

IPICYT

**INSTITUTO POTOSINO DE INVESTIGACIÓN
CIENTÍFICA Y TECNOLÓGICA, A.C.**

POSGRADO EN CIENCIAS APLICADAS

**Net Ecosystem Exchange of carbon and water
vapor among contrasting land-uses types in the
semiarid short-grass steppe in Central Mexico.**

Tesis que presenta

Josué Delgado Balbuena

Para obtener el grado de

Maestro en Ciencias Aplicadas

En la opción de

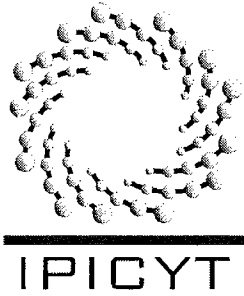
Ciencias Ambientales

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San Luis Potosí, S.L.P., enero de 2010



Constancia de aprobación de la tesis

La tesis "**Net Ecosystem Exchange of carbon and water vapor among contrasting land-uses types in the semiarid short-grass steppe in Central Mexico**" presentada para obtener el Grado de de Maestro en Ciencias Aplicadas en la opción de Ciencias Ambientales fue elaborada por **Josué Delgado Balbuena** y aprobada el **30 de enero de 2010** por los suscritos, designados por el Colegio de Profesores de la División de Ciencias Ambientales del Instituto Potosino de Investigación Científica y Tecnológica, A.C.

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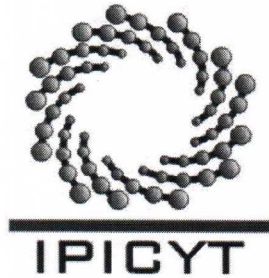


Créditos Institucionales

Esta tesis fue elaborada en el Laboratorio de Ecología de la División de Ciencias Ambientales del Instituto Potosino de Investigación Científica y Tecnológica, A.C., bajo la codirección de los doctores José Tulio Arredondo Moreno y Henry W. Loescher.

Durante la realización del trabajo el autor recibió una beca académica del Consejo Nacional de Ciencia y Tecnología (No. de registro **070278**) y del Instituto Potosino de Investigación Científica y Tecnológica, A. C.

La investigación de esta tesis fue financiada como parte del proyecto SEMARNAT num. ref. **23421**.



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Net Ecosystem Exchange of carbon and water vapor among contrasting land-use types in the semiarid short-grass steppe in Central Mexico

que se desarrolló bajo la dirección de

Dr. José Tulio Arredondo Moreno
Dr. Henry William Loescher (NEON)

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Secretario Académico



A mis padres: Cecilia y Alfonso

y

a mis hermanos: Dante, Laura y Sabatíel

gracias por brindarme su apoyo en todo momento

Agradecimientos

Quiero agradecer al Dr. Tulio Arredondo Moreno por su apoyo en el trabajo de campo y por su asesoría y revisión durante el transcurso de esta tesis.

Al Dr. Henry W. Loescher por sus comentarios y el tiempo invertido en la revisión de este trabajo.

A la Dra. Elisabeth Huber-Sannwald por sus valiosos comentarios que sin duda enriquecieron el trabajo de tesis.

A la M. C. Griselda Chávez Aguilar por su apoyo durante todo el trabajo de campo, fue un largo tiempo, pero agradable.

A Kenia, Dante (hijo) y Jose por los buenos momentos compartidos.

Gracias Jetza por compartir tu tiempo conmigo.

A mis amigos con quienes he compartido magníficos momentos en SLP: Felipe, Gris, Marlín, Rebeca, Reyes, Laura, Manuel, Sosa, Bety, y aquellos que desde lugares más distantes aún siguen apoyando: Aressia, Oli, Lety, Ale, Laura, José Miguel, Eva, Yanek y a los amigos de la Rondalla Chevalier. Gracias a todos.

Agradezco al Laboratorio de Ecología del IPICYT y al Campo Experimental "Vaquerías" del INIFAP por las facilidades otorgadas para el desarrollo del presente trabajo

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Resumen

Intercambio neto de carbono y vapor de agua entre diferentes tipos de uso de suelo en el pastizal mediano abierto del Altiplano Mexicano

Palabras clave: *Dióxido de carbono, evapotranspiración, cambio de uso de suelo, sobrepastoreo, invasión.*

Ecosistemas áridos como los pastizales cubren el 47% de la superficie terrestre y almacenan el 15% del carbono (C) global del suelo. El cambio de uso de suelo (LUC) es la principal actividad humana que controla el intercambio de C, agua y energía entre el continuo suelo-atmósfera. Se requiere incrementar nuestro conocimiento sobre el impacto del LUC sobre el intercambio y almacenamiento de C por los ecosistemas para desarrollar herramientas de predicción y estrategias de mitigación del cambio ambiental global. En este estudio se determinó el intercambio neto de CO₂ (NEE) y vapor de agua (ET) a escala diurna y estacional en cinco sitios de pastizal mediano abierto en los Llanos de Ojuelos, Jalisco: 1) una exclusión de ganado de 28 años (Exclusión), 2) un sitio con dominancia de especies de gramíneas generalmente subordinadas (Cambio de especies), 3) un sitio sobrepastoreado (sobrepastoreo), 4) un sitio sobrepastoreado invadido por arbustivas perennes y herbáceas exóticas (Invasión de arbustos), y 5) un sitio con agricultura de temporal (Agricultura). Se midió el índice de área foliar (LAI), la temperatura del aire (T), la densidad de flujo fotónico fotosintético (PPFD) y contenido volumétrico de agua en el suelo (SWC) como controles bióticos y abióticos de NEE y ET. Se midió el NEE y ET durante ocho fechas de octubre de 2008 a julio de 2009 usando el método del domo geodésico. Se establecieron 6 parcelas por sitio, sobre las que se hicieron 4 mediciones al día (08:00, 12:00, 16:00 y 20:00 h). Se usó un análisis de medidas repetidas (ANOVA, $\alpha=0.05$) para comparar los flujos entre sitios. Se realizaron análisis de regresión lineares y no lineares entre los flujos y sus controles. No fue observado un patrón claro del NEE a través del gradiente de disturbio: el sitio Cambio de especies mostró mayores tasas de NEE diurnas y nocturnas con un balance positivo de captura de CO₂ de $0.781 \mu\text{mol m}^{-2} \text{s}^{-1}$; el sitio sobrepastoreo mostró bajas tasas de intercambio, pero aún con captura de CO₂ ($0.236 \mu\text{mol m}^{-2} \text{s}^{-1}$); en contraste, la Exclusión mostró pérdida de CO₂ ($0.719 \mu\text{mol m}^{-2} \text{s}^{-1}$). Los sitios Cambio de especies y Exclusión mostraron las más altas tasas de ET (1.353 y $1.221 \text{ mmol m}^{-2} \text{s}^{-1}$, respectivamente). El patrón diario de NEE y ET diurnos fueron controlados por el PPFD ($R^2=0.95$ y 0.93 , respectivamente) en los meses húmedos (octubre, junio y julio) y por T en los meses cálidos y secos (marzo-mayo). El SWC y LAI fueron los principales controles estacionales del NEE y ET; sin embargo, LAI sólo estuvo significativamente correlacionado con ET en los sitios exclusión y cambio de especies. Los resultados sugieren que el LUC puede afectar los flujos de C y vapor de agua por modificaciones en la cobertura de las plantas y la capacidad de los ecosistemas para almacenar agua; además, que la acumulación de biomasa muerta en los pastizales puede reducir su capacidad para capturar C.

Abstract

Net Ecosystem Exchange of carbon and water vapor among contrasting land-uses types in the semiarid short-grass steppe in Central Mexico.

Key words: Carbon dioxide, evapotranspiration, land-use change, overgrazing, shrub encroachment.

Dryland ecosystems such as grasslands cover up to 47% of terrestrial land and store around 15% of the global soil carbon. Land-use change (LUC) is the main human activity that controls the carbon, water and energy fluxes in the soil-atmosphere continuum. International research agendas request to increase our understanding on the impact of LUC on the capacity of ecosystems to capture and store carbon to improve forecasting tools and mitigation strategies. In the region “Llanos de Ojuelos”, Jalisco, this study measured at diurnal and seasonal scales, net ecosystem exchange (NEE) and evapotranspiration (ET) of the short-grass steppe. Five different sites were included; 1) a 28 year enclosure (Enclosure), 2) a site dominated by commonly subordinated grasses (Species-shift), 3) an overgrazed site (Overgrazed), 4) an overgrazed site with shrub encroachment and exotic species invasion (Shrub encroachment) and 5) a site converted to rainfed oat crop (Oat crop). Biotic (leaf area index, LAI) and abiotic drivers (air temperature T, photosynthetic photon flux density PPFD, and volumetric soil water content SWC) were measured. NEE and ET were recorded on eight dates from October 2008 to July 2009 using the geodesic dome method. Six plots per site were established and gas exchange was measured on four times during the day (08:00, 12:00, 16:00 and 20:00 h). A repeated measures ANOVA ($\alpha=0.05$) was performed to compare NEE and ET among sites. Linear and non-linear regression analyses between fluxes and drivers were performed. Results showed not clear trends for NEE following the gradient of disturbance; still, species-shift exhibited the highest diurnal and nocturnal NEE rates with a positive CO_2 balance of $0.781 \mu\text{mol m}^{-2} \text{s}^{-2}$. The overgrazed site showed significantly lower rates but still a positive CO_2 balance ($0.236 \mu\text{mol m}^{-2} \text{s}^{-1}$). In contrast, the Enclosure site showed in this period a net CO_2 efflux of $0.719 \mu\text{mol m}^{-2} \text{s}^{-1}$. Regarding ET rates, the Species shift and the Enclosure sites observed the largest rates (1.353 and $1.221 \text{mmol m}^{-2} \text{s}^{-1}$, respectively) that was attributable to a significant larger leaf area index (LAI). Diel time patterns of NEE and ET were driven by PPFD ($R^2=0.95$ y 0.93 , respectively) during the wet months (October, June and July); while in the dry and warm months (March-May) the main driver was air temperature. SWC and LAI on the other hand, acted as the main seasonal drivers of NEE and ET; however LAI was only significantly correlated with ET in the Enclosure and the Species shift sites. These results suggest that LUC can affect water and carbon fluxes by modifications of plant cover and the soil water storage capacity of ecosystems. Moreover, that large accumulation of standing dead biomass can reduce the C uptake capacity of the short-grass prairie.

1. Introduction

Changes in land use is the main human activity that controls long-term net terrestrial fluxes of carbon, water vapor and energy. The consequence of which are that the expansive spatial distribution of carbon, C, sources and sinks is dominated by changes in land use (Houghton, 2003). However, despite of the importance of land-use change in the global carbon balance and thereby in local and regional forecasting of climate change scenarios (Lambin *et al.*, 2006; Koomen and Stillwell, 2007), the magnitude and distribution of emissions from different sources across a mosaic landscape result in large uncertainties (Levy *et al.*, 2004).

Changes in land use are broadly defined as conversion or management of various ecosystems, i.e., forest, grassland, shrubland, agriculture, coastal estuarines, urban and exurban types (Houghton and Goodale, 1999; Houghton, 2003). Changes in land management cause alterations in both the community structure and ecosystem function (Houghton and Goodale, 1999) through the loss of plant cover and changes in species composition, leading to direct and indirect alterations to key ecosystem processes, e.g., biogeochemical cycling of carbon and hydrology (Arredondo *et al.*, 2005; Medina *et al.*, 2008). This in turn changes the amount of carbon stored and the associated process rates in vegetation and soils as compared to a nature, undisturbed system (Houghton and Goodale, 1999). Land-use change also alters the hydrological cycle through several mechanisms, changing i) the amount of energy absorbed by the ecosystem (albedo), ii) the quantity of stored energy, iii) the pathways of energy transformation into sensible and latent heat flux, and iv) the water content and temperature of the atmosphere (Gash and Nobre, 1997). Between the years of 1850 – 1990, global changes in land use have released as much as 156 Pg C into the atmosphere which is about half the amount released from fossil fuels combustion (Houghton and Goodale, 1999). Moreover, between the years 2000 and 2005, fluxes from different land use types (deforestation, afforestation, reforestation, harvest management, fire suppression, non-forest changes in land-use and management) resulted in global emissions of 1.47 -1.5 Gt C y⁻¹ (Raupach *et al.*, 2007; Houghton, 2008). Even

though these studies are widely acknowledged, they are based on inventories, and its parameterization and verification are still active areas of research.

Hence, being able to estimate the drivers, responses and feedback mechanisms of C and H₂O exchange are needed to assess ecosystem sink-source status among key regional land use types among temporal and spatial scales (Flanagan *et al.*, 2002). The Net Ecosystem Exchange (NEE) of carbon through the continuum of soil-vegetation-atmosphere can be estimated through direct measurements. The NEE is the balance between the gross ecosystem productivity (GEP) and the total ecosystem respiration (E_R). E_R comprises both autotrophic (above-ground plant tissues and roots) and heterotrophic respiration (soil microorganisms, micorrhiza and micro and meso fauna; Chapin *et al.*, 2002; Nieder and Benbi, 2008). It is also important to that gross primary productivity (GPP) is often used interchangeably with GEP, they do differ however, GEP includes the photorespiration component, biogenic volatile compounds, and root exudates, while GPP does not (Hymus and Valentini, 2007).

Evapotranspiration (ET) is defined as the sum of water loss from non-vegetated soil surface (soil evaporation) plus water loss through transpiration by the vegetation (Chapin *et al.*, 2002). ET is a key component of ecosystem water balance and is strongly related to GEP in terrestrial ecosystems mainly in arid and semiarid ecosystems (Williams *et al.*, 2004). Moreover, ET is coupled to the energy exchange through the energy required to evaporate the water in leaves and soil surface (Campbell and Norman, 1998). Fluxes of water vapor from ET account for more than 75% of turbulent energy transfer from Earth to the atmosphere in form of latent heat flux (W/m^2) (Fitzharris, 1974).

Several factors including physico-chemical (biotic factors) and microclimatic (abiotic factors), can affect CO₂ an ET exchange through controlling GEP, ER and by modifying the amount of radiant energy available for evaporation. However, the relationships between controlling variables and net terrestrial CO₂ flux and ET are only partially known at the ecosystem-process level.

At the leaf level, abiotic factors as nitrogen availability, light, temperature, air humidity, precipitation and soil water potential are the main factors controlling gross photosynthesis, whereas biotic factors such as phenology, leaf plasticity, leaf area density and canopy structure control gross photosynthesis at the stand level (Lindroth *et al.*, 2008). Landscape factors such fire management, and land use change have impacts on plant community structure and diversity (Belsky, 1992; Noy-Meir, 1995). At the leaf level, abiotic factors mentioned above, affect photosynthesis through effects on stomatal aperture and Rubisco activity, as well as, ultimately, on leaf area. On the other hand, phenology, leaf area and canopy structure act in conjunction and determine the amount of light absorbed by plants (Lindroth *et al.*, 2008). Likewise, abiotic factors also exert a strong control on productivity of ecosystems; for instance, precipitation enhances ecosystem productivity (carbon acquisition), mainly in semiarid regions (Sala *et al.*, 1988), above all by incrementing the soil water content, due to ecosystems are more sensitive to soil moisture than to precipitation (Chapin *et al.*, 2002); however this carbon uptake can be offset by increases in decomposition and subsequent CO₂ emissions (by heterotrophic respiration). In addition to soil moisture, ecosystem respiration is also controlled by temperature and nutrient supply but at different extent (Chapin *et al.*, 2002). For instance, temperature exerts a stronger control over respiration than over NPP (Luo *et al.*, 2001), in contrast with nutrient inputs into ecosystems have larger effects on GEP than on soil respiration (Chapin *et al.*, 2002). Several studies also indicate that respiration increases exponentially with temperature but this response varies through the season (Lindroth *et al.*, 2008).

Factors controlling evapotranspiration at ecosystem level include net radiation, wind speed, soil moisture, how dry the atmosphere is (vapor pressure deficit), reflective land-surface characteristics and season of the year, as well as density and type of vegetation cover (e.g., canopy conductance and surface roughness) and root depth (Hanson, 1991). Changes in vegetation type may influence the amount of water available to evapotranspiration throughout altering interception and the storage of precipitation, and increasing runoff in turn (Chapin *et al.*, 2002).

This may be due to either inherent physiological traits such as differences in water use efficiency (ratio between above-ground gain in biomass and loss of water during the production of that biomass or alteration of soil structure by the addition of organic matter changing the soil capacity to store and transfer water (Fitzharris, 1974; Lambers *et al.*, 2008).

Also, water and energy balances are linked through evapotranspiration. For instance, land-cover change imposes differences in surface albedo that in turn, influences the amount of net energy that can be partitioned into latent and sensible heat and thus the surface-atmosphere energy exchanges impacting the local-to-regional climate (Loescher *et al.* 2006). Changes in structure vegetation, moreover, may alter the emissivity of the surface and its ability to exchange mass and energy in the air just above it, i.e., surface boundary-layer (Fitzharris, 1974).

Dryland ecosystems cover 47.2% of the total land area of the Earth, among these, semiarid regions, including the semiarid grassland biome cover ci. 17.7% of the global land (Lal, 2004). These regions are characterized by share precipitation:potential evapotranspiration ratios (Aridity index, AI) ranging from 0.20 to 0.50, which in addition to highly variable and unpredictable precipitation (Noy-Meir, 1973), makes them vulnerable to disturbance events, such as land-use change; in addition, the majority of grasslands are over used and poorly managed (DeFries *et al.* 1999). In Mexico, the semiarid grassland extends from the North American Midwest along a narrow strip that goes along the *Sierra Madre Occidental* base through the *Chihuahuan* Dessert until the sub-province *Llanos de Ojuelos*, located Northeast of *Jalisco* state. This ecosystem presents summer rain regime with 6 to 9 dry months; hence, the growing season is controlled by available water in the wet months of summer, with low productivity rates during the rest of the year. The vegetation is dominated by grasses, with *Bouteloua gracilis* H.B.K. Lag ex Steud (blue grama) as the most common species, forming almost monospecific stands under moderate use. In the presence of disturbance through land use change (ex. overgrazing, fire suppression) there might be an increase of other grass species usually observed as subordinated species and shrubs

(Rzedowski, 1978). A land cover assessment from 1970's reported that arid and semiarid grasslands covered ci. 5% of Mexico territory based in an historical cartography analysis (even though Rzedowski (1978) estimate 10-11% of cover for the same year); however, changes in land use have reduced grassland cover to only a 4.4% (SEMARNAT, 2002; Velásquez *et al.*, 2002). Grazing by domestic cattle and grassland conversions to rainfed agriculture are the main factors associated to degradation and loss of grasslands (Rzedowski, 1978; Velásquez *et al.*, 2002). Grazing is an essential component of nutrient cycling and contributes to the maintenance of grasslands productivity and structure; however, when grazing exceeds the recovery capacity of grasslands, causes a disruption between soil and plant processes, promoting a decline of plant cover and leaving soils exposed to environmental factors (Rzedowski, 1978; Schlesinger *et al.*, 1990). Overgrazing can reduce soil moisture, organic matter and nitrogen content (Abril and Bucher, 1999). Moreover, long term heavy grazing may also promote encroachment of woody (dessert shrubs) and succulent species into the grass matrix of semiarid grasslands (Lal, 2001; Brown and Archer, 1999). In the case of land converted to rainfed agriculture, soils remain uncovered most part of the year. Under these circumstances processes such as wind and water erosion contribute to the loss of soil organic matter (SOM) and CO₂ emissions, as well as enhancement soil evaporation. On the other hand, management practices intended to increase forage production usually increase soil carbon (Conant *et al.*, 2001). Moreover, is reported that simply cessation of overgrazing can contribute to sequester of 45 Tg C yr⁻¹ (Conant and Paustian, 2002).

Estimations of C flux in grasslands range from about 800 g C m⁻² for uptake and 521 g C m⁻² for emissions, with most grassland ecosystems in the range of 0 ± 200 g C m⁻² (Jaksic *et al.*, 2002). Thus grasslands behave as both sinks and sources of carbon depending on the season. However, recent studies in desert ecosystems (Jasoni *et al.*, 2005; Wohlfahrt *et al.*, 2008) reported carbon uptake rates similar to some forest ecosystems that exhibit much higher biomass. According to these authors, these rates suggest that deserts and semiarid ecosystems can play a

much important role in the global carbon cycle. Therefore, it is crucial to determine through regional studies the role of grassland in the carbon balance as well as the effect of land-use change on NEE.

Overall, considering the direct effects of land-use change on ecosystems, it should be expected to observe concomitant decreases in carbon and water vapor fluxes following an increase gradient of disturbance, driven by a reduction of photosynthetic and transpiring surface area (leaf area index) and changes in species composition (Hypothesis 1). In this sense is hypothesized that sites of short-grass prairie with similar conditions to a pristine ecosystem (exclosures or recovered sites) will trend to capture more CO₂ than degraded sites (i.e. overgrazed or converted to rainfed agriculture) distinguished by loss of plant cover and productivity; thus, is expected that those more conserved grassland sites show a positive C balance throughout the year (Hypothesis 2). In contrast, ET is expected to be lower in more degraded sites by reduction in live and dead plant biomass and soil organic matter, which in turn increase runoff and reduce soil storage capacity, which will be reflected in the lower soil water content through the time (Hypothesis 3).

Thus, the objectives of this study were: 1) to compare the NEE and ET among contrasting land-use types in a semiarid, high elevation grassland ecosystem and 2) quantify short-term and long-term biotic (Leaf area index, LAI) and abiotic (air temperature, photosynthetic photon flux density and soil water content) controls of NEE and ET dynamics among contrasting land-use types in a semiarid grassland in Mexico.

2. Materials and methods

2.1 Study site

Five sites were located in the physiographic sub-province *Llanos de Ojuelos* in central Mexico (Figure 1). This province constitutes the southernmost part of the North American graminetum (Aguado-Santacruz and García-Moya, 1998). The climate is semi-arid, with a mean annual temperature (MAT) between 12 and 18 °C; temperature ranges from -3 to 18 °C for the coldest and warmest months, respectively. Oscillation of mean annual temperature is large (7 – 14 °C). Mean annual precipitation over the last 30 years is 450 mm with a summer precipitation regime occurring between June and September. Rain distribution is ten times higher in the wettest month (July) than in the driest month, while winter rain accounts for less than 5% from the total annual precipitation. The precipitation regime has a convective origin with humidity sources from westerlies and tropical cyclones (García, 2003). The topography is characterized by valleys and gentle

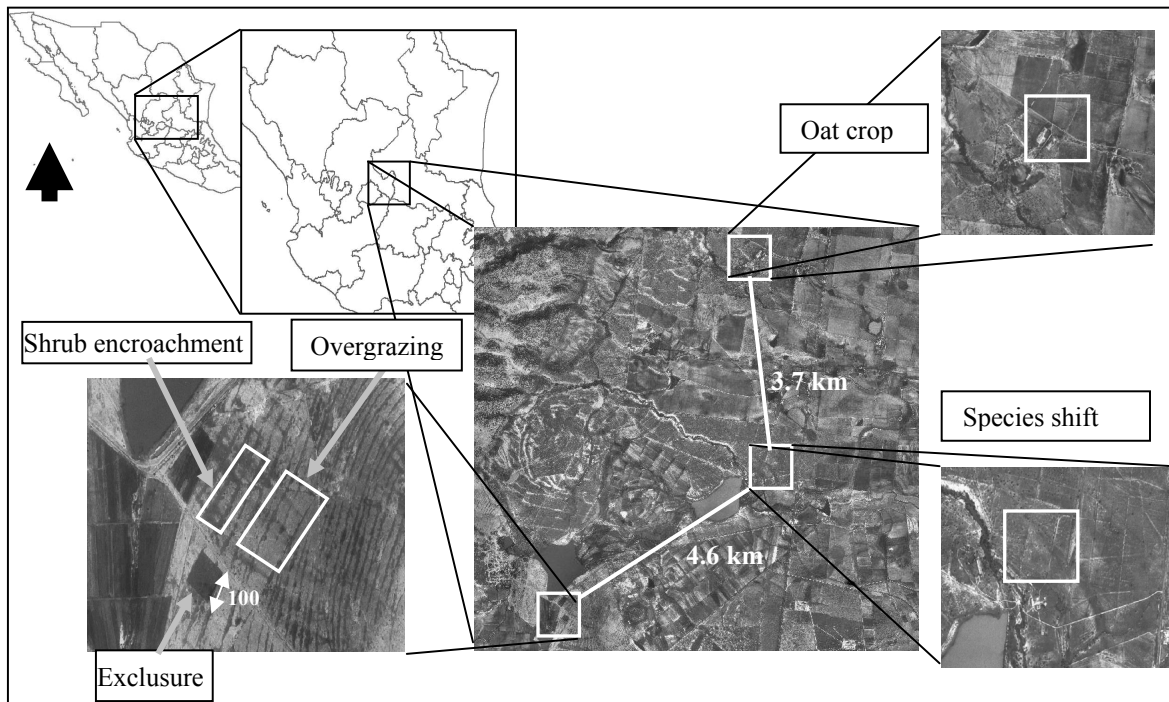


Figure 1. Location of study sites in Llanos de Ojuelos, Jalisco in central Mexico.

rolling hills with soils classified as haplic xerosols associated with lithosols and eutric planosols, and haplic phaeozems associated with lithosols (Aguado, 1993). Soils are shallow with only two horizons at 0-25 cm and 25-40 cm depth (Aguado, 1993) and soil type varying from silty clay to sandy loam textures exhibiting a cemented layer ca. 50 cm depth (COTECOCA, 1979).

Site	Management type	Above ground Productivity (kg dry matter/ha)	Plant cover (%)	Species composition (Dominant species)	Coordinates
Exclosure	28 years non-grazed, exclosure to domestic cattle	800-1200	35 - 40	<i>Bouteloua gracilis</i>	21°45'32.42"N 101°38'32.29"W
Species-shift	A site recovered from agriculture and currently under moderate grazing use	800-1200	35- 40	<i>Bouteloua gracilis</i> , <i>Muhlenbergia rigida</i>	21°46'52.25"N 101°36'29.56"W
Overgrazing	70 years Overgrazed	80-240	5 – 10	<i>Bouteloua gracilis</i> <i>Abundant soil crust</i>	21°45'36.36"N 101°38'20.58"W
Shrub encroachment	70 years overgrazed	440	5 -10	<i>Isocoma veneta</i> , <i>Asphodelus fistulosus</i>	21°45'41.17"N 101°38'24.85"W
Oat crop	Rainfed agriculture	1500-2500	Variable	<i>Avena sativa</i>	21°49'9.53"N 101°36'38.50"W

The five selected sites exhibited contrasting land use change types that imposed drastic differences in species composition, vegetation structure, plant cover, plant phenology and soil resources. Sites included: 1) “Exclosure”: a 28 year old cattle exclosure representing the original shortgrass steppe regarding species composition and vegetation structure (Table 1; Figure 2a); 2) “Species-shift” - a site with long history of heavy grazing and historical agriculture but currently showing a good vegetation cover including a large proportion of subordinate grasses mixed

with the key species, including *Bouteloua gracilis* H.B.K. Lag ex Steud, *Muhlenbergia rigida* (Kunth) Trin. (Purple muhly), *B. scorpioides* Lag., *B. hirsute* Lag., *Aristida* spp., and several herbaceous species (*Astragalus mollissimus* Torr., *Bidens angustissima* Kunth, Table 1, Figure 2b); 3) “overgrazing” – a site with at least 70 years of overgrazing presenting less than 10% of plant cover made up by *Bouteloua gracilis* as the dominant species (Table 1, Figure 2c), 4) “shrub encroachment” - a similar overgrazing site currently presenting invasion by the sub-shrub *Isocoma veneta* (Kunth) Greene, a native perennial shrub species and *Asphodelus fistulosus* L., an exotic naturalized Mediterranean perennial herb (Liliaceae); in addition, in the growing season, the plant community is composed by



Figure 2. Left: aspects of the five different study sites. In the twelve-sided plots shows the characteristics vegetation at of each site under different land-use type (Left). Differences in plant cover, proportion of bare soil and species composition are some features that characterize each site. To the Right there are images of 0.25 m²: square plots of 0.25 m² for estimate leaf area index. For the shrub encroachment site circular plots of 1 m² were used instead.

annual grasses aside from *B. gracilis* and prostrated herbs (*Dichondra argentea* H.B. & Bonpl. ex Willd, *Astragalus mollissimus* Torr., Table 1, Figure 2d), and 5) “oat crop” - a former grassland converted to rainfed agriculture with oat (*Avena sativa* L.), a typical land conversion type for this area (Table 1, Figure 2e).

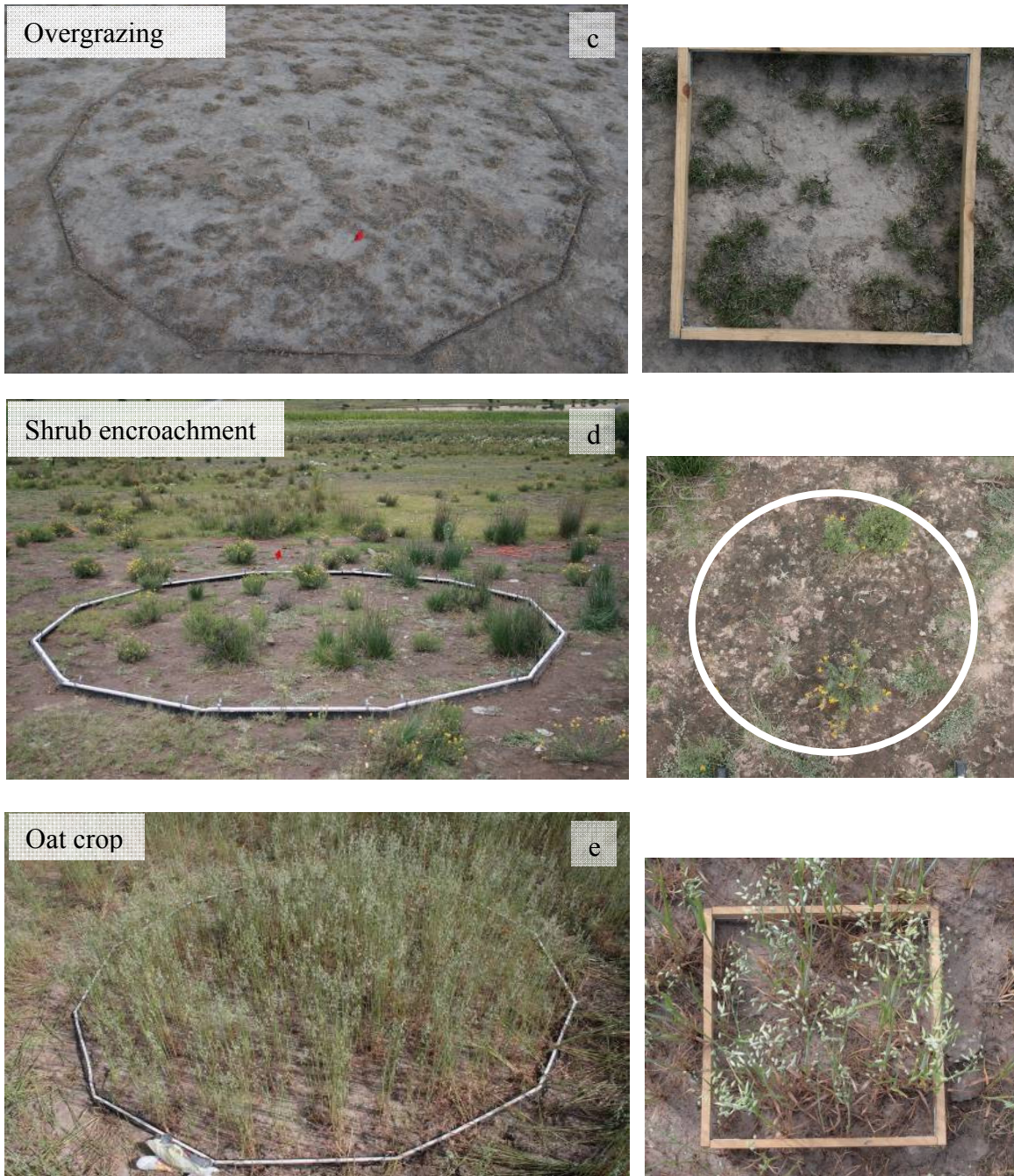


Figure 2. Cont.

2.2 Monitoring of NEE and ET

We used a large static chamber method (geodesic dome; Arnone and Obrist, 2003) to quantify NEE of CO₂ and ET. We used a 4.2 m diameter YurtDome 14 tent (Shelter Systems Inc., Menlo Park CA, USA). The dome covered a ground area of 12.25 m² and a volume of 16.4 m³. The dome's external frame was constructed with 48 individual 3.7 cm diameter PVC tubes (twelve 65 cm tubes and thirty six 107 cm tubes) joined together with fifty-four 7 cm long X 2.5 cm diameter PVC tubes. The dome skin is made of eight large individual panels of semitransparent woven ripstop polyethylene that is attached to the PVC frame with 33 nylon grip clips (Shelter Systems Inc., Menlo Park CA, USA), with upper panels overlapping lower panels by about 10 cm. We sealed panel joints from inside with transparent duct tape to avoid gas leakage. We constructed a 12-sided tubular base with twelve 103 cm long X 5 cm diameter hydraulic PVC tubes joined together by twelve 30-degree schedule 40 PVC elbow joints. On each elbow joint, we drilled a 2 cm diameter vertical hole to accept one 2.5 cm schedule 40 PVC male adapter in which we could connect the twelve vertical PVC tent poles. To attach the dome to the ground we constructed a 12-sided base similar in dimensions and shape to the PVC base. This was made with 12 iron angles using sections of 103 cm long and 5 cm wide joint together with screws. The upper side of the iron angle was in a horizontal position to support the dome's base, and the other one was inserted 3 cm into the soil. We soldered in vertical position, two pairs of 1 cm wide X 5 cm long metal pieces on the top of the metal base, as a clip, to adjust the PVC dome base rapidly. Additionally, we stacked a foam rubber along the top of the base to provide a better seal to the dome (Figure 3d).

Within each site, six plots were established randomly with similar vegetation characteristics for a total of 30 dome plots. Each dome plot enclosed a representative sample of land and vegetation that contained the main features of each community. Before each measurement, two air fans (Mytek, mod. 3306; 20"; 180 W) were positioned on opposite sides of the plot at 30 to 50 cm from the dome wall. Above the canopy, one fan was horizontally oriented and the other was

vertically oriented to obtain a better mix of the air inside the dome (flow rate = $54.3 \text{ m}^3\text{h}^{-1}$). An open-path infrared $\text{CO}_2/\text{H}_2\text{O}$ gas analyzer (IRGA; Li-7500, Li-Cor Inc., Lincoln NE) was located at the center of the plot mounted on a tripod 50 cm above the ground. One photosynthetic photon flux density (PPFD) sensor (PARLITE, Kipp and Zonen Delft, Holland) and one thermocouple (PRT type) were located next to the IRGA. Another set of PPFD and thermocouple sensors were located outside the dome plot at similar heights. To communicate and provide energy to sensors and fans with the PC located outside the dome, wires were passed through a groove in the rubber gasket. Data from all sensors were logged into a datalogger (CR1000, Campbell Scientific Inc. Logan, Utah, USA). The IRGA, PPFD and thermocouple sensors were set up to record data at a frequency of 1 Hertz.

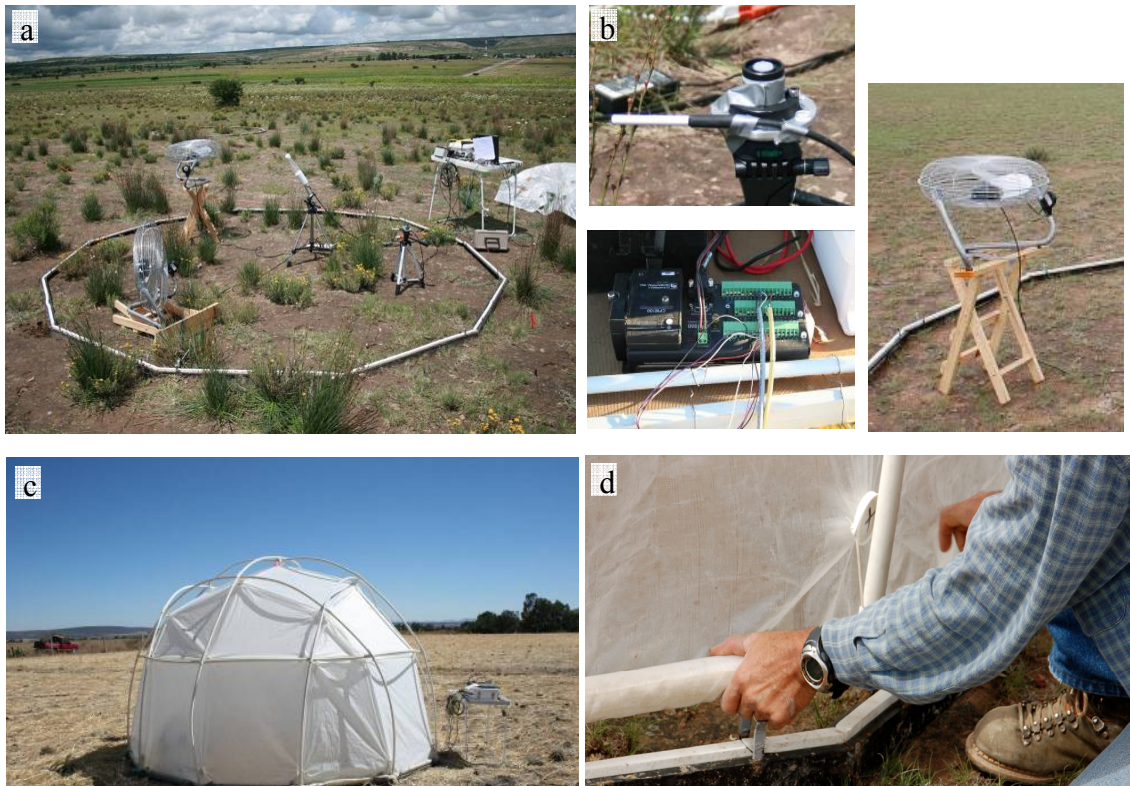


Figure 3. Dome technique. a) Sensor arrangement inside the 12-sided plot; b) ParLite, thermocouple, CR1000 and fan; c) dome on the base frame plot; d) metal base with rubber gasket and clip.

Measurements for NEE and ET were carried out monthly from October 2008 to July 2009 at each site. Each measurement campaign included 4 sampling periods throughout the day: at 08:00, 12:00, 16:00 and 20:00 hr solar time allowing us to construct a daily time course for NEE and ET. The time for diurnal measurements of individual dome plots was about 120 s, and for nocturnal measurements around 180 s.

Calculations of land-area-based CO₂ fluxes considered the slopes of CO₂ time series for each dome plot according to the equation (1):

$$(1) \quad C' = C / (1 - W/1000)$$

where C refers to the mole fraction of CO₂ (μmol mol⁻¹) and W to the mole fraction of H₂O (mmol mol⁻¹). Then CO₂ flux was calculated according to equation (2):

$$(2) \quad F_c = \frac{VP_{av}(1000 - W_{av})}{RS(T_{av} + 273)} * \frac{dW}{dt}$$

Where F_c refers to the CO₂ flux (μmol m⁻² s⁻¹); V is dome's volume (m³); P_{av} is the average inside dome pressure (kPa) during measurement periods; W_{av} the average water mole fraction (mmol mol⁻¹) during measurement periods; R is the ideal gas constant (8.314 J mol⁻¹ K⁻¹); S is the surface area covered by dome (m²); T_{av} is the average temperature (°C) during measurement period; and dC'/dt is the slope of least square linear regressions of C' above time (Jasoni *et al.*, 2005).

To calculate ET equation (3) was used:

$$(3) \quad ET = \frac{VP_{av}(1000)}{RS(T_{av} + 273)} * \frac{dW}{dt}$$

Where ET is the evapotranspiration (mmol m⁻² s⁻¹); dW/dt is the slope of least square line regressions of water vapor concentration on time; V, P_{av} , R, S and T_{av} as above.

To estimate plant cover, biomass production and LAI by site, six 50-cm² quadrants were established outside the dome plots. In the overgrazing and invaded site the

size of the quadrant was 1 m². All live biomass was removed and kept in Ziplock-type bags containing humid pads to maintain the leaves water saturated until analysis. All collected live leaves were passed through a leaf area meter (Li3000C, Li-Cor Inc., Lincoln NE) to determine leaf area and estimate LAI.

Volumetric soil water content was monitored with 15 cm long probes using Time Domain Reflectometry (Mini Trase, SoilMoisture Equipment Corp.). One pair of probes was inserted at the center of each plot, while another pair was inserted outside the plot to about 1 m away. Soil water content measurements were carried out with similar frequency to NEE measurements.

To describe the response of CO₂ net ecosystem exchange to PPFD a rectangular hyperbola function was employed:

$$(4) \quad NEE = y_0 + \frac{\alpha * PPFD * b}{\alpha * PPFD + b}$$

Where:

α is the apparent quantum yield at low light conditions, b is the maximum assimilation rate at light saturation conditions (A_{max}), y_0 is the daytime dark respiration (R_d); and PPFD is the photosynthetic photon flux density observed.

Additionally, an A_{2500} parameter was obtained from the above equation, which is a reference maximum CO₂ assimilation rate at a real PPFD level, because A_{max} is calculated by the model to an infinite PPFD level.

For March and May, an exponential function (5) was used to describe the relationship between daytime NEE and air temperature.

$$(5) \quad NEE = b_0 * \exp(b * T_{air})$$

where b_0 and b are empirical coefficients.

Then, b coefficients were used to estimate the Q_{10} values with equation (6). Q_{10} is the factor by which ecosystem respiration increases with an increase of 10 °C in air temperature.

$$(6) \quad Q_{10} = \exp(10 * b)$$

A polynomial quadratic function was applied to evaluate the effect of volumetric soil water content (SWC) on monthly NEE_{daytime} (7)

$$(7) \quad (NEE_{\text{monthly}} = y_0 + a * SWC + b * SWC^2)$$

while a simple linear model was used to correlate monthly NEE_{daytime} with LAI. On the other hand, monthly $NEE_{\text{nighttime}}$ and SWC were fitted to a logarithmic function (8):

$$(8) \quad NEE_{\text{nighttime}} = y_0 + a * \ln(SWC)$$

Monthly daytime ET was correlated to LAI by an exponential function:

$$(9) \quad ET_{\text{daytime}} = a * \exp(b * LAI)$$

To describe the relationship between the diel time course of ET_{daytime} and PPFD, as well as between monthly ET_{daytime} and SWC, a simple linear fit was applied.

2.3 Normalization of NEE

Daytime and night time NEE at recording times was affected by incident radiation (measured as PPFD) and temperature. To avoid the confounding effects of differences in radiation and temperature a normalization process was incorporated prior to statistical analysis. For daytime, NEE normalization was carried out using available PPFD. NEE was normalized with the following equation:

$$NEE_{\text{norm}} = NEE / (PPFD_{\text{obs}}/PPFD_{\text{max}}).$$

Where:

PPFD_{obs}: PPFD inside the dome at each measured plot.

PPFD_{max}: Maximum PPFD observed at each day of measurement.

Positive NEE fluxes observed at the afternoon as a result of very low light were not normalized.

2.4 Statistical analyses

All NEE and ET data were normally distributed, so a repeated measures analysis of variance (ANOVA) was implemented to compare all flux measurements using the PROC MIXED procedure of SAS (SAS Institute Inc., Cary, NC. USA).. Classification variables included Site (n=5; enclosure, species-shift, overgrazing, shrub encroachment and oat crop) and time of the day (n=4; 08, 12, 16 and 20 h) as between subject factors, and dates (n=7, October, November, January, February, May, June and July) as within-subject factor and Plot (n=6) as the subject variable. Analyses were separated into diurnal and nocturnal fluxes for both NEE and ET (NEE_{daytime} , $NEE_{\text{nighttime}}$, ET_{daytime} and $ET_{\text{nighttime}}$). Post hoc multiple comparisons were done with the Least square means (LS-means) at $\alpha=0.05$.

To describe the relationship between response variables (NEE and ET) and factors (PPFD, air temperature, soil water content and LAI), linear and non-linear regression analysis were performed. To determine short-term drivers of diel time NEE and ET patterns, data of individual plots were used; whilst to determine the long-term drivers (through eight measured months), averages of daily NEE and ET fluxes were employed, separating nighttime and daytime fluxes as above.

Even though in March there was a sampling date, there were many loss data due to hard weather conditions, so, this month was not used in the repeated measures analysis; but available data could be used in regression analysis.

3. Results

3.1 Net ecosystem CO₂ exchange

For the measurements carried out between October 2008 and July 2009, average rates of daytime NEE revealed significant differences between the species-shift site compared to all of the sites (Fig 4, $P < 0.05$; Site main effect, Table 2). Species-shift plots displayed more than twice as much NEE_{daytime} (net uptake; $-2.323 \pm 0.113 \mu\text{mol m}^{-2} \text{s}^{-2}$) in comparison to fluxes of less than $-1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the other sites. In contrast, nighttime NEE rates were similar between the enclosure and species-shift plots and significantly higher than for overgrazing, shrub encroachment and oat crop (Fig. 7, $P < 0.05$). The $NEE_{\text{nighttime}}$ rates fluctuated between 1.54 ± 0.06 and $0.2692 \pm 0.06 \mu\text{mol m}^{-2} \text{s}^{-2}$, for the species-shift and overgrazing sites respectively.

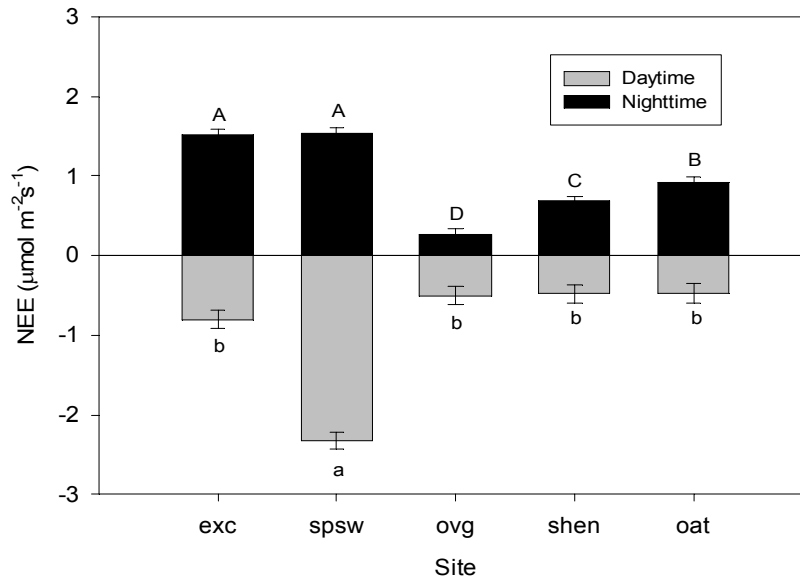


Figure 4. Average rates of NEE (mean \pm 1SE) in a short-grass prairie in Mexico subjected to different land-use types. Negative values represent fluxes from the atmosphere to the ecosystem. Different letters on bars indicate significant differences among sites ($p < 0.05$, capital letters refer to differences in nighttime fluxes and lowercase refers to daytime fluxes). Abbreviations refer to: exc = enclosure, spsw = species-shift, ovg = overgrazing, shen = shrub encroachment and oat = oat crop.

Table 2. Summary of repeated measures ANOVA for NEE and ET including five different land-use change types in a short-grass prairie in Mexico. Effects of Site (Exclosure, species-shift, overgrazing, shrub encroachment and oat crop), time of the day (TOD, 08:00, 12:00, 16:00 and 20:00 hrs), Date (October, November, January, February, May, June and July) on both daytime and nighttime NEE and ET. Degrees of freedom (df) for Daytime and nighttime NEE are the same for ET.

Effect	NEE						ET			
	Daytime			Nighttime			Daytime		Nighttime	
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
SITE	4	48.77	<.0001	4	81.53	<.0001	55.66	<.0001	19	<.0001
TOD	2	87.93	<.0001	6	208.95	<.0001	533.13	<.0001	283	<.0001
DATE	6	140.04	<.0001				166.29	<.0001		
SITE*DATE	24	19.56	<.0001	24	15.01	<.0001	15.81	<.0001	31	<.0001
SITE*DATE*TOD	68	8.68	<.0001				13.25	<.0001		

NEE exhibited both diel and seasonal fluctuations (Table 2, Site*Date*TOD, $P < 0.05$). For the growing season (October, June and July) the diel NEE variation was characterized by two C uptake patterns, one in which rates at the early morning (08:00) and afternoon (16:00) were the lowest in the day whereas maximum NEE was observed at midday (12:00) such as in the Exclosure and Overgrazing sites (Figure 5a). Midday maximum NEE rates reached $\text{ci. } -3.5 \mu\text{mol m}^{-2} \text{ s}^{-2}$ in October in the Exclosure site. The other pattern was characterized by similarly high NEE rates for the morning and midday records followed by a decline in the afternoon as observed in the Species shift, shrub encroachment and oat crop sites (Figure 5a, g). During the dry season, from January to May 2009, diurnal positive NEE fluxes were recorded with larger NEE rates at midday than in the morning or night for all sites (Fig. 5d-h).

At a monthly scale, daytime net ecosystem CO_2 exchange differed among the five sites on five of the seven months included in this analysis (Site*Date $P < 0.05$, Table 2). There was a clear seasonal pattern, with highest negative NEE rates coinciding with the wettest months (October, June and July) compared to either neutral or positive CO_2 fluxes recorded for the dry season.

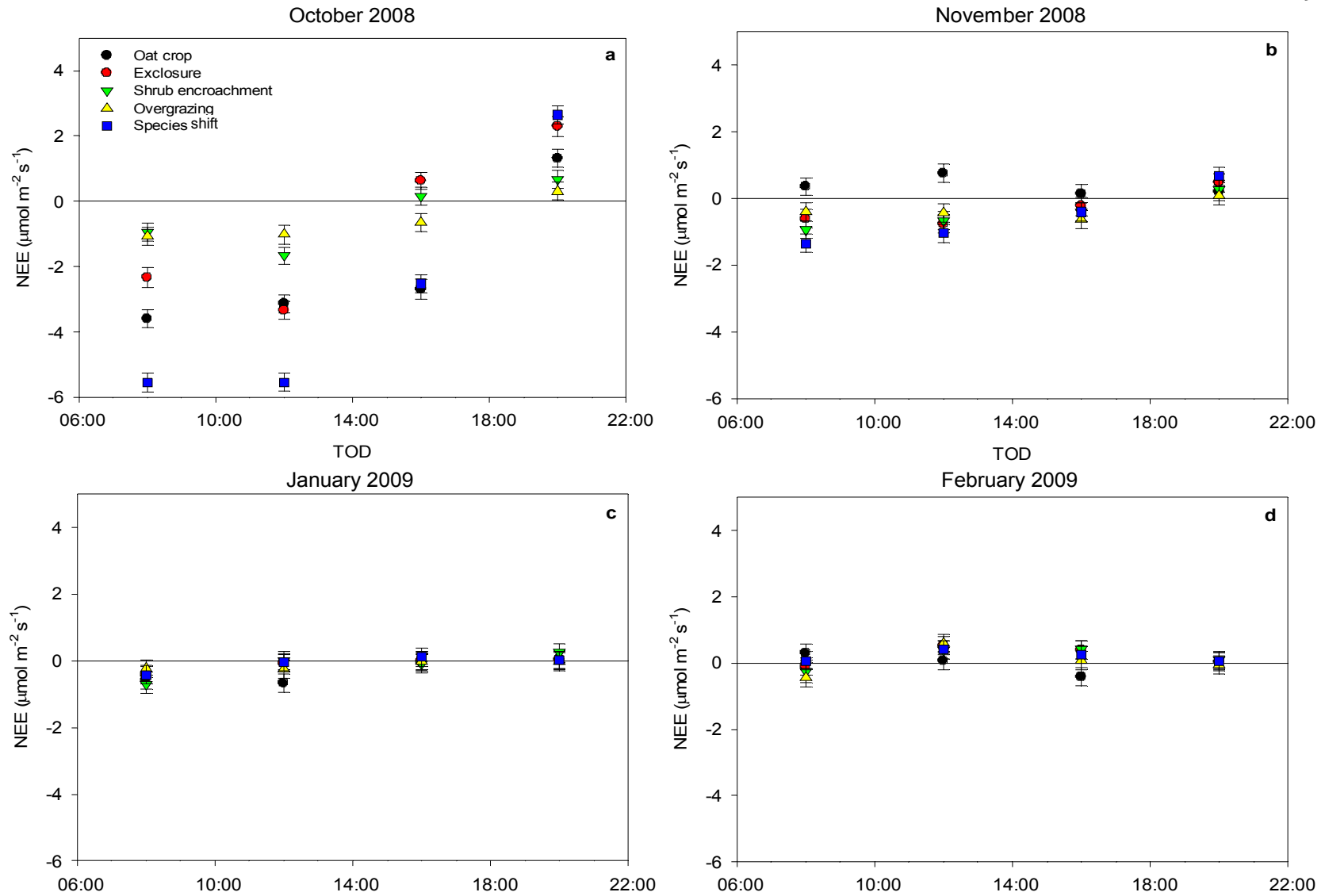


Figure 5. Diel time courses of net ecosystem CO₂ exchange (NEE) in five sites of a short-grass prairie subjected to five different land use types. Each data point represents the average of six plots \pm 1 SE. Observations for overgrazing site in May are missing because of adverse weather conditions. Negative values indicate CO₂ uptake by ecosystem from the atmosphere.

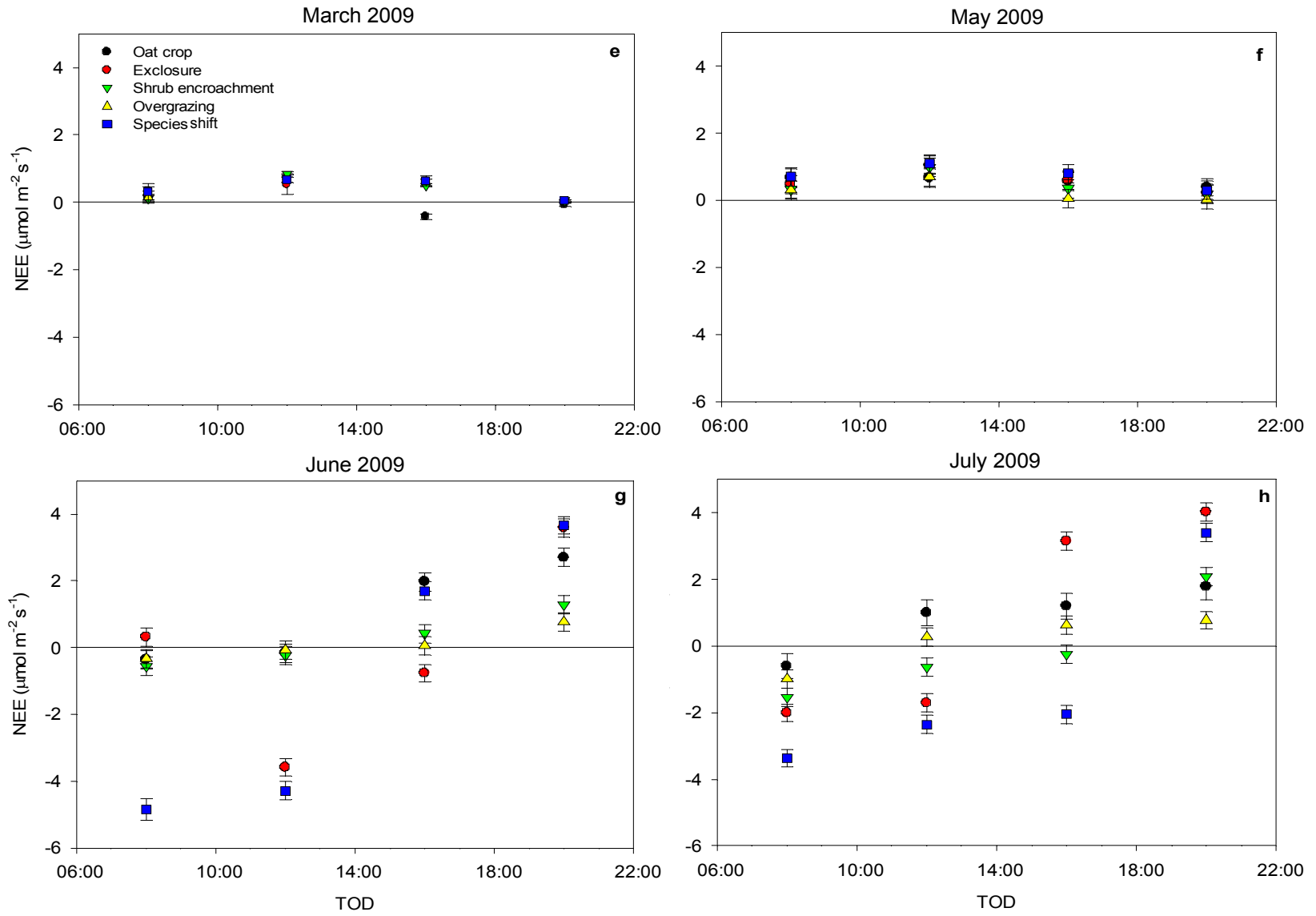


Figure 5. Cont.

Species-shift plots showed the largest negative NEE_{daytime} flux in October, June and July ($p < 0.05$, Site*Date*TOD, Table 2), with maximum rates of $-7.9 \pm 0.29 \mu\text{mol m}^{-2} \text{s}^{-2}$ recorded in October (Figure 6b). The Oat crop plots also exhibited a high negative NEE rate but it was restricted to October when the crop was fully growing, afterward fluxes fell close to zero. In May when the oat was seeded and there was a rain event, fluxes indicated reinitiation of NEE activity. However, rather than fixation there was a release of CO_2 (up to $0.783 \pm 0.409 \mu\text{mol m}^{-2} \text{s}^{-2}$) that was maintained in June and July by the exclosure, the overgrazing and the oat crop. For the Exclosure, intermediate negative fluxes were recorded with maximum rates in October ($-3.091 \pm 0.298 \mu\text{mol m}^{-2} \text{s}^{-2}$), that turned into positive fluxes from February to May, recovering carbon uptake in June ($-2.2722 \pm 0.2899 \mu\text{mol m}^{-2} \text{s}^{-2}$) but even was significantly lower than in Species-shift plots ($p < 0.05$). In comparison, fluxes for overgrazing and shrub encroachment sites were the least negative and generally similar between them, differing significantly only in May and July (Figure 6b, $P < 0.05$).

For $NEE_{\text{nighttime}}$ fluxes there were significant differences among the land use types and dates ($p < 0.05$, Site*Date, Table 2). Major positive fluxes were detected at the wet months (October, June and July), whereas fluxes were near to zero for the dry month (January to May). However no significant differences in fluxes among sites were observed for these dry and cold months (January-May), but only for fall and summer. A significant higher $NEE_{\text{nighttime}}$ was recorded for the species-shift plots compared to all other sites for October ($2.6458 \pm 0.1672 \mu\text{mol m}^{-2} \text{s}^{-2}$) and July ($3.4038 \pm 0.1672 \mu\text{mol m}^{-2} \text{s}^{-2}$; $p < 0.05$, Figure 6a). In contrast to the moderate to low NEE_{daytime} fluxes recorded in the wet months in the exclosure site, $NEE_{\text{nighttime}}$ fluxes in the same season were larger and only slightly lower than species-shift plots (Fig. 6a).

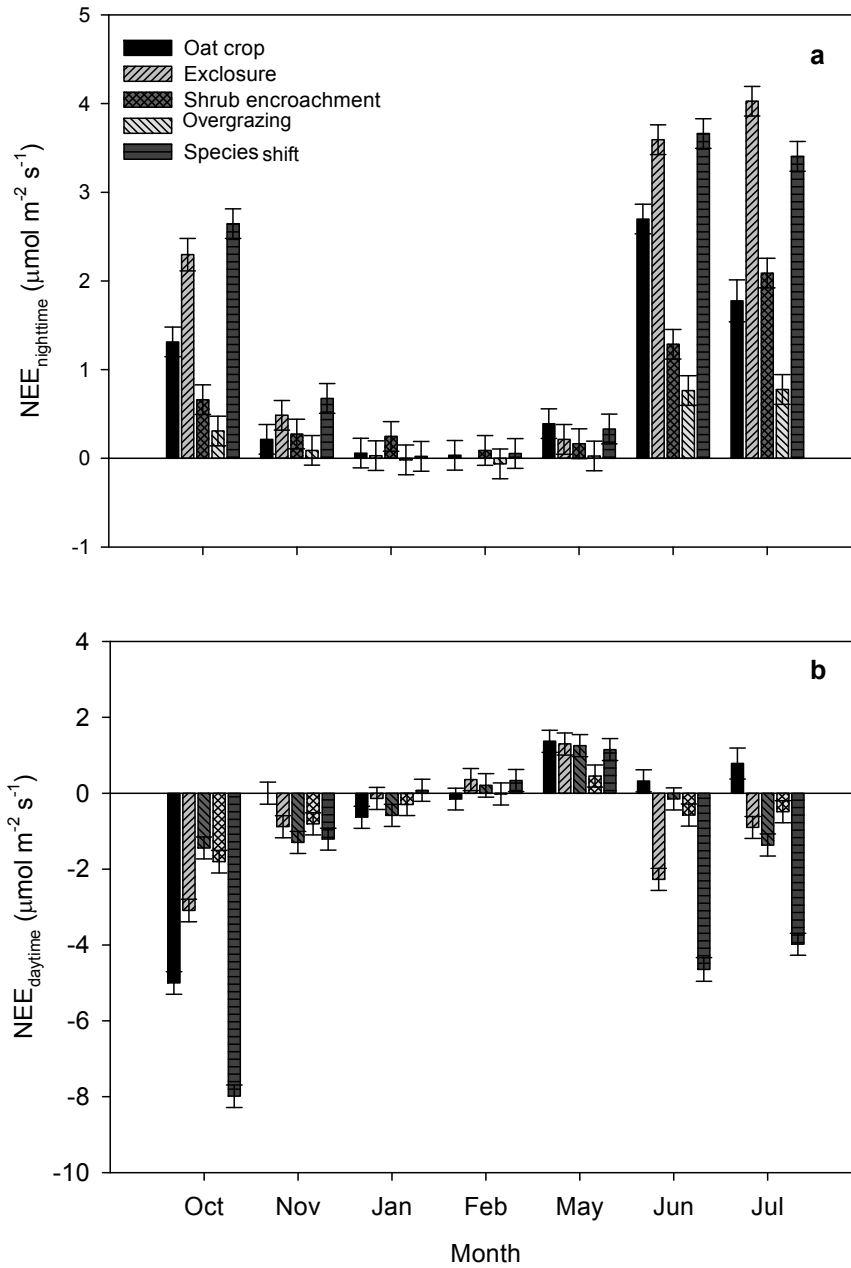


Figure 6. Daily nighttime (a) and daytime (b) net ecosystem CO₂ exchange (NEE) at different months in a short-grass prairie under different land-use types in Central Mexico (mean ± 1SE), measured from October 2008 to June 2009.

3.2 Evapotranspiration

There were significant differences for global ET_{daytime} and $ET_{\text{nighttime}}$ among the five land use types ($P < 0.05$; Figure 7; Site main effect, Table 2). Both, Species-shift and exclosure plots exhibited highest ET_{daytime} rates (1.28 ± 0.029 and 1.099 ± 0.03 $\text{mmol m}^{-2} \text{s}^{-1}$) that were significantly different from Shrub encroachment, overgrazing and Oat crop plots (0.928 ± 0.030 , 0.754 ± 0.03 , 0.776 ± 0.032 , respectively; Figure 8). On the other hand, nighttime ET rates were not higher than 0.12 $\text{mmol m}^{-2} \text{s}^{-1}$. The highest $ET_{\text{nighttime}}$ rates were seen in Exclosure and Shrub encroachment ($0.122 \pm 8.340\text{E-}3$ and $0.116 \pm 8.23\text{E-}3$, respectively), significantly different from the other sites (Figure 7).

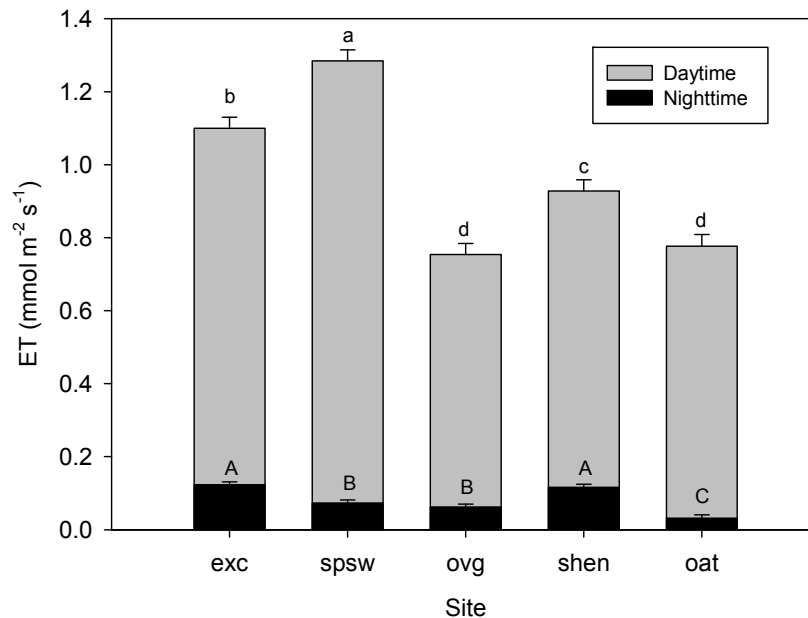


Figure 7. ET rates (mean \pm 1SE) in a short-grass prairie in Mexico exposed below to five different land-use types through 8 month of measurement. Negative values represent fluxes from the atmosphere to the ecosystem. Different letters on top of bars indicate statistical differences among sites with at $p < 0.05$ (Capital letter refer to differences in nighttime fluxes and lowercase refer to daytime fluxes). Abbreviations refer to; Exc = exclosure, spsw = species-shift, ovg = overgrazing, shen = shrub encroachment and oat = oat crop.

Analogous to NEE, the evapotranspiration in all five land use types followed both daily and seasonal distinctive fluxes (Table 2, $P < 0.01$, Site*Date*TOD). Daily fluctuations included a maximum ET flux observed at midday for wet months, falling close to zero at night (Figure 8a, g, h,). In contrast, during the dry months there was not fluctuation in diurnal ET and it was almost indistinguishable from the nocturnal ET flux (Fig. 8c, d, e, f). Seasonally, the largest ET fluxes coincided with the wettest months (October, June and July) whereas the smallest fluxes were observed during January to May (dry months). In both, diurnal and seasonal fluctuations significant differences in ET fluxes were observed among land use types ($p < 0.05$), however there was not a clear ET flux pattern of them (Figure 9b). For instance, the greatest ET fluxes during wet months (October, June and July) were mostly observed for the species-shift and exclosure plots (Figure 9b). In contrast, land use types with the least plant cover such as overgrazing, shrub encroachment and oat crop exhibited the lowest ET fluxes except for some inconsistent peaks. Nighttime ET fluxes were overall almost nil from October to May (Figure 9a), showing small ET fluxes in June and July for all five land use types (Figure 9a). In the particular case of Oat crop in May, negative $ET_{\text{nighttime}}$ fluxes indicated a significant water uptake from the atmosphere by the ecosystem ($-0.219 \pm 0.02 \text{ mmol m}^{-2}\text{s}^{-1}$).

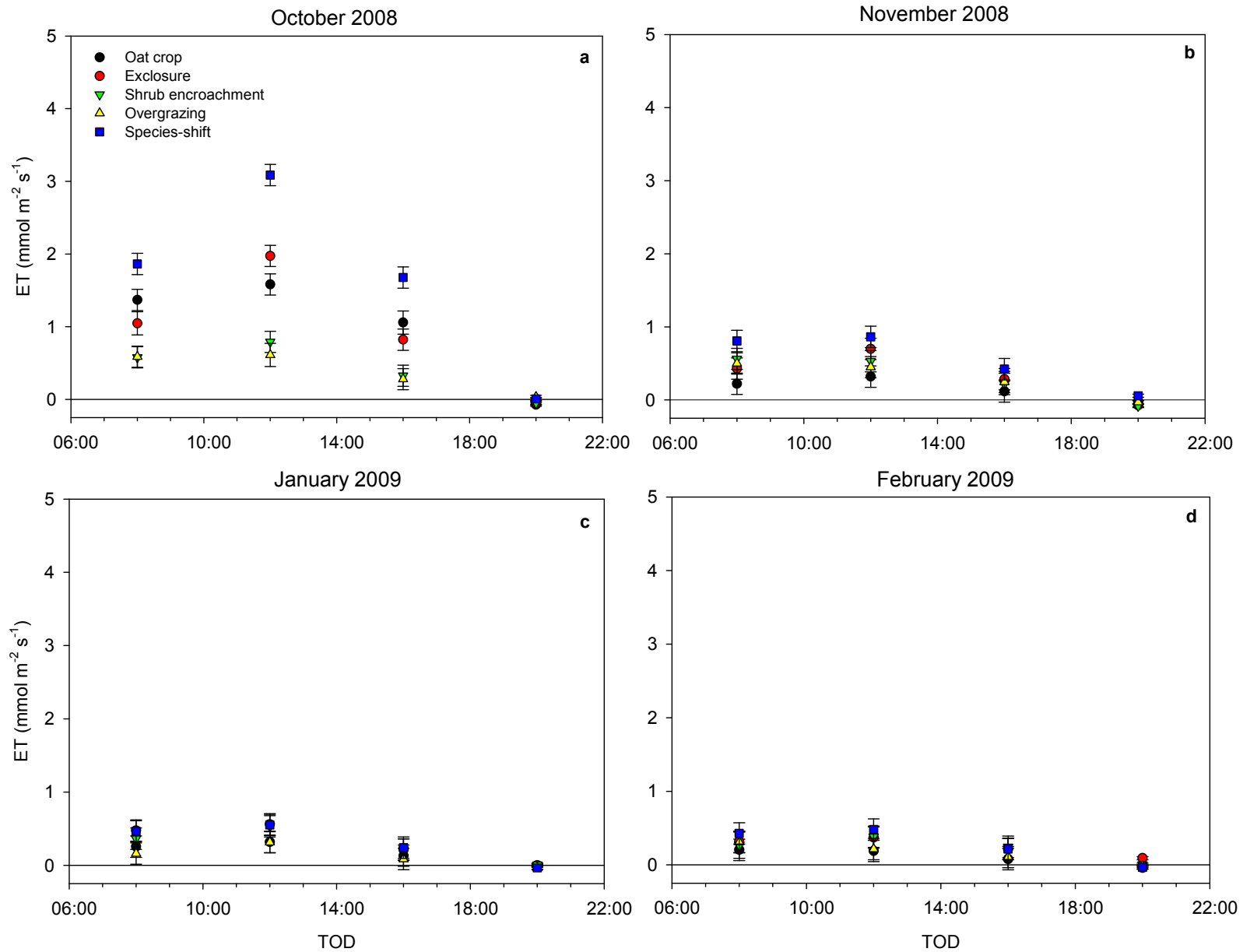


Figure 8. Diel time courses of Evapotranspiration (ET) in a short-grass prairie under five different land use types across eight months of monitoring. Each data point represents one individual plot measurement. For March, data from the overgrazing site are missing because of adverse weather conditions to measure.

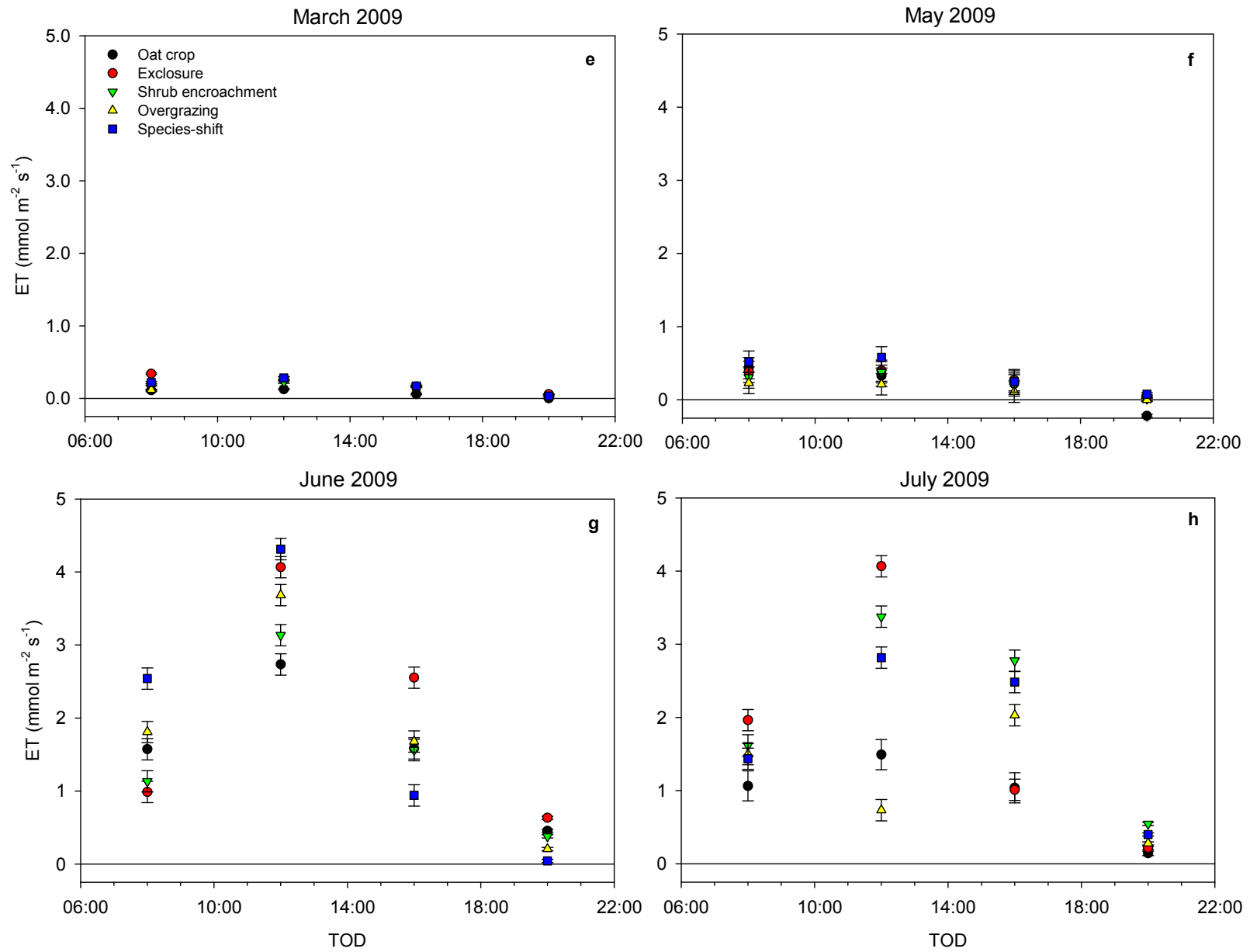


Figure 8. Cont.

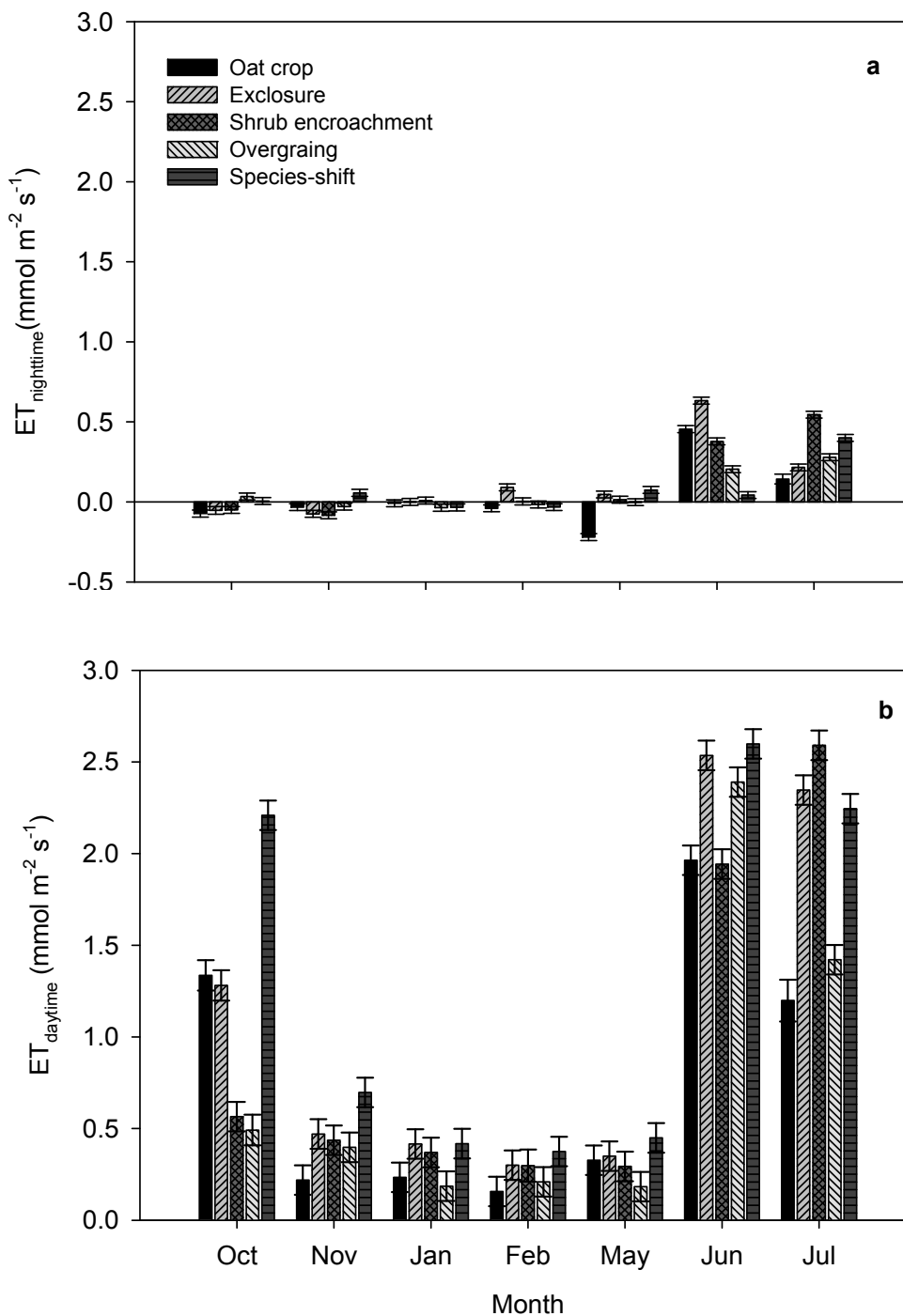


Figure 9. Daily nighttime (a) and daytime (b) evapotranspiration rates (ET) at different months in a short-grass steppe prairie under different land-use types in Central Mexico (mean \pm 1SE), measuring from October 2008 to June 2009.

3.3 Abiotic drivers

Precipitation

Cumulative annual precipitation was very similar for the two years when this study was carried out and also very similar to the 30 years regional average. In 2008, cumulative annual precipitation was 443 mm whereas it reached 442 mm for 2009 (until September 15). However, the distribution pattern of precipitation was distinctive for each year with August being the wettest month in 2008 with 230.4 mm (52% of annual precipitation), compared to September with 206.5 mm (47% of annual precipitation) in 2009 (Figure 10). Comparing those records with the average pattern, there was a displacement for the most raining month.

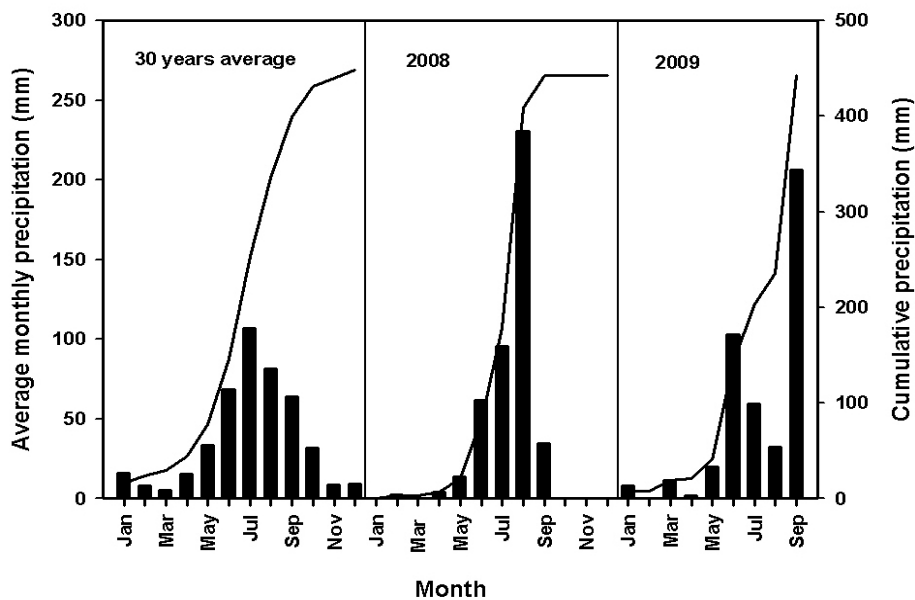


Figure 10. Average monthly (left axis) and cumulative precipitation (right axis) over a 30 year recording period (left panel) and during the study period (October 2008 – July 2009, central and right panels) in Los Llanos de Ojuelos, Mexico.

Soil water content

Soil water content (SWC) in the upper 15 cm soil layer followed the precipitation pattern, with the highest water content observed in October (2008), June and July (2009), whereas records in winter and spring exhibited the lowest SWC for all sites (Figure 12). Significant differences in SWC were registered among sites but only for the wet season ($p < 0.05$), while SWC remained very similar the rest of the year. Thus, from November to May SWC in all sites was maintained below 9% of volumetric soil water content. For the wet months, the exclosure plots exhibited the most efficient soil water recharge as observed in October, June and July ($19.01 \pm 1.6\%$ and $29.3 \pm 1.07\%$, respectively), followed by the species-shift site ($16.28 \pm 0.66\%$, and $26.3 \pm 0.66\%$ for October and June respectively). In particular, overgrazing, shrub encroachment and oat crop were less efficient recharging the upper soil layer following rain events.

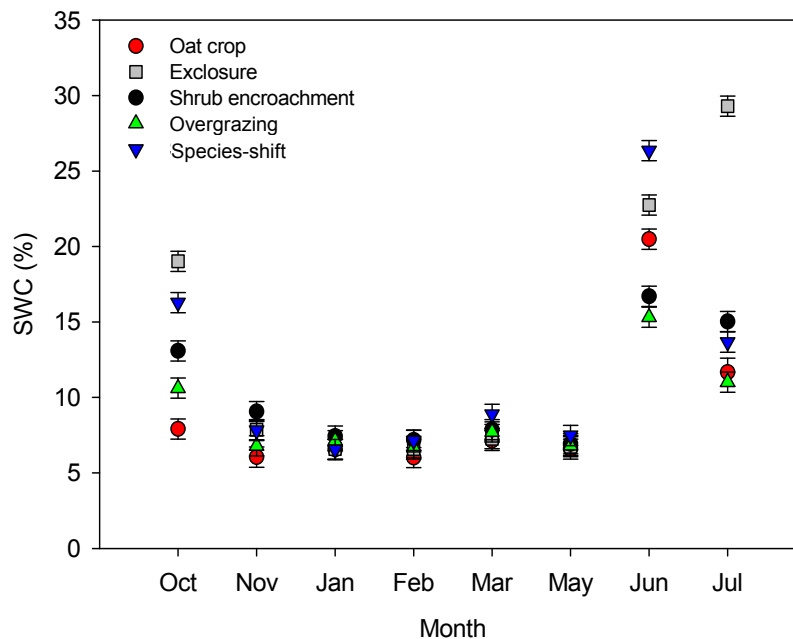


Figure 11. Volumetric soil water content (%) at the five sites of a short-grass prairie in Mexico subjected to different land-use types, across eight months of monitoring from October 2008 to June 2009 (mean \pm 1SE).

3.4 Biotic drivers

Leaf area Index

The Leaf area index (LAI) differed among land use types and dates ($p < 0.05$). Maximum LAI appeared to corresponded with SWC peaks in October, June and July. For dry and wet seasons, both the enclosure and the species-shift sites displayed similar LAI, except for July in which the species-shift site exhibited higher LAI values. For October, the species-shift, the enclosure and the Oat Crop reached the maximum LAI (0.608 ± 0.124 , 0.602 ± 0.052 and $0.527 \pm 0.066 \text{ m}^2/\text{m}^2$, respectively); whilst the shrub encroachment and overgrazing plots showed a 30% less LAI (0.207 ± 0.017 and $0.180 \pm 0.023 \text{ m}^2/\text{m}^2$). The LAI for the shrub encroachment stayed very stable during the recording time because the major plant component were the evergreen perennial herb *Asfodelos fistulosus* and the shrub *Isocoma veneta*, that accounted for ci. 56 to 75% of the leaf area. In the case of the Oat Crop, LAI was overall low exhibiting values close to zero after the crop was harvested (November to May). Non-zero LAI in this land use type was the result of growth by annual species responding to isolated rain events. For the overgrazing site, the plant community maintained overall a very low LAI with a decrease following the end of the rainy season (Figure 12).

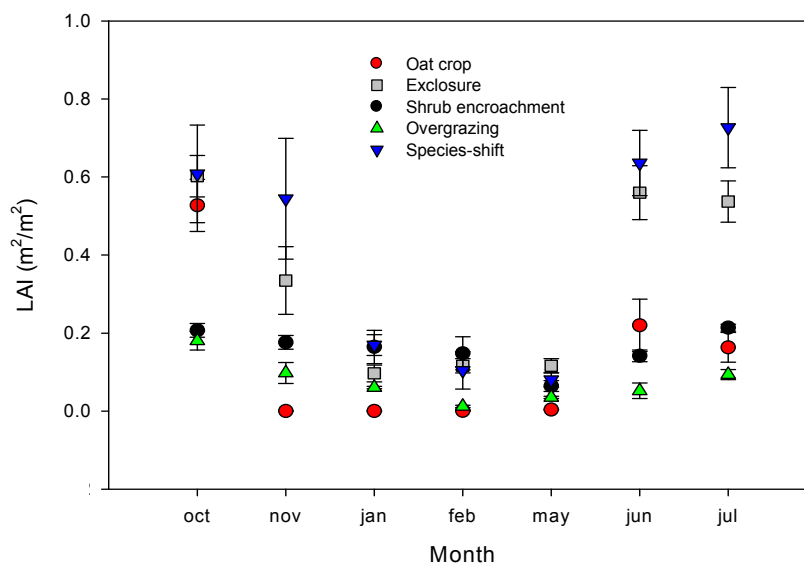


Figure 12. Leaf area index (LAI, mean \pm 1SE) in a short-grass prairie in Mexico under five different land-use types from October 2008 to June 2009.

3.5 Environmental and biotic drivers of ecosystem fluxes

For all sites, PPFD was the factor that explained NEE diel time variation (up to 95% in Exclosure), but it was restricted only to October, November, June and July. Responses by the different land use types to PPFD included those in which NEE reached an asymptote (saturation) and those in which NEE still responded almost linearly to increase PPFD (Figure 13). Thus, for October 2008 the exclosure and the species-shift plots showed a constant NEE increase well beyond a PPFD of $1000 \mu\text{mol m}^2 \text{seg}^{-1}$. In contrast, sites including overgrazing, shrub encroachment and Oat crop reached NEE saturation (asymptote) at a low PPFD (between 500 to $1000 \mu\text{mol m}^2 \text{seg}^{-1}$, Figure 13a), reaching a relatively low A_{max} values (ranging from 1.7 – 6.3, Table 3). Unsaturated light response curves were again observed for the exclosure and the oat crop in June 2009 (Figure 13c). Overall, species-shift showed higher apparent quantum yield (α) and dark respiration (R_d) values (Table 3).

When the vegetation was almost inactive and air temperatures were high (March to May), air temperature was a better predictor of NEE, except in the case of the Oat crop, which exhibited no relationship between these two variables in March (Figure 14a,b). In general, all sites showed similar responses to air temperature, with relatively slow rates of change to increases of temperature (b coefficients from exponential function < 0.1) up to $30 \text{ }^\circ\text{C}$ with faster rates afterward. In particular, shrub encroachment stood out from the other sites with higher b values in both months. This was later on confirmed by estimation of higher Q_{10} values, that allowed to predict increases of 5.4 and 4.4 fold (for March and May, respectively) in respiration (positive $\text{NEE}_{\text{daytime}}$) by a $10 \text{ }^\circ\text{C}$ increase of air temperature compared to 2.5 fold in the other sites (Table 4).

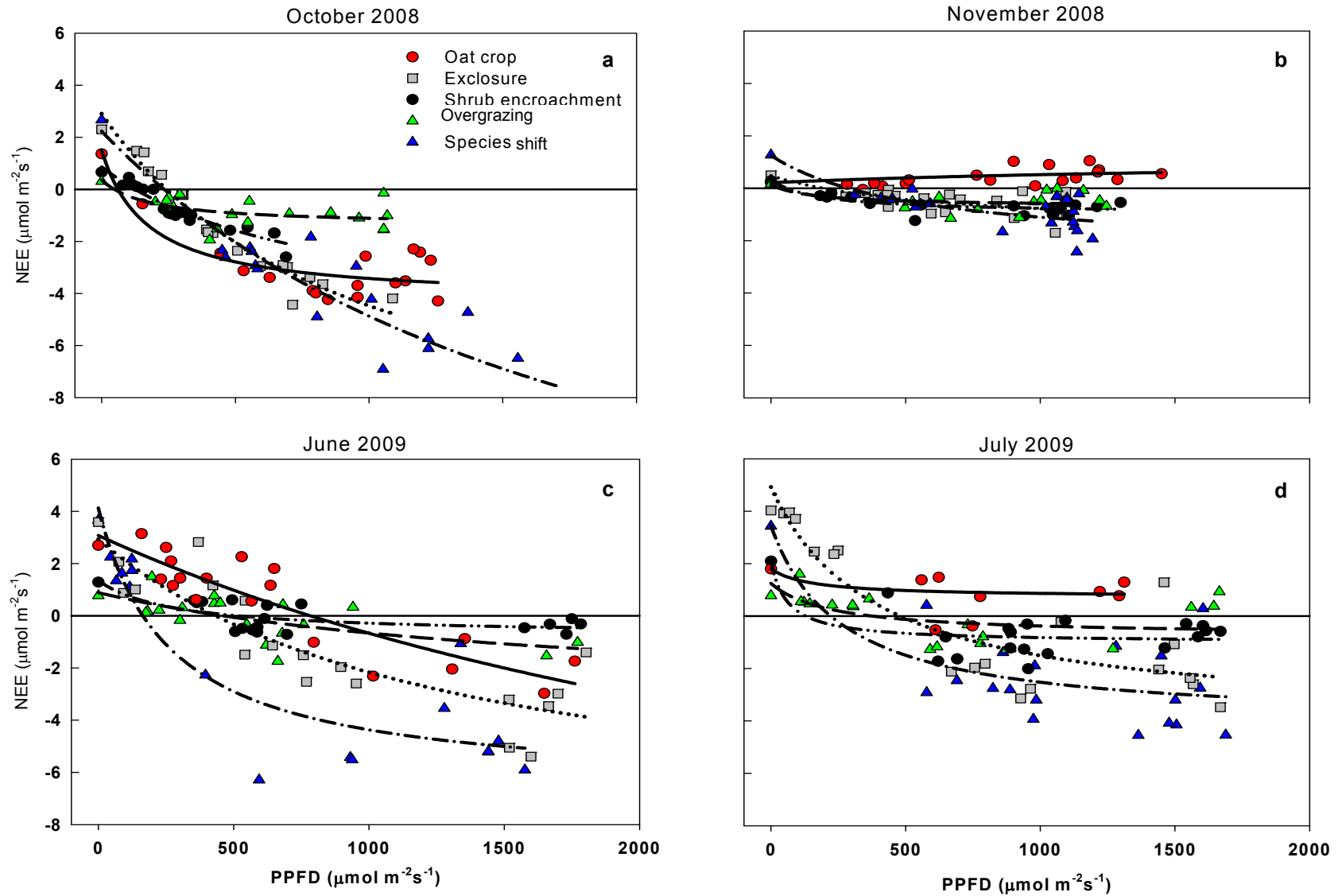


Figure 13. Regression between observed net ecosystem CO_2 exchange (NEE) and photosynthetic photon flux density (PPFD) using a rectangular hyperbola function (Eq. 4 in methods) for five sites on a short-grass steppe in Central Mexico. For the coefficients and p values consult Table 3. Line symbols correspond to: \cdots Exclosure, $- - -$ Species-shift, $- - -$ overgrazing, $- \cdot -$ Shrub encroachment and $—$ Oat crop.

Table 3. Parameter estimates (mean \pm 1 SE) and statistics from the rectangular hyperbolic light response function (Eq. 4 in methods) for five sites under different land-use type in a short-grass steppe. Values correspond to averages over 4 months. Abbreviations refer to the following; Exc = exclosure, Spsh = species-shift, Ovg = overgrazing, Shen = shrub encroachment and oat = oat crop.

Month	Site	$\alpha \pm 1SE$	$A_{max} \pm 1SE$	$R_d \pm 1SE$	R^2	p	A_{2500}
Oct	Exc	-0.015 \pm 0.003	-14.560 \pm 2.579	2.906 \pm 0.406	0.95	<0.0001	-7.58
	Spsh	-0.011 \pm 0.004	-21.188 \pm 7.323	2.235 \pm 1.069	0.85	<0.0001	-9.59
	Ovg	-0.010 \pm 0.011	-1.735 \pm 0.605	0.358 \pm 0.501	0.36	0.0346	-1.26
	Shen	-0.008 \pm 0.002	-6.297 \pm 1.690	0.864 \pm 0.216	0.92	<0.0001	-3.93
	Oat	-0.033 \pm 0.020	-5.776 \pm 0.862	1.495 \pm 0.723	0.77	<0.0001	-3.9
Nov	Exc	-0.003 \pm 0.003	-2.056 \pm 1.021	0.476 \pm 0.403	0.39	0.0194	-1.16
	Spsh	-0.007 \pm 0.005	-3.650 \pm 1.100	1.245 \pm 0.587	0.56	0.0015	-1.74
	Ovg	-0.005 \pm 0.012	-0.812 \pm 0.605	0.125 \pm 0.446	0.27	0.0801	-0.64
	Shen	-0.007 \pm 0.005	-1.267 \pm 0.254	0.308 \pm 0.233	0.61	0.0006	-0.87
	Oat	0.001 \pm 0.001	0.949 \pm 3.027	0.210 \pm 0.272	0.25	0.101	0.75
Jun	Exc	-0.009 \pm 0.005	-11.700 \pm 3.970	2.939 \pm 0.856	0.77	<0.0001	-4.79
	Spsh	-0.041 \pm 0.026	-10.744 \pm 1.256	4.128 \pm 1.289	0.84	<0.0001	-5.59
	Ovg	-0.002 \pm 0.002	-4.249 \pm 3.764	0.883 \pm 0.492	0.43	0.0108	-1.6
	Shen	-0.007 \pm 0.006	-2.092 \pm 0.564	1.347 \pm 0.449	0.47	0.006	-0.53
	Oat	-0.006 \pm 0.004	-13.6800 \pm 9.999	3.4087 \pm 1.020	0.78	<0.0001	-4.08
Jul	Exc	-0.023 \pm 0.014	-8.965 \pm 1.281	4.924 \pm 1.002	0.80	<0.0001	-2.82
	Spsh	-0.029 \pm 0.028	-7.550 \pm 2.082	3.447 \pm 1.456	0.53	0.0025	-3.38
	Ovg	-0.009 \pm 0.013	-1.986 \pm 0.755	1.245 \pm 0.736	0.30	0.0551	-0.58
	Shen	-0.049 \pm 0.120	-3.101 \pm 0.869	2.097 \pm 0.707	0.50	0.0037	-0.93
	Oat	-0.007 \pm 0.042	-1.077 \pm 1.311	1.800 \pm 0.688	0.24	0.5	0.79

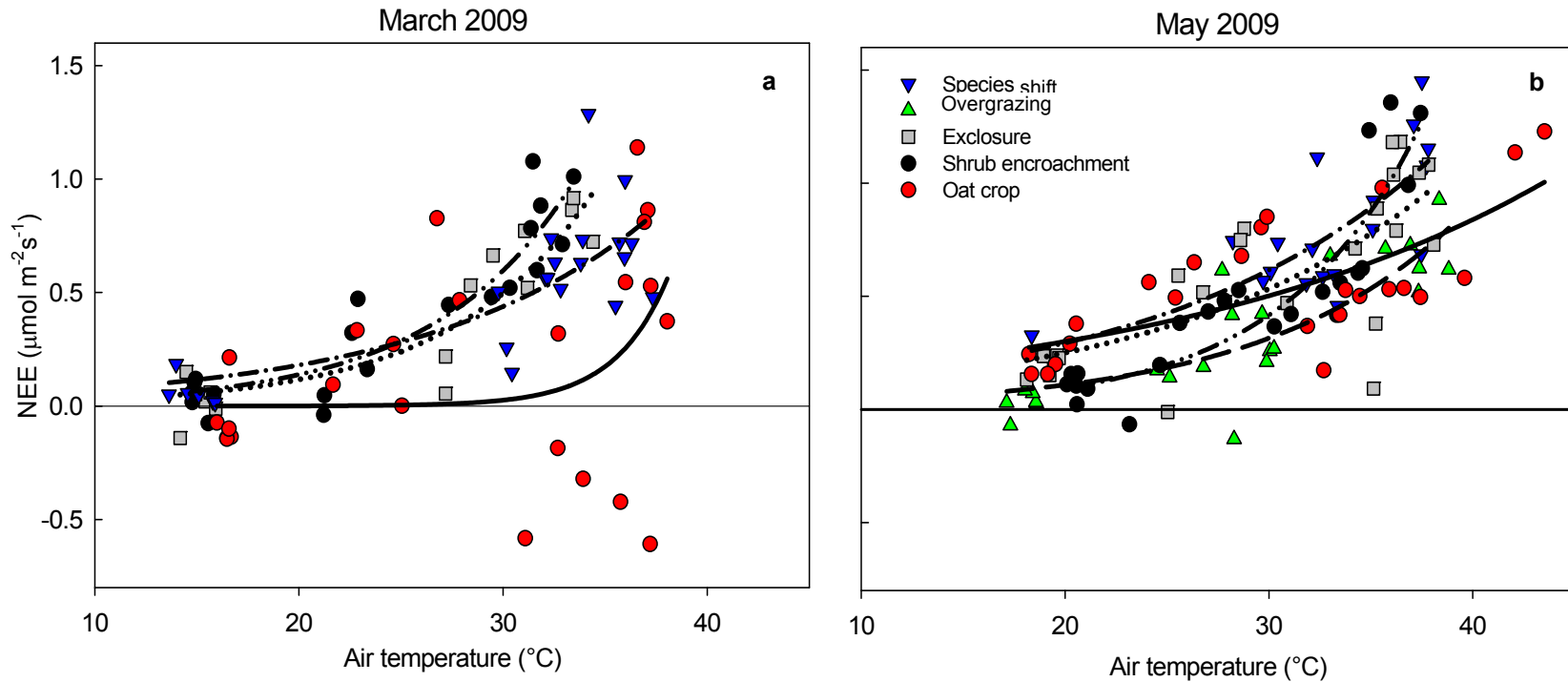


Figure 14. Exponential relationships between daytime NEE and air temperature in March (a) and May (b) in a short grass-prairie under different land use recorded during two dry months. All regressions were statistically significant ($p < 0.05$), with the exception of the Oat crop site in March. Also, the overgrazing site in March is missing because there were not available data. For coefficients calculated and p values consult Table 4. Line symbols correspond to: \cdots Exclosure, $-\cdot-$ Species-shift, $- -$ overgrazing, $- \cdot -$ Shrub encroachment and $—$ Oat crop.

Table 4. Coefficients and least square residuals (R^2) of exponential relationships between daytime NEE and air temperature. Q_{10} values were estimated from equation (6).

Month	Site	$b_0 \pm 1SE$	$b \pm 1SE$	R^2	p	Q_{10}
Mar	Exclosure	0.0241 \pm 0.0467	0.0946 \pm 0.0605	0.34	0.0177	2.57
	Species-shift	0.0305 \pm 0.0273	0.0888 \pm 0.0261	0.62	<0.0001	2.43
	overgrazing		n.a.			
	Shrub encroachment	0.0036 \pm 0.0042	0.169 \pm 0.0368	0.79	<0.0001	5.41
	Oat crop	2.49E-07 \pm 4.45E-06	0.3845 \pm 0.4805	0.09	0.1403	
May	Exclosure	0.0555 \pm 0.0363	0.0754 \pm 0.0188	0.56	<0.0001	2.12
	Species-shift	0.067 \pm 0.0468	0.0739 \pm 0.0199	0.52	0.0007	2.09
	overgrazing	0.0131 \pm 0.0092	0.106 \pm 0.0197	0.71	<0.0001	2.88
	Shrub encroachment	0.0049 \pm 0.0037	0.1484 \pm 0.0217	0.81	<0.0001	4.41
	Oat crop	0.1077 \pm 0.0454	0.0513 \pm 0.0118	0.48	0.0001	1.67

n.a. = data not available.

On the other hand, variation in PPDF explained up to 93% of the variation in daytime ET ($P < 0.05$, Table 5). There was a stronger linear relationship between ET and PPDF in October, November, June and July (Figure 15a,b,g,h; Table 5). Rates of ET increased per unit of PPDF were significantly different for the land use types with the largest plant cover (LAI) such as enclosure and species-shift. Their slopes were more than twofold higher than Shrub encroachment and Oat crop, and up to four-fold than overgrazing (Table 5). In contrast, from January to May, relationship between ET and PPDF was better explained with a polynomial function (Figure 15c,d,e,f; Table 6). Unexpected high ET rates per unit PPDF were observed in June and July by overgrazing and shrub encroachment plots. Across the dry season (November to May), the response of NEE to PPDF was weaker, with slopes under 0.0005; nevertheless, correlation was still strong ($R^2 > 0.4$; $P < 0.05$; Figure 15, Table 6).

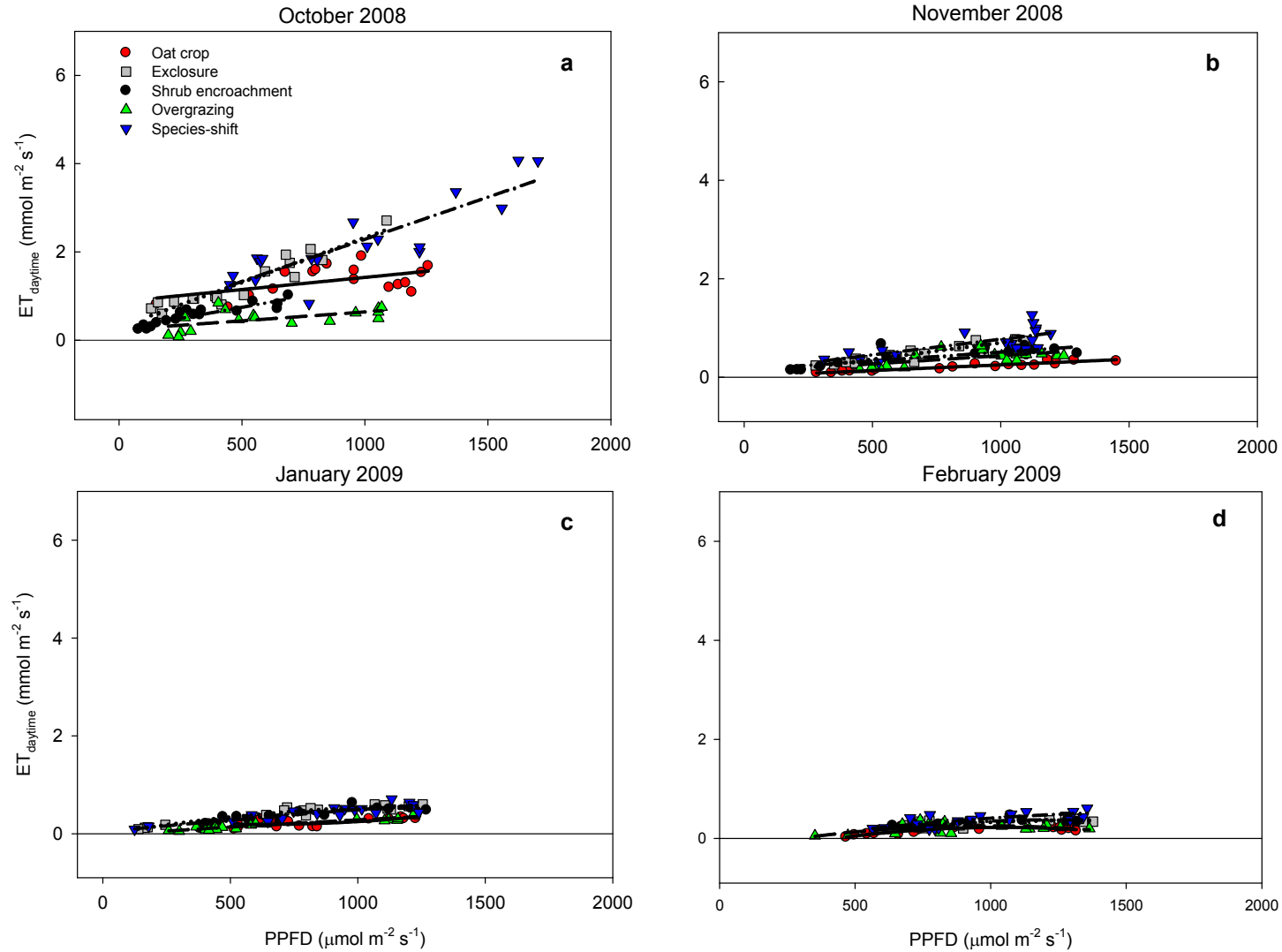


Figure 15. Regressions between daytime Evapotranspiration and Photosynthetic photon flux density in five different land-use change types in a short-grass prairie ecosystem. Linear regressions were used in all months with the exception of May in which a polynomial quadratic function was performed. Line symbols correspond to: $\cdot \cdot \cdot$ Exclosure, $- \cdot -$ Species-shift, $- - -$ overgrazing, $- \cdot \cdot -$ Shrub encroachment and $- - -$ Oat crop.

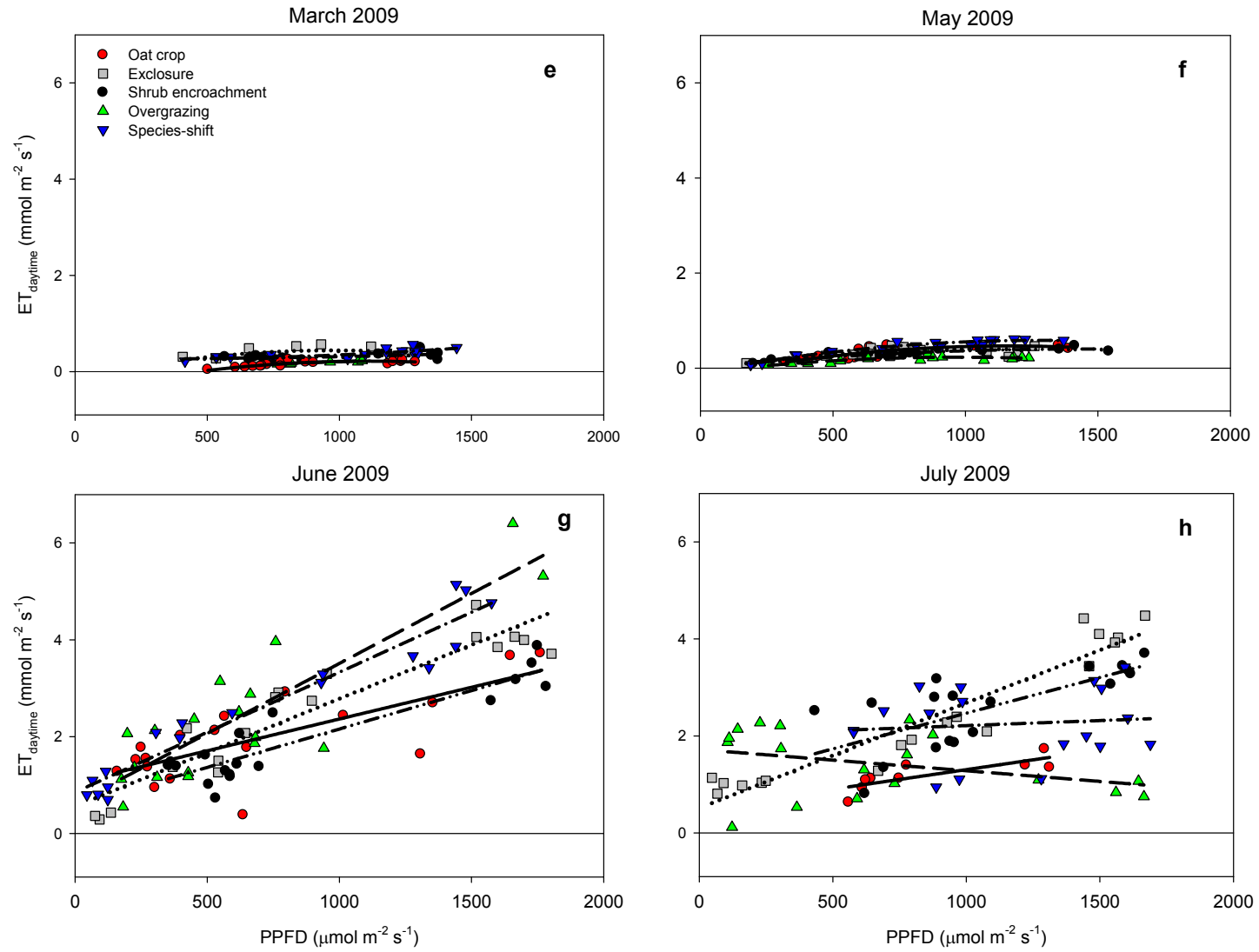


Figure 15. Cont.

Table 5. Regression coefficients and least square residuals (R^2) from linear regressions between ET_{daytime} and PPFD.

Month		intercept (y0) \pm 1SE	slope (a) \pm 1SE	R^2	p
Oct	Exclosure	0.2935 \pm 0.1034	0.0020 \pm 0.0002	0.8894	<0.0001
	Species shift	0.3771 \pm 0.2836	0.0019 \pm 0.0003	0.7537	<0.0001
	overgrazing	0.2377 \pm 0.1010	0.0004 \pm 0.0001	0.3361	0.0129
	Shrub encroachment	0.2439 \pm 0.0417	0.0010 \pm 0.0001	0.8350	<0.0001
	Oat crop	0.8727 \pm 0.2126	0.0006 \pm 0.0002	0.2761	0.0284
Nov	Exclosure	0.0264 \pm 0.0449	0.0007 \pm 6.3470E-005	0.8758	<0.0001
	Species shift	0.1336 \pm 0.1393	0.0006 \pm 0.0001	0.5333	0.0006
	overgrazing	0.1018 \pm 0.0989	0.0003 \pm 0.0001	0.3774	<0.0001
	Shrub encroachment	0.1500 \pm 0.0573	0.0004 \pm 6.4878E-05	0.6584	<0.0001
	Oat crop	0.0195 \pm 0.0211	0.0002 \pm 2.2602E-5	0.8678	0.006
Jun	Exclosure	0.5589 \pm 0.2174	0.0022 \pm 0.0002	0.8805	<0.0001
	Species shift	0.8517 \pm 0.1514	0.0025 \pm 0.0002	0.9323	<0.0001
	overgrazing	0.6201 \pm 0.3100	0.0029 \pm 0.0004	0.7569	<0.0001
	Shrub encroachment	0.5726 \pm 0.1806	0.0016 \pm 0.0002	0.8319	<0.0001
	Oat crop	1.0520 \pm 0.2474	0.0013 \pm 0.0003	0.5616	0.0003
Jul	Exclosure	0.5100 \pm 0.1719	0.0022 \pm 0.0002	0.9126	0.0006
	Species shift	n.s.			
	overgrazing	n.s.			
	Shrub encroachment	0.9967 \pm 0.4087	0.0015 \pm 0.0004	0.5170	<0.0001
	Oat crop	0.4966 0.2062	0.0008 0.0002	0.6476	0.0089

Table 6. Regression coefficients and least square residuals (R^2) of a polynomial quadratic regression between ET_{daytime} and PPFd.

Month	Site	$y_0 \pm 1SE$	$a \pm 1SE$	$b \pm 1SE$	R^2	p
Jan	Exclosure	-0.0134 \pm 0.0413	0.0009 \pm 0.0001	-3.1069E-07 \pm 9.8085E-08	0.9280	0.0001
	Species shift	0.0383 \pm 0.0851	0.0005 \pm 0.0003	-5.1001E-08 \pm 1.7255E-07	0.7729	0.0001
	overgrazing	-0.0309 \pm 0.0697	0.0004 \pm 0.0002	-3.7032E-08 \pm 1.4293E-07	0.8808	0.0001
	Shrub encroachment	-0.2179 \pm 0.1336	0.0012 \pm 0.0004	-4.9898E-07 \pm 2.2362E-07	0.8300	0.0001
	Oat crop	0.3570 \pm 0.2526	-0.0005 \pm 0.0006	4.1855E-07 \pm 3.4947E-07	0.4830	0.0001
Feb	Exclosure	-0.1140 \pm 0.3115	0.0007 \pm 0.0007	-2.4044E-07 \pm 3.2064E-7	0.5275	0.0029
	Species shift	-0.1961 \pm 0.3915	0.0008 \pm 0.0008	-2.3113E-07 \pm 4.1927E-7	0.5421	0.0027
	overgrazing	-0.2637 \pm 0.1854	0.0011 \pm 0.0004	-5.4143E-07 \pm 2.4409E-7	0.3149	0.0569
	Shrub encroachment	-0.3356 \pm 0.3332	0.0011 \pm 0.0007	-4.6009E-07 \pm 3.5804E-7	0.6314	0.0013
	Oat crop	-0.4149 \pm 0.0860	0.0012 \pm 0.0002	-5.8880E-07 \pm 1.0825E-7	0.8069	<0.0001
Mar	Exclosure	-0.1542 \pm 0.4422	0.0012 \pm 0.0011	-6.2513E-07 \pm 6.4237E-7	0.2151	0.4284
	Species shift	0.2796 \pm 0.1611	-0.0001 \pm 0.0004	1.6953E-07 \pm 2.0485E-7	0.5872	0.0013
	overgrazing		Not available			
	Shrub encroachment	0.2743 \pm 0.3339	-3.82E-5 \pm 0.0007	7.4434E-08 \pm 3.5965E-7	0.2825	0.1364
	Oat crop	-0.4305 \pm 0.1440	0.0012 \pm 0.0003	-5.2958E-07 \pm 1.7354E-7	0.7394	<0.0001
May	Exclosure	-0.0353 \pm 0.1192	0.0008 \pm 0.0003	-4.0614E-07 \pm 1.9450E-7	0.4813	<0.0001
	Species shift	-0.0834 \pm 0.0535	0.0010 \pm 0.0002	-4.0992E-07 \pm 1.0480E-7	0.9281	0.0072
	overgrazing	-0.0948 \pm 0.0533	0.0007 \pm 0.0002	-2.06E-07 \pm 5.95E-08	0.7301	<0.0001
	Shrub encroachment	0.0115 \pm 0.0429	0.0005 \pm 0.0001	-1.8869E-07 \pm 6.0361E-8	0.8348	<0.0001
	Oat crop	-0.1876 \pm 0.1358	0.0011 \pm 0.0003	-4.8662E-07 \pm 1.9454E-7	0.6203	0.0006

Throughout the year, the main environmental control of NEE_{daytime} was the volumetric soil water content that explained more than 79% of NEE_{daytime} variation with a quadratic fitting (Eq. 7, Table 7). The fit displays two groups for maximum NEE_{daytime} as dependent on SWC. In one group conformed by enclosure and species-shift sites maximum NEE_{daytime} was observed at around 20% SWC, while for the overgrazing and shrub encroachment sites maximum NEE_{daytime} coincided with a 12% of SWC (Figure 16). The oat crop did not show a pattern in NEE_{daytime} in relation to SWC.

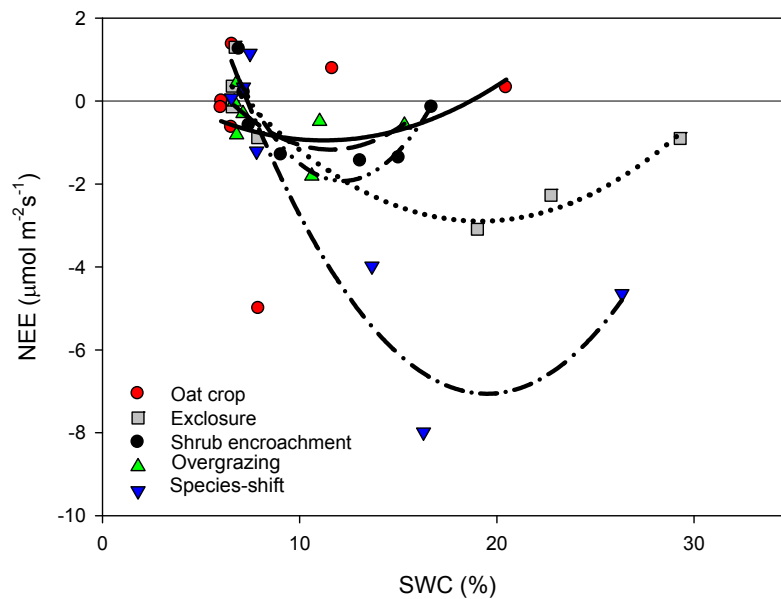


Figure 16. Regressions between monthly daytime NEE and volumetric soil water content across five land-use change types. A polynomial quadratic function was used to fit the data (All p-values<0.05, except for the Oat crop p=0.13). Line symbols correspond to: . . . Exclosure, — · — Species-shift, — — overgrazing, — · · — Shrub encroachment and ——— Oat crop.

Table 7. Regression coefficients and least square residuals (R^2) of a polynomial quadratic regression between NEE_{daytime} and soil water content.

Site	Intercept (y_0) \pm 1SE	$a \pm$ 1SE	$b \pm$ 1SE	R^2	p
Exclosure	4.6348 \pm 1.1861	-0.7867 \pm 0.1872	0.0205 \pm 0.0055	0.86	0.0182
Species shift	11.1591 \pm 2.7877	-1.8699 \pm 0.4289	0.048 \pm 0.0132	0.89	0.0115
overgrazing	4.8019 \pm 3.3947	-1.0317 \pm 0.6949	0.0445 \pm 0.0324	0.42	0.3306
Shrub enc.	11.2136 \pm 3.1934	-2.1586 \pm 0.6138	0.0886 \pm 0.0265	0.79	0.0425
Oat crop	1.21 \pm 7.7473	-0.3844 \pm 1.4796	0.0171 \pm 0.0558	0.05	0.9035

Leaf area index was also a good predictor of NEE and maintained linear relationships with NEE_{daytime} throughout the year (Fig. 18, $R^2 > 0.64$, $P < 0.05$). A high steep slope in shrub encroachment plots indicates that carbon uptake increased faster per unit LAI gain (slope = -19.0457 ± 2.59), even though other sites exhibited higher LAI (Figure 17, Table 8).

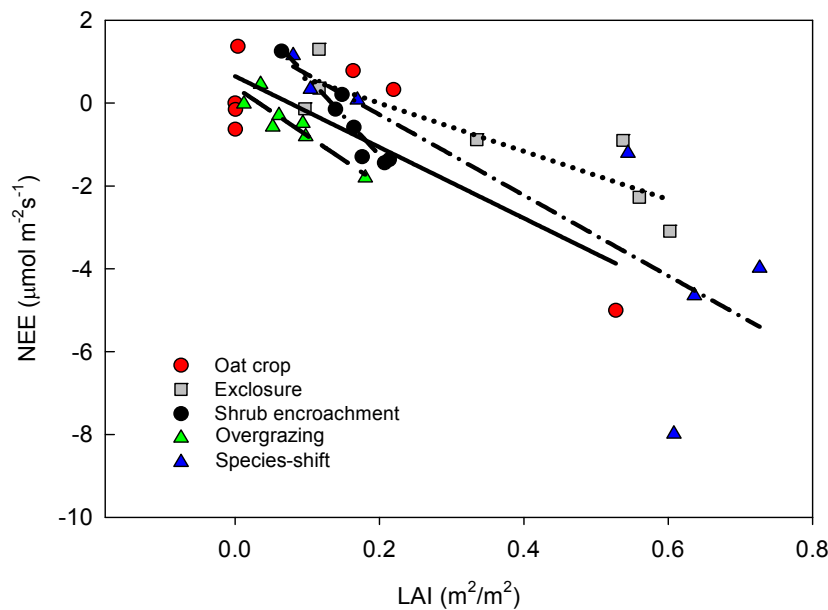


Figure 17. Linear regressions between daytime monthly NEE and leaf are index for across five different land-use change types in a short-grass steppe in Los Llanos de Ojuelos, Jal., Mexico. All regressions were statistically significant ($p < 0.05$). Line symbols correspond to: \cdots Exclosure, $- \cdot -$ Species-shift, $- - -$ overgrazing, $- - -$ Shrub encroachment and $- - -$ Oat crop.

Table 8. Regression coefficients and least square residuals (R^2) of a linear regression for $NEE_{daytime}$ and Leaf area index.

Site	intercept (y_0) \pm 1SE	slope (a) \pm 1SE	R^2	p
Exclosure	1.1595 \pm 0.5457	-5.817 \pm 1.3685	0.78	0.0081
Species shift	1.6617 \pm 1.4863	-9.7243 \pm 3.0666	0.66	0.0248
overgrazing	0.3849 \pm 0.2106	-11.7172 \pm 2.3004	0.83	0.0038
Shrub encroachment	2.5443 \pm 0.43	-19.0457 \pm 2.5965	0.91	0.0007
Oat crop	0.6477 \pm 0.6351	-8.5704 \pm 2.8283	0.64	0.0291

On the other hand, $NEE_{nighttime}$ was associated to SWC in a logarithmic way ($p < 0.05$, $R^2 > 73\%$, Figure 18). Unlike the relationship between $NEE_{daytime}$ and SWC in which it was clear that there was an optimum SWC to perform maximum carbon uptake, at night time, increases of SWC resulted in more carbon release to the atmosphere. The relationship also displayed to groups of slopes with one including shrub encroachment and overgrazing (1.0167 ± 0.1932 and 1.7024 ± 0.458 , respectively), that exhibited significantly lower slopes than exclosure, species-shift and oat crop (Table 9).

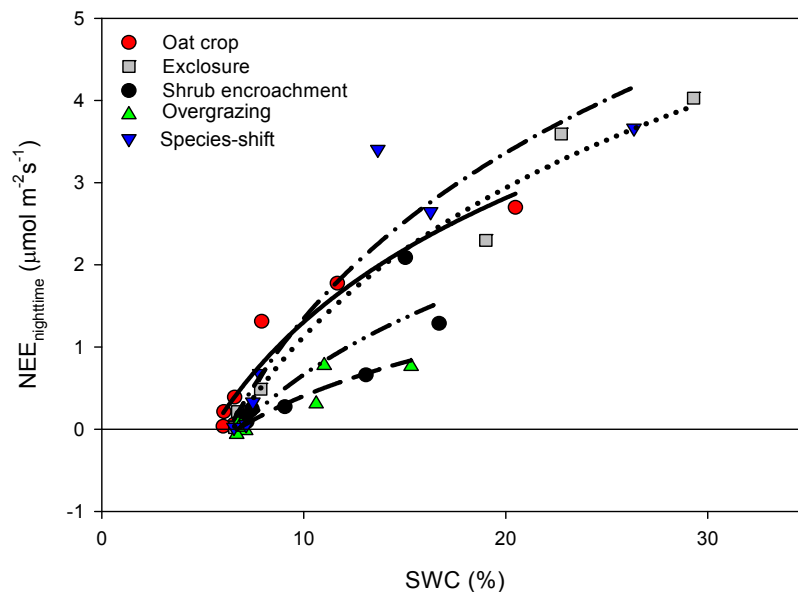


Figure 18. Logarithmic regressions between nighttime NEE and volumetric soil water content. All regressions were significant at ($p < 0.05$). Line symbols correspond to: \cdots Exclosure; $- \cdot -$ Shift species; \cdots Exclosure, $- \cdot -$ Species-shift, $- -$ overgrazing, $- \cdot -$ Shrub encroachment and $- - -$ Oat crop.

Table 9. Regression coefficients and least square residuals (R^2) of logarithmic regression for $NEE_{\text{nighttime}}$ and soil water content.

Site	intercept (y_0) \pm 1SE	a \pm 1SE	R^2	p
Exclosure	-4.8887 \pm 0.4313	2.6117 \pm 0.1704	0.97	<0.0001
Species shift	-5.3519 \pm 1.098	2.9084 \pm 0.4537	0.89	0.0014
overgrazing	-1.9373 \pm 0.4234	1.0167 \pm 0.1932	0.84	0.0033
Shrub encroachment	-3.2564 \pm 1.0727	1.7024 \pm 0.458	0.73	0.0138
Oat crop	-3.7091 \pm 0.5806	2.1771 \pm 0.2675	0.92	0.0005

Seasonal changes in volumetric soil water content explained a fair proportion of seasonal changes in ET_{daytime} (Fig. 20, Table 10. $p < 0.05$, $r^2 > 0.73$). In this case, a linear fit also identified two groups of similar slopes. In one group, the overgrazing and shrub encroachment plots exhibited almost a two fold increase in ET rate per unit SWC than the species-shift, exclosure and oat crop sites.

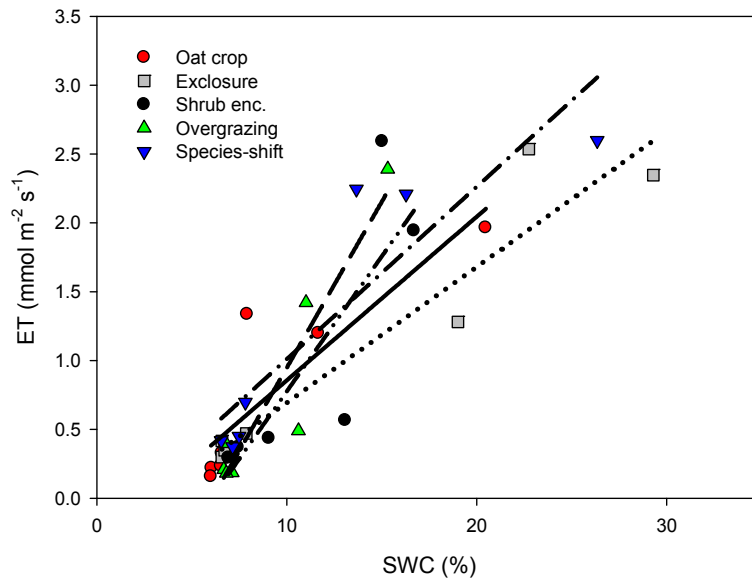


Figure 19. Linear regressions between daytime monthly ET and volumetric soil water content in a short-grass prairie in Central Mexico under for five different land-use change types. Line symbols correspond to: \cdots Exclosure, $- \cdot -$ Species-shift, $- -$ overgrazing, $- \cdot \cdot -$ Shrub encroachment and $- - -$ Oat crop.

Table 10. Regression coefficients and least square residuals (R^2) of linear regression for daytime evapotranspiration (ET) and soil water content (SWC).

Site	intercept (y_0) \pm 1SE	slope (a) \pm 1SE	R^2	p
Exclosure	-0.2922 \pm 0.2275	0.0986 \pm 0.0137	0.9120	0.0008
Species shift	-0.2400 \pm 0.3742	0.1251 \pm 0.0269	0.8126	0.0056
overgrazing	-1.4620 \pm 0.3810	0.2410 \pm 0.0393	0.8824	0.0017
Shrub encroachment	-1.1843 \pm 0.6089	0.1960 \pm 0.0533	0.7300	0.0143
Oat crop	-0.3311 \pm 0.3051	0.1188 \pm 0.0289	0.7711	0.0093

Leaf area index explained 69% and 78% of variation of daytime ET in Exclosure and Species shift, respectively, related through an exponential function ($p < 0.05$; Table 11). Overgrazing, Shrub encroachment and Oat crop did not show significant relation between LAI and ET (Figure 20).

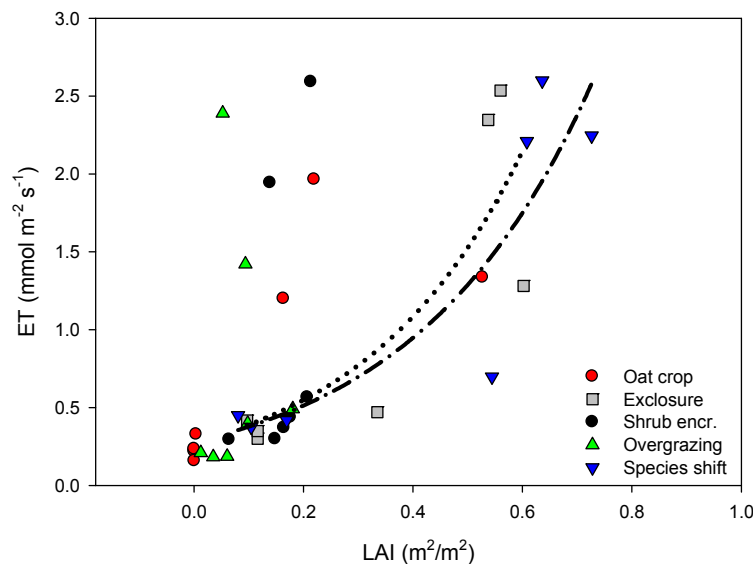


Figure 20. Exponential regressions between monthly daytime ET and leaf area index across five land-use change types ($p < 0.05$ in Species shift and Exclosure alone). Line symbols correspond to: ●●● Exclosure: ··· Exclosure, — · — Species-shift, — — overgrazing, — · · — Shrub encroachment and — Oat crop.

Table 11. Coefficients and least square residuals (R^2) of exponential regression for ET_{daytime} and leaf area index (LAI). Equation 9

Site	$a \pm 1SE$	$b \pm 1SE$	R^2	p
Exclosure	0.2772 ± 0.2409	3.4107 ± 1.5820	0.6905	0.0205
Species-shift	0.2777 ± 0.2053	3.0679 ± 1.1383	0.7853	0.0079
Overgrazing	0.4558 ± 0.3799	0.3178 ± 8.9315	0.0003	0.9685
Shrub encroachment	0.0544 ± 0.1409	13.6171 ± 13.2399	0.1985	0.3164
Oat crop	0.3544 ± 0.1605	2.0179 ± 1.1726	0.3965	0.1297

Temperature and SWC appeared to enhance the $ET_{\text{nighttime}}$ (Temperature with a more clearly exponential tendency, Figure 21); however, very low $ET_{\text{nighttime}}$ rates with high both air temperature and SWC values resulted in a weak correlation, in addition to relatively high $NEE_{\text{nighttime}}$ in presence of low SWC (Figure 22).

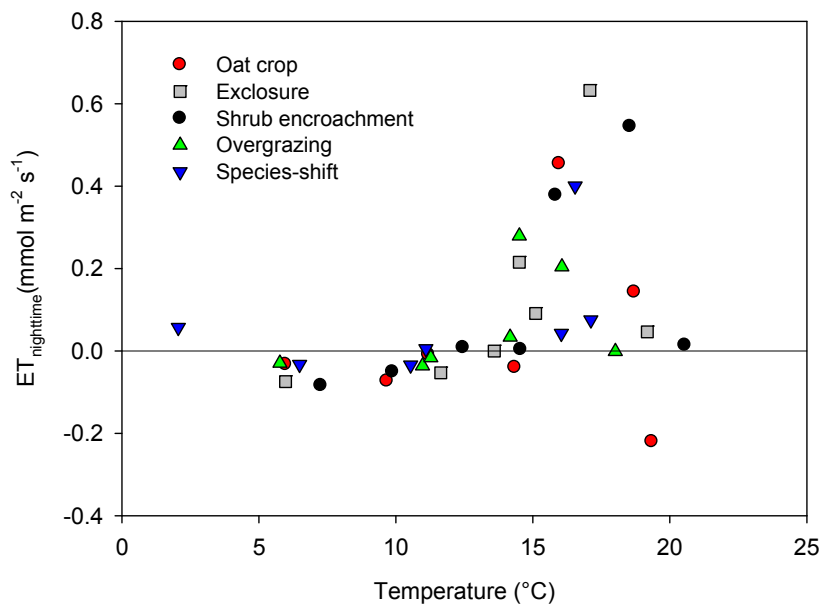


Figure 21. Relationship between nighttime ET and air temperature. Lines were not fitted because no significant relationship was found.

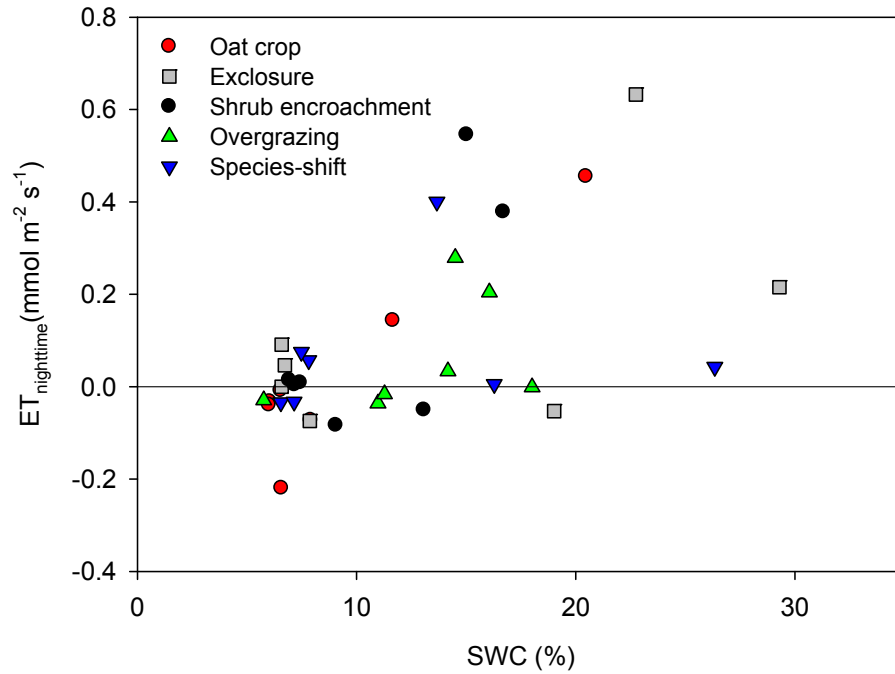


Figure 22. Relationship between nighttime ET and volumetric soil water content. Lines were not fitted because no significant relationship was found.

4. Discussion

Land use change is globally contributing with 1.2 PgC y⁻¹ to the total 9.9 PgC y⁻¹ (12%) emitted to the atmosphere (The global carbon project, 2009). Natural grasslands are an extensive biome covering 40% of all free ice terrestrial surface (Novick *et al.*, 2004). Due to a predominance of herbaceous cover, carbon pools from grasslands are located in the soil. The predominant ways of land use change such as, overgrazing, fire suppression and conversion to agriculture tend to negatively affect both the size of carbon pools and their potential for carbon uptake. There is still large uncertainty on how the effect of land use change on plant cover and species composition will alter the carbon cycling and the carbon budget of this important biome.

4.1 Effect of land-use change on NEE

There were significantly effects of land-use change on NEE such as was predicted in hypothesis 1. However, contrary to was hypothesized (H2), results from this study did not show a clear pattern of effect of plant cover loss and change of species composition by land-use change on daytime and nighttime net CO₂ ecosystem exchange (NEE, Figure 5). It was expected that Exclosure and species-shift were sinks of carbon; however, through a roughly Net CO₂ balance (mean NEE_{daytime} + mean NEE_{nighttime}), Species shift and Overgrazing sites showed be potential sinks of carbon (-0.7818 and -0.2368 μmol CO₂ m⁻²s⁻¹, respectively), whilst Exclosure, Oat crop and Shrub encroachment did function as carbon sources (0.7192, 0.4529 and 0.2049 μmol CO₂ m⁻²s⁻¹, respectively). Mean NEE across eight months (October 2008 to June 2009) indicated a large daytime C uptake capacity for the Species-shift in comparison to the other sites (Figure 5). Since both the exclosure and species-shift sites shared similar ecosystem characteristics (Table 1) including productivity (around 1000 kg MS/ha), plant cover (≈ 28%) and LAI (≈ 0.6, Figure 13), it was expected that both sites would exhibited

similar carbon exchange rates. Surprisingly, daytime NEE for the Exclosure was significantly lower than the one observed for the Species-shift and did not differ from Overgrazing, Shrub encroachment and Oat crop sites.

Differences in LAI values among species-shift and all sites may help to explain the occurrence of higher mean daytime NEE ($-2.323 \pm 0.113 \mu\text{mol m}^{-2}\text{s}^{-1}$), relative to that observed in the other sites; but these differences do not support NEE rates measured in the Exclosure which were much lower than the expected when compared to Overgrazing and Shrub encroachment LAI (Figure 12).

Even though the Exclosure was the representative site for the short-grass prairie, 28 years of protection favored an excessive accumulation of standing litter as a result of the elimination of grazing and wild fire, both natural disturbances that rejuvenate the biomass in this ecosystem (Noy-Meir, 1995). Thus, this large accumulation of standing leaf biomass (1500 Kg/ha) probably contributed to block direct PPFD to active leaves, resulting in the lower daytime NEE for the exclosure as compared to species-shift site. This was not the case for the other sites that were subjected to recent fire (species-shift), grazing (overgrazing and shrub encroachment) and seeding (oat crop) that helped them maintain an active plant cover. In Overgrazing and Shrub encroachment sites, the permanent pressure of grazing kept a single leaf layer and almost no standing grass litter; likewise, the spacing among oat plants and its erectophile leaves, avoided any effect of shading for the oat site. Evidence of the interfering role of standing litter at the exclosure is suggested by the positive NEE fluxes at the late evening time (Figure 5a), the lower NEE rates at similar PPFD and the high light compensation point compared to the Species-shift site (Figure 13a). Moreover Knapp and Seastedt (1986) argued that in addition to restrictions of PAR to emerging shoots (until 58% less PAR), large amounts of standing dead biomass can decrease productivity (until 32%) through reduction of photosynthetic capacity by modification of leaf traits, alteration

of microclimate (temperature, soil moisture) and modifications of nitrogen dynamic; thus, any of these effects also could have taken place reducing C uptake in the Exclosure site. Likewise, a recent study argues that photochemical induced CO₂ (by UV radiation) could account for a significant proportion of annual carbon loss from litter in arid ecosystems (Brandt *et al.*, 2009), in according to several works that refer to aboveground litter photodegradation as a key decomposition process in arid environments (Austin and Vivanco, 2006; Martínez-Yrizar *et al.*, 2007; Parton *et al.*, 2007; Hugh *et al.*, 2008).

There is also the possibility that the large amount of soil litter present at the Exclosure may have played an important role promoting the heterotrophic fraction of Ecosystem respiration. In dryland ecosystems, activity of soil biota and vegetation is mainly limited by soil moisture; hence increase of soil water availability during October, June and July in this study (Fig. 12) is congruent with increasing CO₂ efflux due to soil microorganism activity at the Exclosure. Although plants would have also responded to the increase of soil moisture with subsequent gain in C uptake, the balance between NEE and soil water content suggest that there is a balance favoring ER rather than GEP, particularly when soil water content is above 19% (Figure 20).

Maximum daytime negative NEE rates (carbon uptake up to $-8 \mu\text{mol m}^{-2}\text{s}^{-1}$ in the Species-shift site) observed in this study were consistent with rates reported for similar ecosystems in the growing season (Lecain *et al.*, 2000; Zhang *et al.*, 2008) , and up to 5-fold larger than the sagebrush steppe (Obrist *et al.*, 2003) and the arid shrubland in Mojave Desert (Jasoni *et al.*, 2005). However, these large daytime carbon uptake rates were balanced by equivalent large ER rates (positive NEE); therefore, in net terms , NEE rates were in the range of $\pm 1 \mu\text{mol m}^{-2}\text{s}^{-1}$, which are close to reports from the studies mentioned below (0.5-0.6 $\mu\text{mol m}^{-2}\text{s}^{-1}$). Likewise, maximum NEE rates from the above ecosystems were analogous to the Shrub

encroachment site ($\approx 2.0 \mu\text{mol m}^{-2}\text{s}^{-1}$) which is a more similar system.

Daytime NEE for the Oat crop was characterized by the dominance of the respiratory fraction of C fluxes except for October 2008 (Fig. 6). Active assimilation by the Oat crop in October, occurred only when the oat reached anthesis. A soil covered by actively growing oat seedlings in July was not enough to function as a sink, likely because soil respiration was promoted by soil tillage before sowing (Mermut, 2000; Paustian *et al.*, 2000). The unusual C uptake observed in January (less than $1.0 \mu\text{mol m}^{-2}\text{s}^{-1}$) was promoted by several herbs growing after winter rains. So, it is important to emphasize the functional role of the herbaceous species to fix carbon during the intercrop period offsetting the large loss of C by soil respiration as expected for a bare soil most of the year.

A homogeneous increase of soil respiration observed in May resulted from the usual high temperatures of that month and unusually early rains that triggered positive $\text{NEE}_{\text{daytime}}$ (ranging from 1.36 ± 0.28 to $1.14 \pm 0.28 \mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 6b) that was also observed in nighttime NEE (Figure 6a). This result suggest that precipitation may promote soil activity before GEP is enhanced (Emmerich, 2003; Flanagan *et al.*, 2002) Implications of this mechanism under climate change scenarios where rain will preferentially fall as isolated events (Jentsch *et al.* 2007) suggest that a more spaced rain distribution may favor ER fraction of grassland fluxes.

Contrary to daytime observations, both the Species-shift and the Exclosure sites exhibited similar nighttime NEE, which were higher than the remaining sites (Figure 4). This is probably associated to a much larger root biomass in vegetation with a good and uniform plant cover. Examining a long-term grazing gradient Medina-Roldan *et al.* (2007) reported 2 to 4 times more root biomass in a well preserved grassland compared to more open and degraded grasslands in the same region. This larger root biomass may contribute with proportionally more autotrophic CO_2

emissions to the atmosphere (Raich and Schlesinger, 1992). Similar magnitude of nighttime NEE rates between Exclosure and Species-shift sites suggest that net C uptake is defined by a large contribution of ER in addition to lower GEP at low PPFD levels for the Exclosure as suggested by assimilation rates at standard PPFD ($2500 \mu\text{mol m}^{-2}\text{s}^{-1}$, A_{2500} , Table 3) and low photosynthetic efficiency (slightly lower apparent quantum yield, α , Table 3). Nevertheless, direct measures of daytime respiration could solve this issue.

Overgrazing and Shrub encroachment followed similar low daytime NEE rates, but differed significantly in nocturnal fluxes (Figure 4), where Shrub encroachment showed more respiration. The two-fold increasing night NEE but similar daytime NEE by the Shrub encroachment, may have resulted from all year long maintenance cost of an evergreen canopy that includes adaptations to withstand environmental factors and mechanisms of grazing avoidance (Wardle *et al.*, 1998; Díaz *et al.*, 2007; Zheng *et al.*, 2009). These adaptations include leaves with low nutrients content, high C:N ratios with recalcitrant carbon compounds, low specific leaf area (SLA), and low relative growth rates (RGR) which together lead to a relatively high cost of maintenance when compared to herbs and grasses with deciduous leaves (Poorter *et al.*, 1990; Grime *et al.*, 1997; Gulías *et al.*, 2003). In this study, SLA in Overgrazing site measured in October was $0.0337 \text{ m}^2 \text{ g}^{-1}$ in contrast to 0.0047 from Shrub encroachment, and was even higher than the Exclosure and Species-shift (0.023 and 0.018 , respectively) which is related to higher photosynthetic rates (Reich *et al.*, 1998). Thus, in spite of maintain a yearlong C assimilation due to its evergreen cover, this system functions as a net C source ($0.204 \mu\text{mol m}^{-2}\text{s}^{-1}$) in contrast to the overgrazing site that functions as a small sink ($-0.237 \mu\text{mol m}^{-2}\text{s}^{-1}$). This response run in accordance to reductions of productivity in grasslands due to shrub encroachment (Lett and Knapp, 2005) and contrast with observations found by Scott *et al.* (2006) in another grassland

invaded by woody shrubs with different functional attributes (i.e. *Prosopis velutina*). Likewise, it has been reported that grasslands can respond to grazing pressure in variable ways (Frank, 2002; Owensby *et al.* 2004; Li *et al.*, 2005) performing like both sinks or sources of carbon, even changing from one year to another, as a function of variations of climate, soil properties, plant community composition and landscape (Haferkamp and Macneil, 2004).

Additionally to low nighttime respiration rates in Overgrazing site, the slight sink of CO₂ observed may have been the result of the contribution of soil crusts to photosynthesis (Jasoni *et al.*, 2005; Housman *et al.*, 2006), which are key components of nutrient cycles in arid ecosystems (Lange *et al.*, 1998; Veluci *et al.*, 2006)

4.2 Effects of land-use change on ET

Water vapor fluxes between the vegetation and the atmosphere are mediated through factors associated to transpiring leaves and evaporation at the soil surfaces. Preponderance of either one would depend on either biological factors that alter leaf transpiration or factors associated to soil water evaporation. In this study, a pattern in ET throughout the eight months of monitoring among the 5 different sites was not clearly defined, probably because the two ET components, Evaporation (E) and Transpiration (T), significantly varied among the sites and throughout the year in time and space (through the soil profile; Boulet *et al.*, 1997).

Differences in daytime ET rates among the five sites of contrasting land-use change types of the shortgrass steppe coincided with the first hypothesis stating that increased degradation would affect negatively ET. Observed differences in ET could be the result of i) modifications in plant cover, ii) vegetation structure, iii) change of plant species with different water use patterns, iv) the proportion of the bare soil, or v) changes in the ecosystem capacity to store water in soils, all as a

result of land-use change (Emmerich, 2007). Accordingly, the Species-shift site showed the average greatest daytime ET rates followed by the Exclosure, Shrub encroachment, and with similar rates the Overgrazing and the Oat crop sites (Figure 7).

The Species-shift plots for instance, showed a pronounced high ET rate in October coinciding with the NEE peak, with both fluxes performing the best under a high volumetric soil water content (>15%). Interestingly, in November when SWC was similar to the other sites (<10%, Figure 11), the ET rate for Species-shift plots was still the highest (Figure 9). This response appears to relate to its large LAI that was still similar to the one observed in October (Figure 12).

Plant cover influences the partitioning of incoming water into surface runoff and infiltration (Lambers *et al.*, 2008). Since a large amount of live and dead biomass content was present, in addition to probably higher SOM (Miller and Donahue, 1990; Conant and Paustian, 2002), at both the Exclosure and the Species-shift sites it would be expected the largest soil water storing capacity at these sites, coinciding with SWC records in this study (Figure 11). Large water storage in the soil would support higher ET and NEE rates. However, the very high SWC observed at the Exclosure in July's records was not particularly reflected in ET rates, because this site suffered a big storm before soil water content determinations and after flux measurements took place.

For the Shrub encroachment site, water vapor fluxes were relatively low, and they were similar between October and May (Figure 9), increasing 5-fold in July. This increase in ET of approximately $1 \text{ mmol m}^{-2}\text{s}^{-1}$ was probably driven by a larger contribution of evaporation rather than transpiration. Thus, in spite of a 16% increase in soil water content observed in June (Figure 9) there was not an equivalent rise in LAI that remained very low and similar throughout the year. In addition, the dominant element in the Shrub encroachment plots was the bare soil

comprising around 90% of the plot surface. These elements suggest that observed ET rates were driven mostly by soil evaporation rather than plant transpiration. Controls of evaporation were likely the high daytime temperatures (air temperature > 30 °C). This result agrees with Frank (2003) who argues that LAI in grasslands generally is not the dominant factor determining ET rates. However, this is in disagreement respect to observations for the Exclosure and Species-shift plots where LAI appears to be the main controlling factor (Figure 21). Thus, according to this study results the contention by Frank (2003) would operate in grassland communities where the base soil is the dominant element.

On the other hand, based on the presence of evergreen species on such as the Shrub encroachment site, it was expected higher ET rates during the dry season (November-May) as compared to the other sites (Figure 9). In spite of perennial attributes of *Asfodelos fistulosus* and *Haplopappus venetus* the dominant species that maintained physiological activity from November to May, observed ET followed a pattern similar to the other sites; nevertheless mean ET rate was larger than the Overgrazing and the Oat crop sites (Figure 7), which is in accordance to the Hypothesis 3.

ET in Oat crop was higher respect to its SWC observed (<10%) in October, so apparently was a result of more elevated plant transpiration than soil evaporation by oat plants in concordance with Hanks *et al.* (1968); on the contrary, in June and July there was a magnification of ET but probably more enhanced by soil evaporation stimulated by high soil water content (20%), because LAI of herbaceous was much lower (only 0.2 m²/m²) than that observed in October (0.5 m²/m²) and moreover, In July ET decreased as SWC also did.

Overall, nighttime ET was close to zero from October to May with slightly negative fluxes in May for the Oat crop. These negative fluxes are probably due to water condensation on the grass and soil surface (water yield) similar to the reports from

other studies (Schulze *et al.*, 1994; Obrist *et al.*, 2003; Davie *et al.*, 2006).

Water fluxes of this study are in agreement with the magnitude of ET rates reported in grasslands (Potts *et al.*, 2006). It also agrees with the decreases of ET in grasslands subjected to grazing (Bremer *et al.*, 2001; Frank, 2003) where ET rates have declined up to 7%. Equally, the results coincide with water fluxes decline of grasslands converted to croplands (Burba and Verma, 2006). However, the observations for the Shrub encroachment site disagree with Kurc and Small (2007) study, since they did not observed differences in ET between a grassland site and invaded grassland by shrubs.

Observed ET rates under contrasting land-use types support the idea that land-use change modifies energy fluxes in the short grass prairie, promoting a major energy exchange as sensible heat flux as land-use reduces plant cover and at the same time decrease the capacity of ecosystems to store water in the soil. More open plant canopies in ecosystems exposes larger proportion of bare soil promoting a rise in evaporation rates. At the ecosystem level, an increase in evaporation counteracts the reduction of plant transpiration, but only until water in the upper soil layers is depleted. In contrast, a preponderance of transpiration favors longer time of water exploitation because plants can withdraw water from deeper soil layers (Boulet *et al.*, 1997; Donohue *et al.*, 2007). Additionally, a good plant cover is related to better soil water storing capacity by ecosystems by preventing runoff (Kurc and Small, 2004; Scott *et al.*, 2006), which by personal observations was occurred in the Exclosure and the Species-shift sites.

4.3 Biotic and environmental factors controlling NEE and ET

NEE and ET in a shortgrass steppe under contrasting land-use displayed diurnal and seasonal patterns that depend on the different biotic and abiotic controls. At diel time course, photosynthetic photon flux density (PPFD) was the main driver of

daytime NEE, but only for the growing season. The observed NEE peaks coincided with maximum PPFD levels at the morning and midday measurements, followed by a significant decline in NEE in the afternoon, when PPFD was a limiting factor. In February, March and May were more negative NEE rates in the morning rather than the midday records (Figure 5d-f) notwithstanding its higher PPFD levels, likely as a response to other factors limiting the ecosystem capacity to fix C. Peaks of PPFD are intimately related to peaks of temperature and vapor pressure deficit (VPD), which may decrease photosynthesis by several mechanisms such as; inducing stomatic closure due to high transpiration demands , reducing the photosynthetic efficiency by photorespiration and energy dissipation (Lambers *et al.*, 2008). Likewise, a rise in temperature enhances soil respiration leading to an offset of carbon uptake (Davidson *et al.*, 2000)

From February to May, PPFD was not related to NEE; instead, air temperature did appear to control NEE diel time course. So is reasonable suggest that once plants become senescent or at least water stressed, they do not respond any more to PPFD or they do respond with energy dissipation mechanisms; thus, ER become the main component of NEE in the dry season. Ecosystem respiration responds positively to temperature (Davidson *et al.*, 1998), inverting the diel time course of NEE with a larger fraction of positive fluxes at midday when temperatures are maximum.

For the growing season PPFD did explain up to 95% of the variation on NEE_{daytime} , but its degree of control decreased as the months became drier. In June, after the first rains PPFD was again the strongest control of daytime NEE; however, the fit obtained for these data points was weaker than the one obtained with October data. That could be a masking effect of high ecosystem respiration rates, which is evidenced by Dark respiration (R_d) rates of almost twice than that seen in October (Table 3) in addition to the also larger nighttime NEE rates observed the same

moth.

Overall, October was the time when all sites displayed the C uptake peak. In this month, both the Species-shift and the Exclosure sites did not reach the saturation point in the light response curves; while the Oat crop, overgrazing and Shrub encroachment plots reached saturation soon after a PPFD of $500 \mu\text{mol m}^{-2}\text{s}^{-1}$. Likewise, the light compensation points differed among sites with Species shift and Exclosure sites beginning to show CO_2 efflux at c.i. $250 \mu\text{mol m}^{-2}\text{s}^{-1}$ of PPFD, whereas the Oat crop and Overgrazing plots are already taking CO_2 at about $100\text{-}150 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Figure 13a). Despite the above, apparent quantum yield (α) calculated from rectangular hyperbolic model (Equation 3) did not appear differ among sites (Table 3).

In contrast to results reported by several authors (Ruimy *et al.*, 1995; Gilmanov *et al.*, 2007), in this study apparent quantum yield (α) did not increase through the year as plants were more water stress, but in opposition α got lower, which means that vegetation was not more efficient to capture CO_2 in drier soil conditions, maybe due to natural degradation of photosynthetic capacity of old leaves current in the late growing season. Maximum assimilation rates for the Species-shift site was much higher than the other sites due to its almost linear curve, but still in the range of fluxes for grassland ecosystems (23.8, Ruymi *et al.*, 2005). Nonetheless, when this rate is examined at a standard PPFD (A_{2500}) it turns very similar to the Exclosure and not so different from the others (Table 3). This derives from using an infinite PPFD to calculate, A_{max} , however it yields an unreal parameter. Therefore, A_{max} rate is better estimated using a standard PPFD | typical of the site where observations are carried out.

Daytime NEE for March and May was mainly driven by air temperature. Estimated Q_{10} values were similar among sites (2.09-2.88) and very close to the mean value of 2.4 reported for soil respiration in terrestrial ecosystems (Raich and Schlesinger

(1992). An exception was observed for the Shrub encroachment site that showed Q_{10} values twice as larger than the other sites (5.41 and 4.1 for March and May, respectively) whereas, the Q_{10} value for the Oat crop site was the lowest (1.67). These values allow to predict much larger CO_2 releases for the Shrub encroachment site in response to increases in temperature in the dry months, suggesting that this vegetation would function as a large source of carbon in scenarios of global warming.

On the other hand, diel time courses of ET were also driven by PPFD throughout the adjustment of the stomata opening to control CO_2 and water vapor fluxes (Lambers *et al.*, 2008). During the growing season, ET maintained regularly a linear positive relationship to PPFD (Figure 15) except for overgrazing and Shrub encroachment sites that did not respond to a rising PPFD in July (Fig. 15h). This response coincided for these two sites with a very low NEE in July (Fig. 6b). For February and May, the relationship of ET and PPFD fitted to a quadratic curve, which is expected in water stress plants, due to the closing of stomata under high levels of radiation and temperature observed at midday (Figure 15d,f, Table 5; Mooney *et al.* 1975). In July, a weak relationship between ET and PPFD was the result of large soil evaporation rates driven by high temperatures and moist soil conditions observed (Amundson, 2001).

Both nighttime NEE and ET at a diel time scale was not related to any biotic or abiotic factor considered in this study. Some studies report that night NEE (Respiration) is mainly driven by soil temperature from the upper soil layers (Davidson *et al.*, 1998), however, this variable was not measured in this study, air temperature was not related to NEE or ET.

At a higher scale, monthly daytime NEE was driven by soil water content and leaf area index (89% and 91% of variation was explained by SWC and LAI, respectively). NEE was related to SWC in a polynomial quadratic way (Equation 7,

Fig16). All sites except the Oat crop did show this trend, in accordance with the predictions that considered drastic changes of plant cover with different physiological traits through the year. Soil water content enhanced C uptake until reaching an optimum point. Two optimum soil water contents were detected, one including sites with poor plant cover such as overgrazing and Shrub encroachment reaching a 12% of optimum SWC, and the other one included sites with a good plant cover such as Exclosure and Species shift plots where optimum SWC reached a 19% (Figure 17). A study by Medina *et al.* (2007) carried out in the same region showed that shortgrass communities along a disturbance gradient exhibited differences in water content and soil water dynamics. Thus, the plant community with the highest plant cover and the most proportion of the key species (*Bouteloua gracilis*) displayed the fastest soil water recharge and soil water use. They attributed these soil characteristics to the effects of its large root biomass and organic matter incorporation into the soil. Also, these results suggest that SWC higher than the ones required for optimum NEE enhance Ecosystem Respiration rather than photosynthesis. This response was also the cause of the poor fit observed in June and July between NEE and PPFD.

Considering biotic controls, LAI exhibited overall a negative linear relationship with daytime NEE. Larger LAI values resulted in more negative NEE rates. The relation of LAI to NEE exhibits different efficiencies among the five ecosystem types, with Exclosure as the least efficient ($-5 \mu\text{mol m}^{-2} \text{s}^{-1}$ per $1 \text{ m}^2 \text{ m}^{-2}$) and Shrub encroachment as the most ($-19 \mu\text{mol m}^{-2} \text{s}^{-1}$ per $1 \text{ m}^2 \text{ m}^{-2}$) and Species-shift, overgrazed and oat crop with intermediate values. Thus, a unit change in LAI for the Shrub encroachment site induced a fourfold NEE when compared to the Exclosure (Table 8). The fact that vegetations with the largest proportion of bare soil such as the Shrub encroachment and overgrazing plots were the most efficient is perhaps related to the low proportion of standing dead material blocking

incidence of radiation.

Similar to daytime NEE, seasonal night NEE was also controlled by SWC (Figure 18), characterized by a rapid growth of ER under low SWC followed by a decline in ER as soil water increased, however no vegetation type reached an asymptote. In this case, the overgrazing, the Shrub encroachment and the Oat crop conformed one group that responded with higher ER rates to SWC compared to other group conformed by the overgrazing and Shrub encroachment plots. This latest response could be the result of a reduced root biomass and microbial community in soils limiting soil respiration (Raich and Schlesinger, 1992; Medina *et al.*, 2007).

Regarding evapotranspiration, SWC was the main driver (Figure 19). Overgrazing and Shrub encroachment displayed ET rates twofold of those recorded for the Exclosure, Species-shift and Oat crop sites (Table 10, 0.14 vs. 0.07 mmol m² s⁻¹, per unit %). These differences may have resulted from a larger contribution of soil evaporation in the first two sites as a result of a large proportion of bare soil in these sites, because evaporation from soil surfaces increase as LAI decrease (Law *et al.*, 2002, Ruymi *et al.*, 1995). In this study, nighttime ET rates were not related to SWC or air temperature, variables that one would expect to control ET. Air temperatures appeared to exert an exponential control on ET, however during the dry season a low soil moisture favored low ET rates in spite of high air temperature (Figure 21 and 22). This suggests that there was not enough soil water in the upper soil layers to sustain evaporation. Commonly Soil water content and temperature interact and their effects on CO₂ and ET are usually confounded (Davidson *et al.*, 1998); thus, a separated seasonal analysis should be recommended.

5. Conclusions

Land-use change did modify both CO₂ and ET fluxes; however a clear pattern of change derived from loss of vegetation cover and change of species was not obtained. A site characterized by the dominance of grasses commonly subordinated to *Bouteloua gracilis*, the key species in the Mexican shortgrass, functioned as a sink for the eight months period of this study. Equally, the permanent overgrazing pressure despite to reduce plant cover and productivity did maintain the grassland site as a small carbon sink in the same period. In contrast, the site overgrazed and invaded by perennial shrubs and exotic herbs, the site converted to rainfed agriculture (oat) and even a site fenced out to grazing for 28 years and chosen as a representative pristine shortgrass steppe, did work as net sources of CO₂. This later was suggested to be the result of large amount of dead biomass which favored ecosystem respiration over carbon assimilation; so, a historic land-management record is recommended to acquire a better understanding of ecosystem processes.

Land-use did define a more clear response of ET across the gradient of disturbance. ET rates were higher in sites with major plant cover (measured as LAI) and lower as land-use change imposed a decline of transpiring surface and reduction of soil water availability.

Environmental and biotic drivers do control NEE and ET at different time scales. In the dry season, there was an alternation between PPF and air temperature to control NEE; whilst PPF was the main control for daytime NEE and ET in diel time scale in all sites, however at monthly scales LAI and SWC were controlling these fluxes.

For several responses, land use types were grouped into highly degraded and good condition, as a result of plant cover loss and change of species composition, modifying ecosystem responses for NEE and ET to environmental or biotic drivers.

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Appendices

Statistical tables

Table 1. Repeated measures (ANOVA) for NEEdaytime

Effect	Num DF	Den DF	F Value	Pr>F
SITE	4	25	48.77	<.0001
TOD	2	58	87.93	<.0001
DATE	6	147	140.04	<.0001
SITE*DATE	24	147	19.56	<.0001
SITE*DATE*TOD	68	278	8.68	<.0001

Table 2. Effect of site on NEEdaytime from repeated measures (ANOVA)

Effect	SITE	Estimate	Error	DF	t Value	Pr>t
SITE	agr	-0.4733	0.1201	25	-3.94	0.0006
SITE	exc	-0.8043	0.1128	25	-7.13	<.0001
SITE	inv	-0.4831	0.1135	25	-4.26	0.0003
SITE	ovg	-0.506	0.1128	25	-4.49	0.0001
SITE	vaq	-2.3238	0.1139	25	-20.4	<.0001

Table 3. Effect of Date (n=7) on NEEdaytime from repeated measures (ANOVA)

Effect	DATE	Estimate	Error	DF	t Value	Pr>t
DATE	2008_10	-3.8655	0.1327	147	-29.13	<.0001
DATE	2008_11	-0.84	0.1296	147	-6.48	<.0001
DATE	2009_01	-0.3161	0.1296	147	-2.44	0.016
DATE	2009_02	0.1453	0.1315	147	1.1	0.271
DATE	2009_05	1.1045	0.1296	147	8.52	<.0001
DATE	2009_06	-1.464	0.1315	147	-11.13	<.0001
DATE	2009_07	-1.1909	0.142	147	-8.39	<.0001

Table 4. Repeated measures (ANOVA) for daytime ET

Effect	Num DF	Den DF	F Value	Pr>F
SITE	4	25	55.66	<.0001
DATE	6	147	533.13	<.0001
TOD	2	58	166.29	<.0001
SITE*DATE	24	147	15.81	<.0001
SITE*DATE*TOD	68	281	13.25	<.0001

Table 5. Repeated measures (ANOVA) for nighttime ET

Effect	Num DF	Den DF	F Value	Pr>F
SITE	4	25	19.34	<.0001
DATE	6	146	283.28	<.0001
SITE*DATE	24	146	30.89	<.0001

Table 6. Repeated measures (ANOVA) for nighttime NEE

Effect	Num DF	Den DF	F Value	Pr>F
SITE	4	25	81.53	<.0001
DATE	6	146	208.95	<.0001
SITE*DATE	24	146	15.01	<.0001