig. 5), and the high light compensation point of high plant cover sites compared to other sites (e.g. overgrazing, Fig. 5a). In the case of the exclosure (the site with the most death standing litter), our analyses
support the contention that large accumulated litter in grasslands can cause; (i) additional limitations of PPFD to emergent shoots (up to 58 % less PPFD. Fig. 2b), (ii) a decreased uptake (up to 32 %) through a reduction of photosynthetic capacity due to modifications in leaf traits (reductions in leaf thickness, specific leaf mass, stomatal density and conductance), and (iii) modifications to the nitrogen cycling (Knapp and
Seastedt, 1986). If these sites could recover its natural fire cycles, we could expect not only the large pulse of carbon during fire, but also uptake rates and overall carbon balance to increase as well.

4.2 NEE sensitivity to environmental controls as a function of plant cover

To test H_2, we examined threshold conditions including; light compensation points
(LCP), maximum rates of photosynthesis change to increased PPFD, and maximum rates of respiration change to SWC, and T_a. Sites with low plant cover and low LAI showed greater sensitivity to increases in PPFD in support of H_2. According to this pattern, sites with low plant cover had generally smaller LCPs (from 60 to

348 µmol m^{-2} s^{-1}) compared to sites with high plant cover (151 to 485 µmol m^{-2} s^{-1}, Table S1, Supplement). Equally, sites with low plant cover had A_{max} values at lower PPFD than sites with high plant cover (Fig. 5). Overall, sites with low plant cover (and low LAI) are characterized by small plant patches with large open ground interspaces
5 and low stature canopies, all vegetation characteristics that contribute to large canopy radiative transfer and minimum light attenuation (low extinction coefficients), enhancing vegetation sensitivity to lower radiation levels. Therefore, vegetation responses such as light compensation point and light saturation NEE are reached sooner compared to communities with high plant cover. This is also supported by the observed greater
10 efficiency of a unit LAI in the net carbon uptake rates resulted in 2× as large when compared to the high plant cover sites (6.75 µmol m^{-2} s^{-1}, for both overgrazed, and shrub encroachment, and 3.39 and 2.4 µmol m^{-2} s^{-1} for exclosure and moderate grazed, respectively, calculated as the first derivative of a quadratic equation at maximum observed LAI). Although other studies have reported increases in canopy photosynthesis
15 following a growth in LAI (Lai et al., 2002), the efficiency of LAI for carbon uptake would decrease as a function of leaf self-shading and increases in leaf respiration (Lai et al., 2002).

When examining NEE as a function of SWC during the daytime, we only found partial support for H$_2$ (Fig. 7). Thus, moderate grazing site displayed the largest rate of change
20 (uptake) per unit % SWC from all the sites, whereas the exclosure site – with the highest plant cover – showed similar NEE$_{daytime}$ rates to sites with low plant cover. We interpreted this result as the combination of several factors; (i) reduced uptake capacity by the exclosure site due to the large amount of aboveground biomass (live and death) limiting PPFD, increased photodegradation and R_e as mentioned earlier
25 (Brandt et al., 2009), and (ii) live biomass at the moderate grazing site being stimulated by grazing and fire, i.e. disturbance (Coughenour, 1985).

Seasonal NEE$_{nighttime}$ responses to SWC from the low plant cover sites (overgrazed and shrub encroachment), showed lower basal respiration rates (a term of Eq. 6) than sites with high plant cover (Table 3) in support to H$_2$. We attribute this difference to

a combination of, (i) lower maintenance costs of smaller biomass ($\sim 442\,\mathrm{kg\,ha}^{-1}$, Table 1), and (ii) lower inputs to support microbial respiration, for the low plant cover sites. Additional explanations for the low respiration may relate to higher sensibility to air temperature throughout the year (b term of Eq. 6) and poorer capacity to infiltrate and
5   store water in soil (high runoff) by low plant cover sites (Fig. 2, Medina-Roldán et al., 2008), hence resulting in the smallest cumulative night carbon release.

Comparing Q_{10} values to examine $NEE_{nightime}$ sensitivity to T_a from sites with low plant cover, Q_{10} values were similar among most sites (2.09–2.88) and span the mean value of 2.4 reported for soil respiration in terrestrial ecosystems (Raich and
10   Schlesinger, 1992). The exception was observed for the shrub encroachment site that showed a Q_{10} twice as large as those for the overgrazed site (4.39 vs. 2.89 for March and May, respectively). In the shrub encroachment site, C_3 forbs and sub-shrubs were the dominant functional group, characterized by expressing greater daytime respiration sensibility to elevated temperatures, rf. Fig. 6, March and May (Lambers et al., 1998).
15   Seasonal patterns of plant activity, i.e. phenology (Gebremedhin et al., 2012; Curiel yuste et al., 2003) can also induce differences in Q_{10}. In this regard, the shrub encroachment, a C_3 dominant functional group showed photosynthetically-active leaves and stems between March and May, whereas the overgrazed C_4 functional group was dormant in this season (Fig. 6). For daily light response curves from the moderate graz-
20   ing site, we also observed a hysteresis-like loop controlled by T_a (data not shown) suggesting an increase in R_e in the afternoon during the warmer hours, similar to the one reported by Gilmanov et al. (2010). Vegetation at the moderate grazing site included a dense cover of annual C_3 herbs that emerged following early rains in summer. Thus, differences in the degree of control by environmental factors on NEE fluxes between
25   grassland communities emerged from seasonal changes in the preponderance of plant functional groups (C_3 vs. C_4 species). This hysteresis-like loop response was equally observed for the crop site dominated by Oat a C_3 species.

4.3 NEE as a function of species composition

In agreement with H_3, differential effects on NEE fluxes as well as on NEE sensitivity to controlling factors were mediated by plant cover with no clear effects of vegetation's species composition. For example, exclosure and moderate grazing sites displayed very similar NEE rates for both day and nighttime (Figs. 3, 4). For low plant cover plots, there were statistically no differences in net NEE, still the overgrazed site exhibited half the CO_2 efflux than the shrub encroachment site (Fig. 4). The two-fold difference in $NEE_{nightime}$ rates observed in the shrub encroachment site with dominant C_3 native sub-shrubs and exotic perennials may have resulted from; a larger aboveground biomass ($442\,kg\,ha^{-1}$, $2\times$ larger than in the overgrazed site), higher respiration costs from yearlong maintenance an evergreen canopy including adaptations to withstand harsh environmental factors and resistance to herbivory (Wardle et al., 1998; Díaz et al., 2007), and larger temperature sensitivity by C_3 plants in their autotrophic respiration.

Finally, the crop site, characterized by an uniform plant cover and an architecture that includes enough spacing among plants as well as erectophile leaves, more efficient at reducing shading and optimizing photosynthesis per unit leaf area. This feature together with a low belowground biomass typical of an annual species produced the largest net C uptake rates among the five sites (Fig. 4). Net C uptake rates observed in the crop site should be taken with caution since most biomass is removed from the site and decomposed somewhere else, therefore CO_2 emissions from exported biomass are not accounted in this (and other) NEE studies.

5 Conclusions

Site differences in plant cover caused by contrasting land use did influence patterns of net carbon uptake. A combination of factors such as; plant cover, accumulated litter and aboveground live biomass (LAI), species predominance in the vegetation and

the balance between NEE and R_e contributed to the final C budget of the different plant communities. Thus, the overgrazed site with low respiratory fluxes resulted in the greatest net C sink compared to the exclosure, the moderate grazed, and the crop sites, in spite of its low plant cover ($< 8\%$). Plant cover showed some influences on the NEE drivers mostly due to its associated LAI and accumulated biomass. These influences on NEE operated throughout PPFD attenuation and decoupling of vegetation temperature. Finally, no clear influences on NEE were attributed to grassland species composition, still seasonal emergence or dominance of functional groups in which C_3 herbs, sub-shrubs and exotic species prevailed over native C_4 grasses may account for important net NEE differences.

Our results may contribute to an improved understanding of patchy landscapes such as the shortgrass steppe from Central Mexico – for the management of carbon resources. Where biomass harvest is the primary benefit, management should incorporate criteria to optimize biomass harvest (ex. Oat crop, cattle grazing) combined with the maximum capability to store carbon at larger spatial scales. This could be particularly important for converted fields to rainfed agriculture from the semiarid region of central Mexico that could help to contribute towards a neutral or even a carbon sink regionally.

Supplementary material related to this article is available online at:
http://www.biogeosciences-discuss.net/9/17099/2012/
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Table 1. Short-grass steppe characteristics of the study sites in the sub-province Llanos de Ojuelos, located Northeast of Jalisco State, Mexico.

Site	Land use change	Above ground biomass (kg dry matter ha^{-1})	Plant cover (%)	Species composition (dominant species)	Coordinates
Exclosure	28 yr non-grazed, exclosure to domestic cattle	800–1200	35–40	*Bouteloua gracilis*	21° 45′ 32.42″ N 101° 38′ 32.29″ W
Moderate Grazing	Site recovered from heavy grazing; burned 4 yr ago	800–1200	35–40	*Bouteloua gracilis*, *Muhlenbergia rigida*	21° 46′ 52.25″ N 101° 36′ 29.56″ W
Overgrazing	70 yr overgrazed	80–240	5–10	*Bouteloua gracilis*, abundant soil biological crust	21° 45′ 36.36″ N 101° 38′ 20.58″ W
Shrub Enchroachment	70 yr overgrazed	440	5–10	*Isocoma veneta* *Asphodelus fistulosus*	21° 45′ 41.17″ N 101° 38′ 24.85″ W
Crop	Rainfed agriculture	1500–2500[*]	Variable	*Avena sativa*	21° 49′ 9.53″ N 101° 36′ 38.50″ W

[*] Indicates the maximum standing crop at the final harvest in contrast to year round productivity.

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Table 2. Summary of ANOVA table for daily $NEE_{daytime}$ and $NEE_{nighttime}$ contrasting land-use change types in the shortgrass steppe in Central Mexico. Factors included in the model term are; site (exclosure, shrub encroachment, overgrazing, moderate grazing, crop), time of day (TOD, 08:00, 12:00, 16:00 and 20:00), date (October, November, January, February, March May, June, July, August and September).

	Daytime					Nighttime				
Source	df	SS	MS	F	p	df	SS	MS	F	p
Model	4	2.729	0.682	0.54	0.709	4	3.463	0.866	5.41	< 0.01
Error	45	57.061	1.268			45	7.201	0.160		
Total corrected	49	59.790				49	10.664			

df = degrees of freedom, SS = sums of squares; MS = Mean Square.

Table 3. Fitted relationships between daytime and nighttime NEE with leaf area index, soil moisture, and air temperature.

Equation	Site	Fitted parameters	R^2	F
Daytime				
NEE $= a + b \cdot$ LAI	Crop	$a = 0.6477$, $b = -0.0009$	0.65	9.18
	Exclosure	$a = 0.5039$, $b = -3.3852$	0.74	20.22
	Moderate grazing	$a = 0.3240$, $b = -2.4055$	0.56	9.02
NEE $= a + b \cdot$ LAI $+ c \cdot$ LAI^2	Overgrazing	$a = -0.0975$, $b = 3.2000$	0.67	6.11
		$c = -49.7930$		
NEE $= a + b \cdot$ SWC	Exclosure	$a = 0.3492$, $b = -0.0636$	0.64	13.96
	Moderate grazing	$a = 0.6333$, $b = -0.1006$	0.67	16.42
	Shrub encroachment	$a = 0.3849$, $b = -0.0620$	0.47	6.16
Nighttime				
NEE $= a \cdot e^{(b \cdot T)} \cdot$ SWC^c	Crop	$a = 0.0693$, $b = 0.00547$,	0.46	86.62
		$c = 1.177$		
	Exclosure	$a = 0.0768$, $b = 0.0125$,	0.73	266.59
		$c = 1.0671$		
	Moderate grazing	$a = 0.0674$, $b = 0.0106$,	0.55	118.56
		$c = 1.1794$		
	Overgrazing	$a = 0.00365$, $b = 0.0399$,	0.44	51.81
		$c = 1.623$		
	Shrub encroachment	$a = 0.026$, $b = 0.0317$,	0.68	161.12
		$c = 1.1598$		

LAI = Leaf area index, SWC = soil water content, T = air temperature. All regressions are significant at $\alpha = 0.05$.

Oat crop (*Crop*)

3.7 km

Shrub encroachment (*ShEnc*)

Moderate grazing (*Mod*)

4.6 km

100 m

Overgrazing (*Ovg*)

Exclusure (*Exc*)
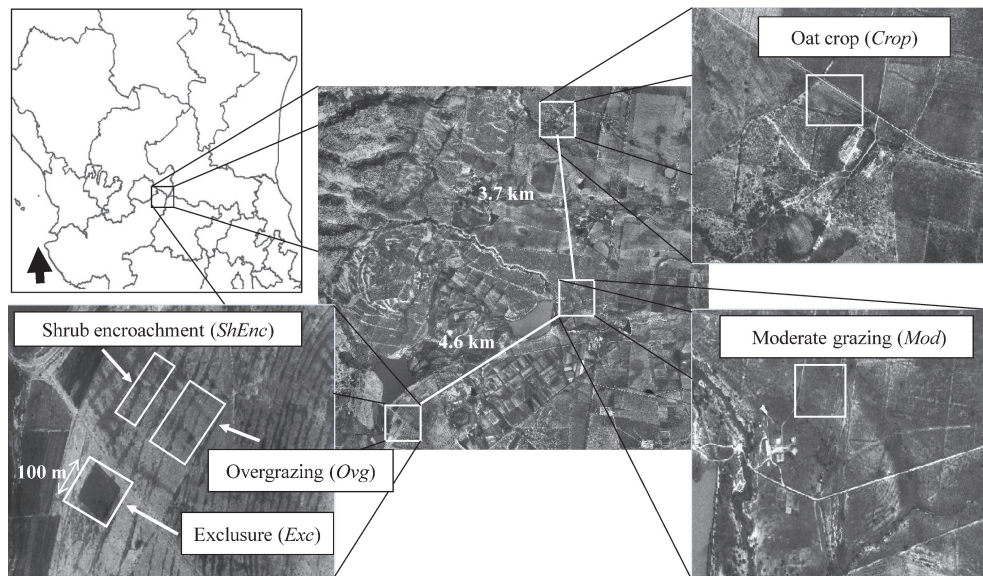
Fig. 1. Location of the study sites in Llanos de Ojuelos, Jalisco in Central Mexico.
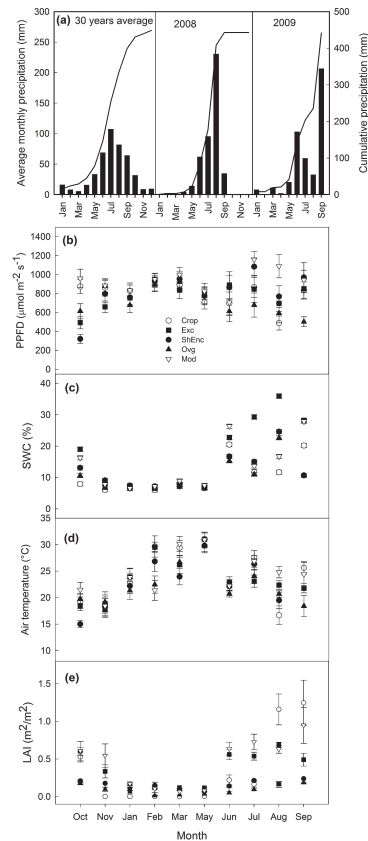
Fig. 2. (a) Average monthly and annual cumulative precipitation over a 30-yr period (left panel) and during the study period October 2008–July 2009 (central and right panels) in Los Llanos de Ojuelos, Mexico. Monthly time series from October 2008 to September 2009 depicting, **(b)** PPFD, **(c)** SWC, **(d)** T_a, and **(e)** LAI at five contrasting land use types in the shortgrass steppe in Central Mexico. All points represent the mean ±1 SE. Acronyms stand for; crop = oat crop, Exc = exclosure, ShEnc = shrub encroachment, Ovg = overgrazing and Mod = moderate grazing.
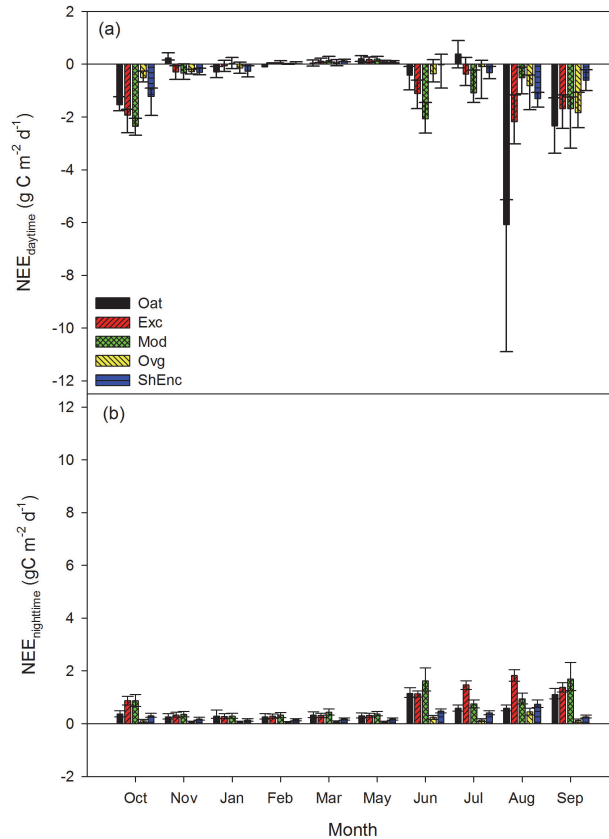
Fig. 3. Daily daytime **(a)** and nighttime **(b)** NEE (mean $\pm$ 1 CI) in five sites with contrasting land-use types in the shortgrass steppe in Central Mexico, recorded from October 2008 to September 2009. For explanation of acronyms please refer to Fig. 2.
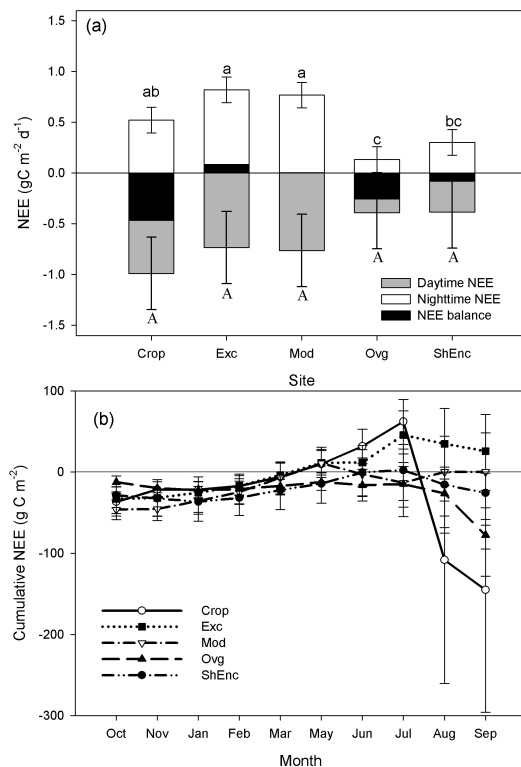
Fig. 4. (a) Average rates of net NEE (mean ± 1 SE) in the shortgrass steppe in Central Mexico associated to five different land-use types. Different letters on both the top and bottom of bars indicate significant differences among sites ($P < 0.05$, capital letters indicate daytime differences whereas lowercase letters refer to nighttime differences in fluxes). **(b)** Cumulative NEE in the five sites, recorded from October 2008 to September 2009. Bars denote the combined uncertainty (95 %) for each cumulative NEE. For explanation of acronyms refer to Fig. 2.

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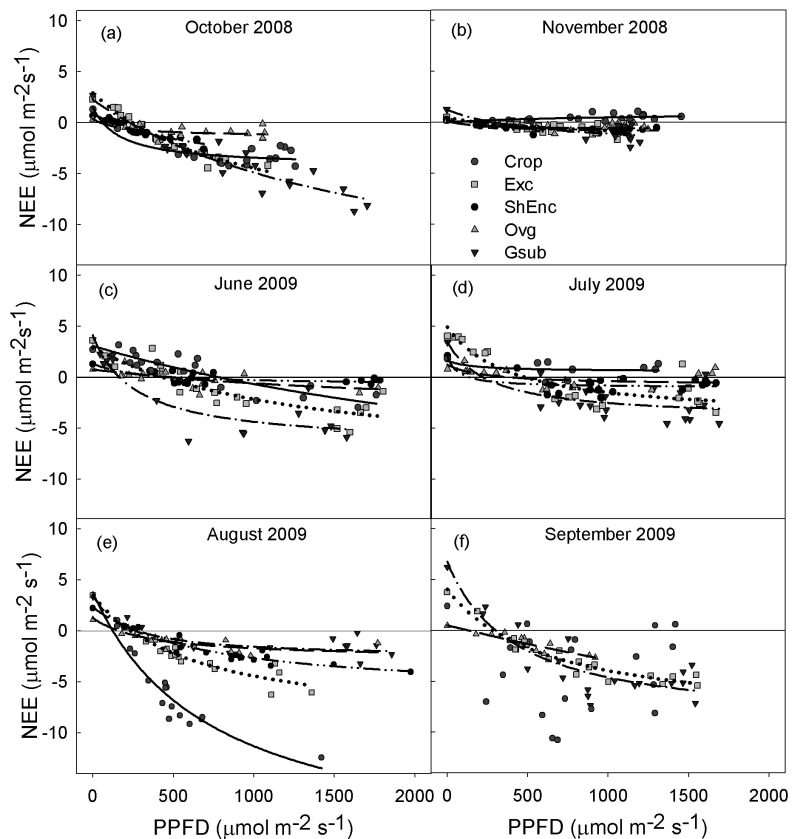Printer-friendly Version

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Fig. 5. Relationships between observed daytime NEE and PPFD fitted to a rectangular hyperbola function (Eq. 3) for five contrasting land use types in the shortgrass steppe in Central Mexico. Line symbols correspond to: ⋯ Exc, – · – Mod, – – Ovg, – ·· – ShEnc, and – Crop. For explanations of acronyms refer to Fig. 2.
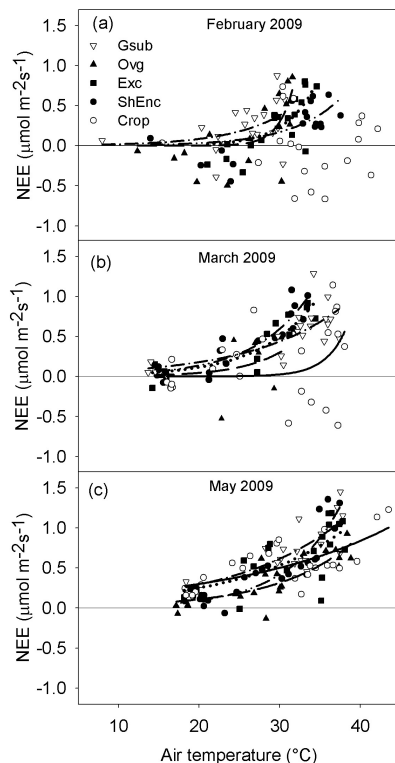
Fig. 6. Exponential relationships between daytime NEE and T_a for February **(a)**, March **(b)** and May **(c)** in five contrasting land use types in the shortgrass steppe in Central Mexico. All regressions were statistically significant at $P < 0.05$, with exception of the Oat crop site in March. Also for March, the Ovg site curve is missing because there were not enough data. Daytime NEE resulted positive (R_e) in this period because vegetation was senescent and LAI was ~ 0, therefore PPFD did not exerted control on NEE. Line symbols correspond to: $\cdots$ Exc, $-\cdot-$ Mod, $--$ Ovg, $-\cdot\cdot-$ ShEnc, and $-$ crop. For explanation of abbreviations refer to Fig. 2.

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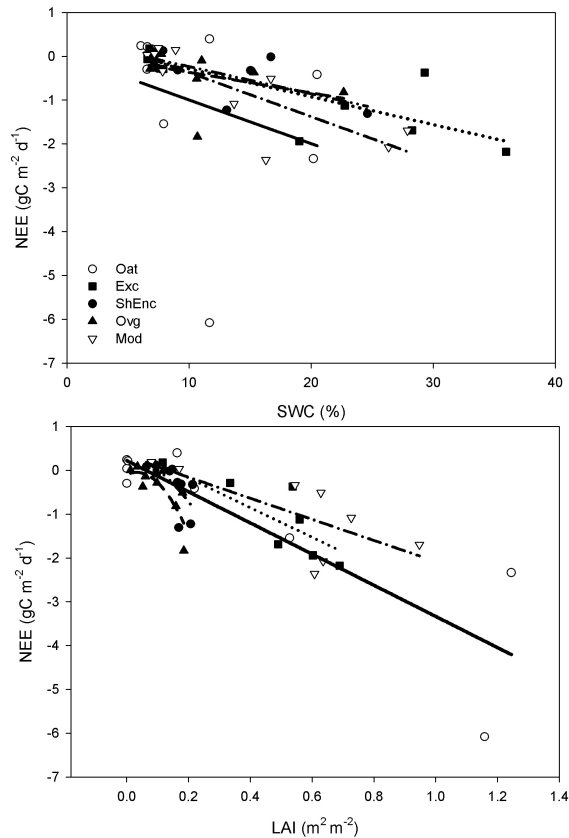Printer-friendly Version

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Fig. 7. (a) Linear regressions between daily daytime NEE and SWC in five contrasting land-use change types measured during ten months. **(b)** Linear regressions between daily daytime NEE and LAI. Line symbols correspond to: ··· Exc, – · – Mod, – – Ovg, – ··– ShEnc, and – crop. For explanations of abbreviations refer to Fig. 2.