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Research Paper

Simple models to predict grassland ecosystem C exchange and actual evapotranspiration using NDVI and environmental variables

Stephen J. Del Grosso[a,b,*], W.J. Parton[b], Justin D. Derner[c], Maosi Chen[b], Compton J. Tucker[d]

[a] USDA ARS PA SMSBR, 2150 Center Ave, Bldg. D, Suite 100, Fort Collins, CO 80526, USA
[b] Natural Resource Ecology Laboratory, Colorado State University, 1231 East Drive, Fort Collins, CO 80523, USA
[c] USDA-ARS High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009-8899, USA
[d] NASA/GSFC, Mail Code: 610.9, Greenbelt, MD 20771, USA

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ABSTRACT

Semiarid grasslands contribute significantly to net terrestrial carbon flux as plant productivity and heterotrophic respiration in these moisture-limited systems are correlated with metrics related to water availability (e.g., precipitation, Actual EvapoTranspiration or AET). These variables are also correlated with remotely sensed metrics such as the Normalized Difference Vegetation Index (NDVI). We used measurements of growing season net ecosystem exchange of carbon (NEE), NDVI from eMODIS and AVHRR, precipitation, and volumetric soil water content (VSWC) from grazed pastures in the semiarid, shortgrass steppe to quantify the correlation of NEE with these driving variables. eMODIS NDVI explained 60 and 40% of the variability in daytime and nighttime NEE, respectively, on non-rain days; these correlations were reduced to 41 and 15%, respectively, on rain days. Daytime NEE was almost always negative (sink) on non-rain days but positive on most rain days. In contrast, nighttime NEE was always positive (source), across rain and non-rain days. A model based on eMODIS NDVI, VSWC, daytime vs. nighttime, and rain vs. non-rain days explained 48% of observed variability in NEE at a daily scale; this increased to 62% and 77%, respectively, at the weekly and monthly scales. eMODIS NDVI explained 50–52% of the variability in AET regardless of rain or non-rain days. A model based on eMODIS NDVI, VSWC, Potential EvapoTranspiration (or PET), and rain vs. non-rain days explained 70% of the observed variability in AET at a daily scale; this increased to 90 and 96%, respectively, at weekly and monthly scales. Models based on AVHRR NDVI showed similar patterns as those using eMODIS, but correlations with observations were lower. We conclude that remotely-sensed NDVI is a robust tool, when combined with VSWC and knowledge of rain events, for predicting NEE and AET across multiple temporal scales (day to season) in semiarid grasslands.

1. Introduction

Grasslands cover over 30% of the Earth's terrestrial surface (Adams et al., 1990; Reynolds et al., 2007), store large amounts of carbon (C) in soil organic matter strongly influence interannual variability in atmospheric carbon dioxide (CO_2) flux (Huang et al., 2016), and support rural economies through livestock grazing (Dunn et al., 2010). Recent analyses suggests that although water-limited, semiarid ecosystems account for only about 16% of global terrestrial NPP, they are responsible for about 29% of interannual variation in NPP, and drought is a primary driver (Huang et al., 2016). Consequently, it is important to improve understanding and better predict how key drivers, such as weather, drive the processes (photosynthesis, plant and microbial respiration) that control biomass production and net carbon flux in these systems. Net primary productivity (NPP) as well as net ecosystem exchange of carbon (NEE) in water-limited, semiarid grasslands are typically controlled by indices related to soil water (e.g., precipitation, soil water content, actual evapotranspiration) to a greater extent than other environmental controls (e.g., temperature, solar radiation). It is well established that NPP and NEE are correlated with normalized difference vegetation index (NDVI) and weather variables, particularly precipitation, at global scales (Del Grosso et al., 2008) and across the US Great Plains (Zhang et al., 2010; Gilmanov et al., 2005). Heterotrophic respiration also is limited by moisture in semiarid ecosystems and is particularly sensitive to rainfall events onto previously dry soil (Huxman et al., 2004).

Previously, Parton et al. (2012) presented empirical equations relating NEE observed in a shortgrass steppe grassland in Colorado, USA,

* Corresponding author at: USDA ARS PA SMSBR, 2150 Center Ave, Bldg. D, Suite 100, Fort Collins, CO 80526, USA.
E-mail addresses: steve.delgrosso@ars.usda.gov (S.J. Del Grosso), William.parton@colostate.edu (W.J. Parton), Justin.Derner@ars.usda.gov (J.D. Derner), compton.j.tucker@nasa.gov (C.J. Tucker).

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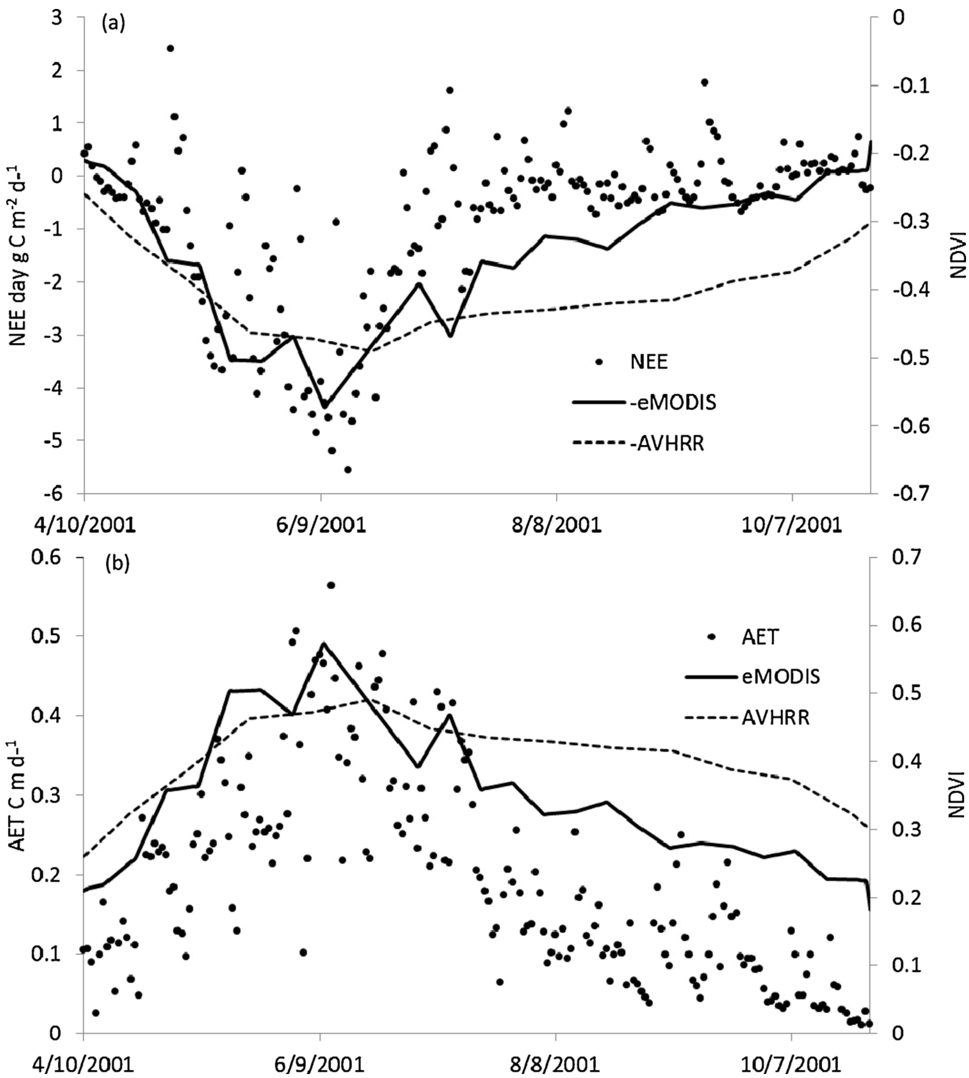

Fig. 1. Net ecosystem carbon exchange (NEE) (a) and actual evapotranspiration (AET) (b) with NDVI from eMODIS and AVHRR for shortgrass steppe during the 2001 growing season.

to soil water content, photosynthetically active radiation, live biomass, air temperature and relative humidity. Models based on these factors explained up to 65% of the variability in observed daytime NEE, but live biomass, which was the most important factor, relied on ground based measurements. In this paper we use flux tower data from shortgrass steppe pastures to demonstrate (1) that NEE is correlated with NDVI and soil water content, (2) that actual evapotranspiration (AET) is correlated with NDVI, soil water content, and potential evapotranspiration (PET), and (3) that precipitation events modify these relationships. We then develop and evaluate models to predict NEE and AET based on remotely-sensed NDVI from two satellite platforms, Moderate Resolution Imaging Spectroradiometer (eMODIS) and Advanced Very High Resolution Radiometer (AVHRR) combined with the weather related variables mentioned above. Lastly, we apply the model to quantify the importance of rain induced respiration on NEE and to compare the impact of increasing rainfall frequency, while keeping seasonal total constant, on NEE.

2. Materials and methods

2.1. Data sets used

NEE, AET and soil water content were observed at the USDA-ARS Central Plains Experimental Range (CPER), lat. 40° 50′ N. long. 104° 43′. The CPER, a Long-Term Agro-ecosystem Research (LTAR) network site, is about 12 km northeast of Nunn, Colorado, USA. Mean annual precipitation is 340 mm with 242 mm occurring during the spring and early summer growing season (April–August) and mean air temperatures are 15.6 °C in summer and 0.6 °C in winter. Vegetative basal cover ranges from 23% to 35% (Milchunas et al., 1989) and is comprised of a mixture of C4 and C3 perennial grasses, a sub-frutescent shrub (*Artemesia frigida*), forbs, and cacti, with the majority of the aboveground plant production coming from *Bouteloua gracilis* (C4 perennial grass). The CPER site, used as an experimental range since 1937, has been grazed by livestock during the past 150 years, with grazing by American Bison prior to European settlement in the 1850s.

Measurements were obtained from two consecutive grazing experiments at the CPER, one conducted from 2001 to 2003, and the other during 2004 to 2006. The earlier grazing study considered three grazing intensities (none, moderate, and heavy) while the latter only had moderate and heavy grazing (Morgan et al., 2016). Bowen ratio CO_2 energy balance (BREB) flux towers were used to infer NEE and AET. Remotely sensed 7-day 250 m resolution NDVI were calculated for the pastures using eMODIS data from the expedited Moderate Resolution Imaging Spectroradiometer (eMODIS) product (Jenkerson et al., 2010) and from bi-weekly 8-km AVHRR (Advanced Very High Resolution Radiometers) data (Tucker et al., 2005). Daily NDVI values for both eMODIS and AVHRR were inferred by linearly interpolating between days with consecutive observations. Volumetric soil water content (VSWC) was measured daily at 0–15 cm depth using calibrated water content reflectometers (Model CS615, Campbell Scientific Inc., Logan, UT, USA). Daily PET was calculated from max/min air temperature and day length based on a simplified Penmen-Montieth equation (Allen et al., 1998).

Observations of NEE, AET, NDVI, and soil water content from the moderately and heavily grazed pastures were averaged. We concentrate on the growing season because NEE during the dormant season was not well correlated with any of the driving variables (Parton et al., 2012). Note that partitioning of daytime vs. nighttime NEE was based on changes in actual day length throughout the growing season. AET from the 2001 to 2003 experiment was used for model calibration while AET from another pasture during 2001 to 2006 was used for model validation. Unfortunately, independent data for NEE validation were not available. However, we used independent biomass observations (Lauenroth, 2013) to test how well above ground NPP was correlated with modeled gross primary productivity (GPP).

2.2. NEE and AET model development

NEE patterns vary diurnally with C uptake due to photosynthesis during daytime typically exceeding respiration leading to negative daytime C flux values while C flux values are always positive during nighttime due to lack of photosynthesis. Consequently, we partitioned the observations diurnally. We then plotted time series of daytime NEE and NDVI for a particular year (2001) and this showed that NEE was negatively correlated with NDVI (Fig. 1a) with maximum C uptake and highest NDVI values occurring in June when plant above ground biomass is also typically at its peak (Parton et al., 2012). AET was positively correlated with NDVI with peak values also occurring during June (Fig. 1b). Fig. 1 also shows that NDVI obtained from eMODIS was more dynamic than NDVI from AVHRR. NEE and AET patterns are also influenced by precipitation events so we partitioned the observations by precipitation (rain days vs. non-rain days). Similar to Parton et al. (2012), precipitation days are defined as those that received any amount of recorded rainfall plus the two subsequent days if the sum of precipitation during the previous two days exceeded 5 mm. This criteria is supported by observations showing that small (2 mm) rainfall events enhance soil respiration rates for about 24 h whereas larger events (5 mm or greater) enhance respiration rates for up to two days (Munson et al., 2010).

Scatterplots and best fitting linear equations of NEE vs. NDVI showed that for a given NDVI value, daytime NEE was more negative and nighttime NEE less positive on non-rain days (Fig. 2a, b). The magnitudes of the correlations between NEE and NDVI were also strongly influenced by precipitation events and day vs. night with the highest coefficients observed during day on non-rain days and lowest values during night on rain days (Fig. 2a, b). For a given value of NDVI, AET was higher in rain days while the correlation coefficients between AET and NDVI differed little between rain and non-rain days (Fig. 2c). In addition to NDVI, NEE was weakly correlated with soil water content except during nighttime on rain days (Fig. 3) but not with temperature (data not shown). AET was weakly correlated with soil water content on both rain and non-rain days and with PET on non-rain days only (Fig. 4).

Because the relationships between NEE and the driving variables were significantly different based on precipitation events and day vs night (Figs. 2 and 3), we optimized four separate eMODIS NDVI, AVHRR NDVI, and water equations (day non-rain, night non-rain, day rain, night rain) by minimizing the root mean square error between modeled [NEE = F(NDVI)*F(VSWC)] and observed NEE. We considered linear and exponential functional forms for both the NDVI and VSWC functions. Note that the four VSWC functions were optimized with the NDVI functions based on eMODIS and AVHRR simultaneously. The models based on eMODIS and AVHRR NDVI were evaluated by comparting observed and predicted total NEE at various temporal scales (daily, weekly, monthly, and annually) and by considering the four sub-

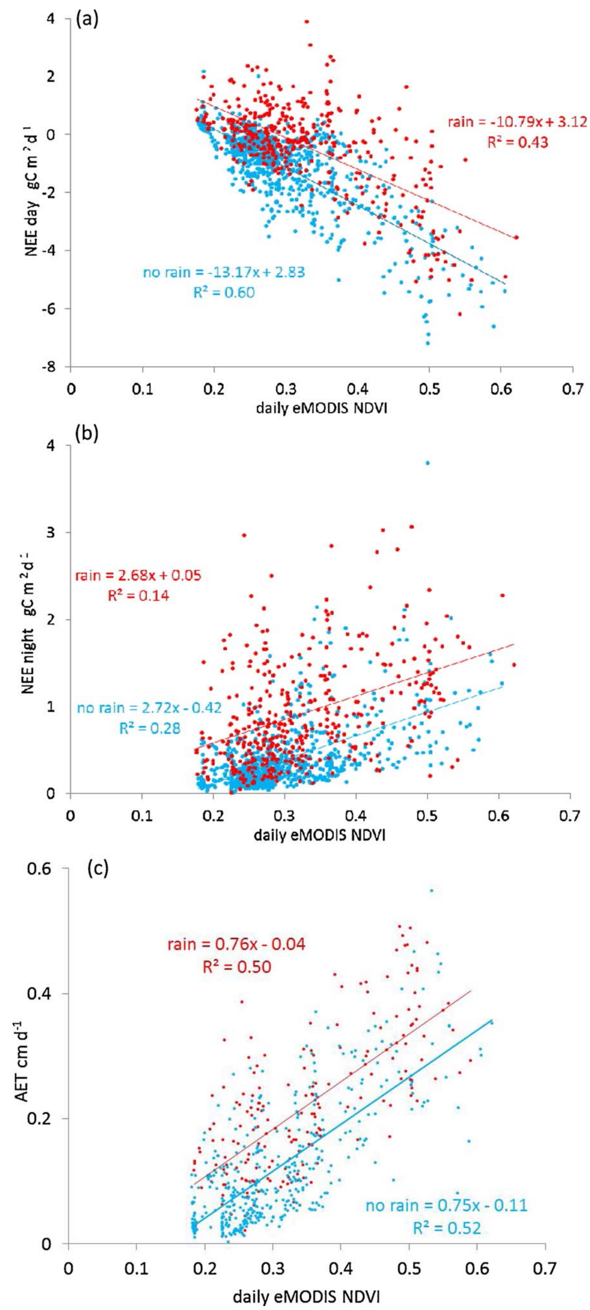

Fig. 2. Net ecosystem carbon exchange (NEE) during daytime (a) and nighttime (b) and actual evapotranspiration (AET) (c) regressed with NDVI from eMODIS for shortgrass steppe on rain and non-rain days. Daily eMODIS NDVI values were inferred by linearly interpolating between days with consecutive observations.

models separately (day no rain, night no rain, day rain, night rain). We also isolated modeled daytime NEE on non-rain days and assumed that this approximates growing season GPP. We then compared how well modeled GPP was correlated with independent observations of above ground NPP from the CPER (Lauenroth, 2013) during 1983–2014 for the AVHRR model and 2000–2014 for the eMODIS model.

Development of the AET models was similar as those for NEE except AET for day and night were combined and PET was included in the equations: [AET = F(NDVI)*F(VSWC)*F(PET)]. PET was included in the AET models because PET is a major driver of AET (Parton et al., 1981). Model evaluation was also similar; i.e. observed and predicted AET were compared at different time scales and for rain and non-rain days separately. In addition, the AET models were validated and tested using independent AET data during 2001–2006 from different pastures.

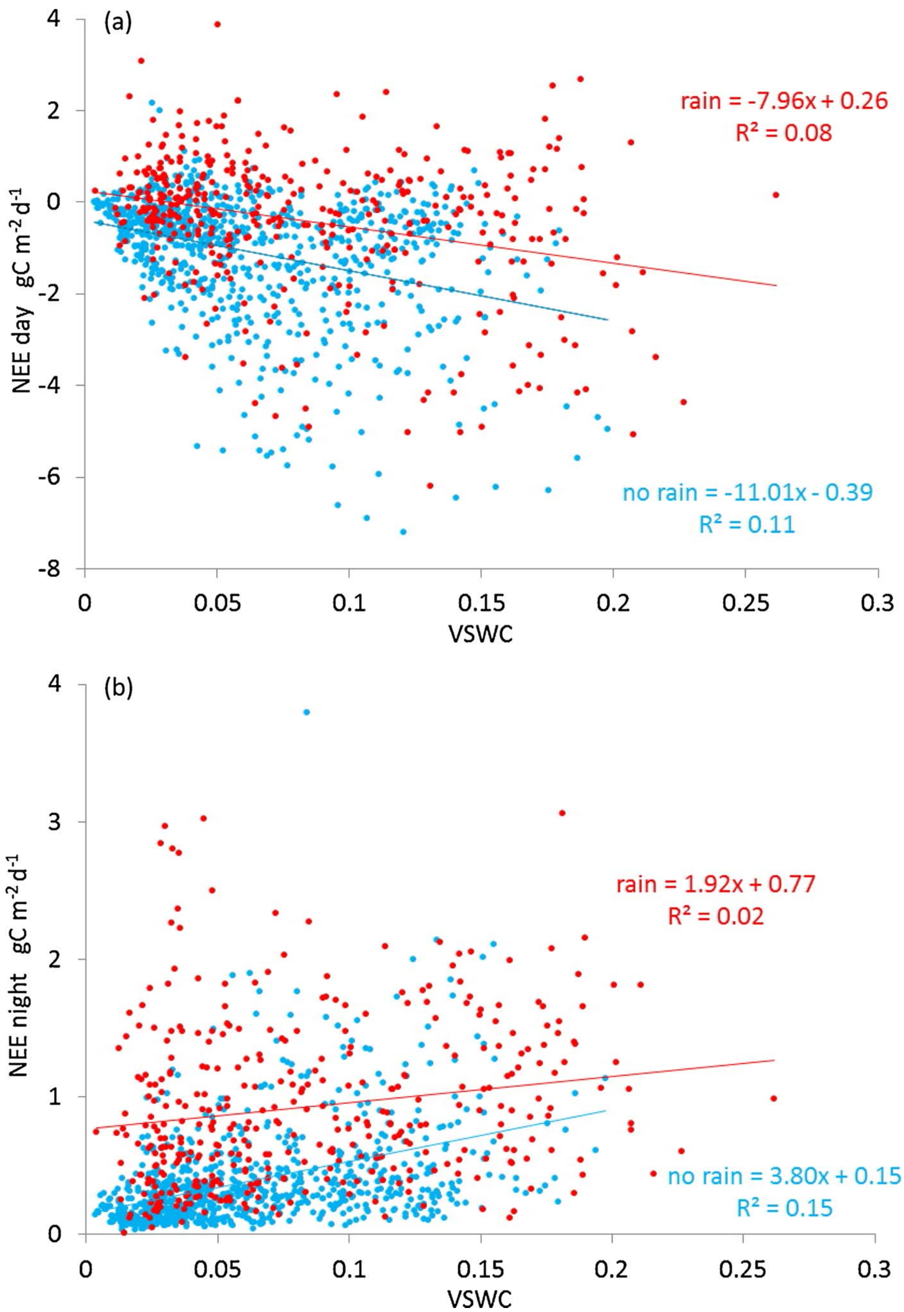

Fig. 3. Net ecosystem carbon exchange (NEE) during daytime (a) and nighttime (b) regressed with volumetric soil water content (VSWC) for shortgrass steppe on rain and non-rain days.

2.3. NEE model application

For a model application, we ran the AVHRR NEE model using NDVI, VSWC, and precipitation data from the CPER during 1983–2014 and the eMODIS NDVI model from 2000 to 2014. We then ran the model assuming no rain days and subtracted these results from those using actual precipitation to isolate rain induced respiration. Rain induced respiration was then compared with modeled NEE to investigate the influence of rain induced respiration on seasonal NEE. To explore the impact of altering rainfall frequency on NEE we aggregated rainfall events so that one event (at the most) occurred per week during the growing season while keeping seasonal rainfall constant. We then compared long-term NEE (1983–2014 for AVHRR and 2000–2014 for eMODIS) predicted using the actual and modified weather files.

3. Results

3.1. Model equations

For NDVI, simple linear functions performed as well as exponential functions but exponential functions performed better than linear for VSWC. Best fitting functions for the response of daytime NEE to NDVI from both eMODIS and AVHRR had nearly identical slopes with the intercept being larger (more positive) on rain days (green and blue lines in Fig. 5a and b) while the functions for nighttime NEE had different slopes and intercepts (purple and red lines in Fig. 5a and b). Best fitting water functions had exponential form with high sensitivity at low VSWC values and decreasing sensitivity as VSWC increased (Fig. 5c). This functional form is consistent with previous results from grasslands showing that soil respiration increased substantially with increasing

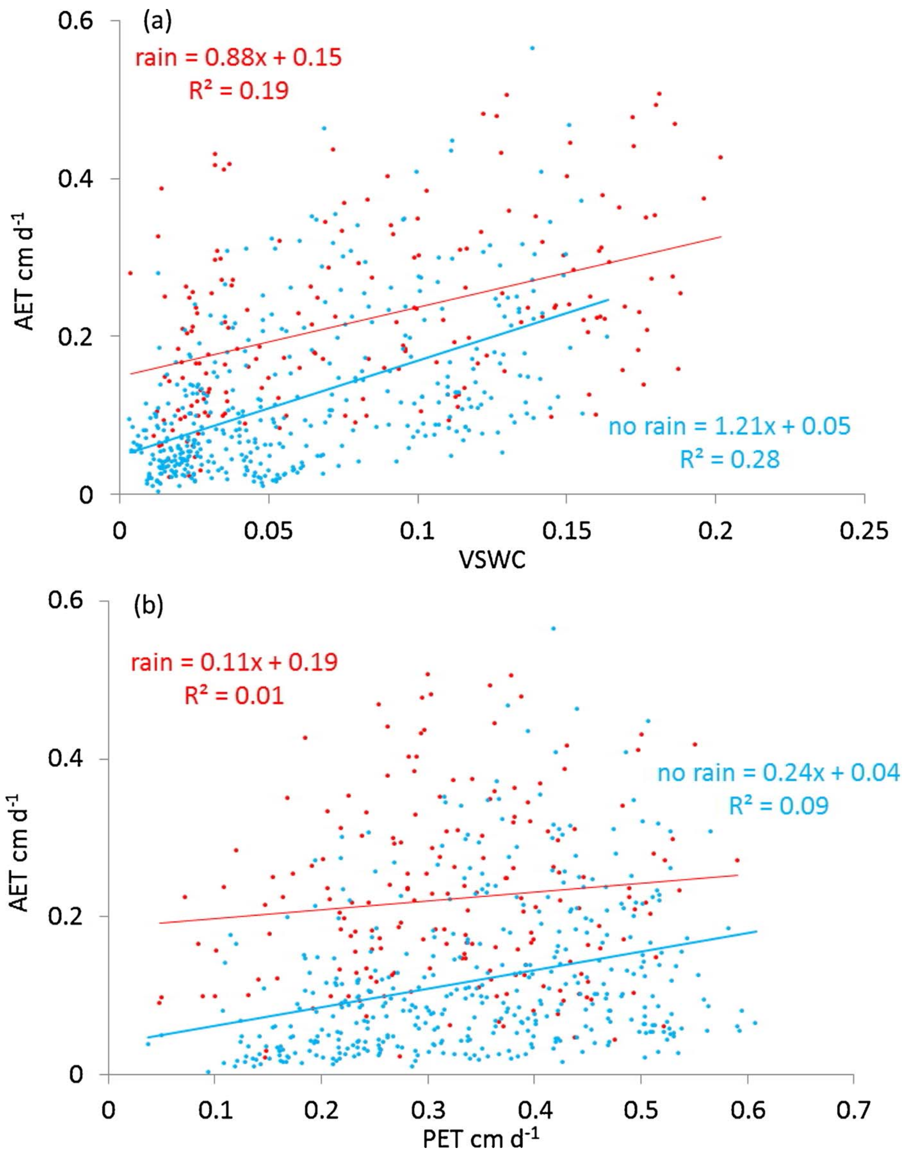

Fig. 4. Actual evapotranspiration (AET) regressed with volumetric soil water content (VSWC) (a) and potential evapotranspiration (PET) (b) for shortgrass steppe on rain and non-rain days.

VSWC at low values and little further increase above about 60% of water holding capacity (Del Grosso et al., 2005).

Best fitting functions for the response of AET to NDVI from both eMODIS and AVHRR had intercepts of 0 and greater slopes on rain than non-rain days (Fig. 6a). The slope of the VSWC function was larger on non-rain days (Fig. 6b), likely due to increased evaporation contributing a larger portion of AET on rain days whereas on non-rain days AET is dominated by transpiration which is more sensitive to soil water content (Parton et al., 1981).

Observations (Fig. 2a, b) and optimized equations show (Fig. 5a, b) that C uptake for a given value of NDVI was greater on non-rain days (e.g. the blue line on Fig. 5a) during the day while C losses at night were greater on rain days (e.g. the purple line on Fig. 5a). Optimized equations show that the impact of volumetric soil water content (0–15 cm depth) on NEE increased rapidly until it exceeded about 10–15% then leveled off (Fig. 5c). As NDVI increased, AET increased at a greater rate on rain than non-rain days (Fig. 6a). Impacts of soil water content and PET on AET increased at a greater rate on non-rain days (Fig. 6b, c).

3.2. Model evaluation and application

On rain days, eMODIS NDVI alone accounted for 41% of NEE variability; including the VSWC multiplier only marginally increased this to 44% (Table 1). NDVI explained a majority (60%) of the variability in daytime NEE on non-rain days; including VSWC in the model improved model performance ($r^2 = 0.70$, Table 1). For night-time NEE, NDVI explained much less variability on both rain (15%) and non-rain (29%) days. Addition of VSWC did not increase model performance on rain days, but did increase for non-rain days to 40%. In sum, the model performed better during daytime compared to night and on non-rain compared to rain days.

When results were combined (i.e, day + night NEE on rain and non-rain days) modeled and observed net NEE were moderately well correlated at the daily time scale (Fig. 7a) and correlations improved as NEE was aggregated to coarser time scales (Fig. 7b and c). When NEE was aggregated to the entire growing season, the model exhibited patterns of the shortgrass steppe functioning as a net sink (C sequestration) during 2001, 2003, 2005, and 2006, and a net source (C loss) in dry years of 2002 and 2004. Sink strength was over-estimated in 2001 and under-estimated in 2006 (Fig. 8a).

To further investigate seasonal patterns we partitioned observed and modeled NEE by daytime vs. nighttime and rain vs. non-rain days (Fig. 8b–e). For seasonal NEE on non-rain days, both observations and the model always showed daytime net C uptake, although the model over-estimated during 2001 and under-estimated in 2006 (Fig. 8b). For rain days, daytime seasonal C exchange can be positive, negative, or

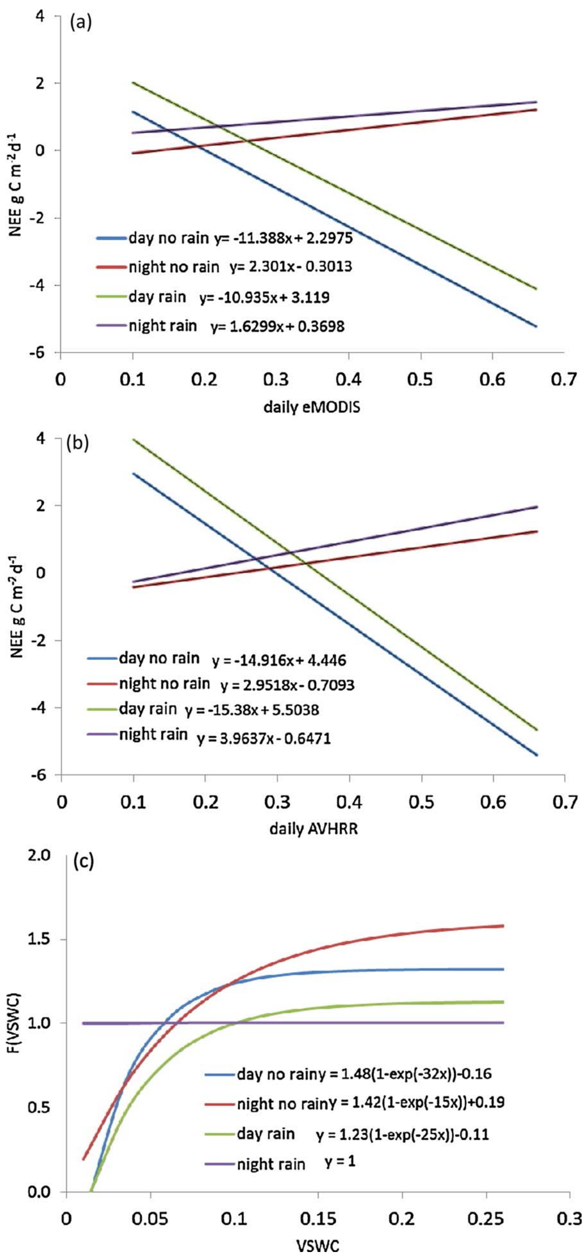

Fig. 5. Best fitting linear equations representing the response of net ecosystem carbon exchange (NEE) to NDVI based on eMODIS (a) and AVHRR (b) and best fitting exponential equations representing the impact of volumetric soil water content (VSWC) on NEE (c). Daily NDVI values for both eMODIS and AVHRR were inferred by linearly interpolating between days with consecutive observations. (For interpretation of the references to color in the text, the reader is referred to the web version of this article.)

neutral (Fig. 8c). The model showed fairly good agreement with the observations except during 2001 when C uptake was over-estimated and 2006, when observations showed a small sink and the model predicted a small source (Fig. 8b). Although the model did not perform very well for nighttime NEE at the daily time scale (Table 1), there was good agreement with observations when aggregating both rain and non-rain days to the seasonal scale (Fig. 8d, e). In aggregate, the model did a very good job (R^2 = 0.93) at representing differences in seasonal NEE related to day vs. night and rain vs. non-rain days (Fig. 7d). We further evaluated the model by comparing seasonal NEE for non-rain days (a surrogate for GPP) with long term above ground NPP observations at the CPER and found good correlations (R^2 = 0.53 for the model based on eMODIS using 15 years of NPP observations and R^2 = 0.56 for the model based on AVHRR using 32 years of NPP

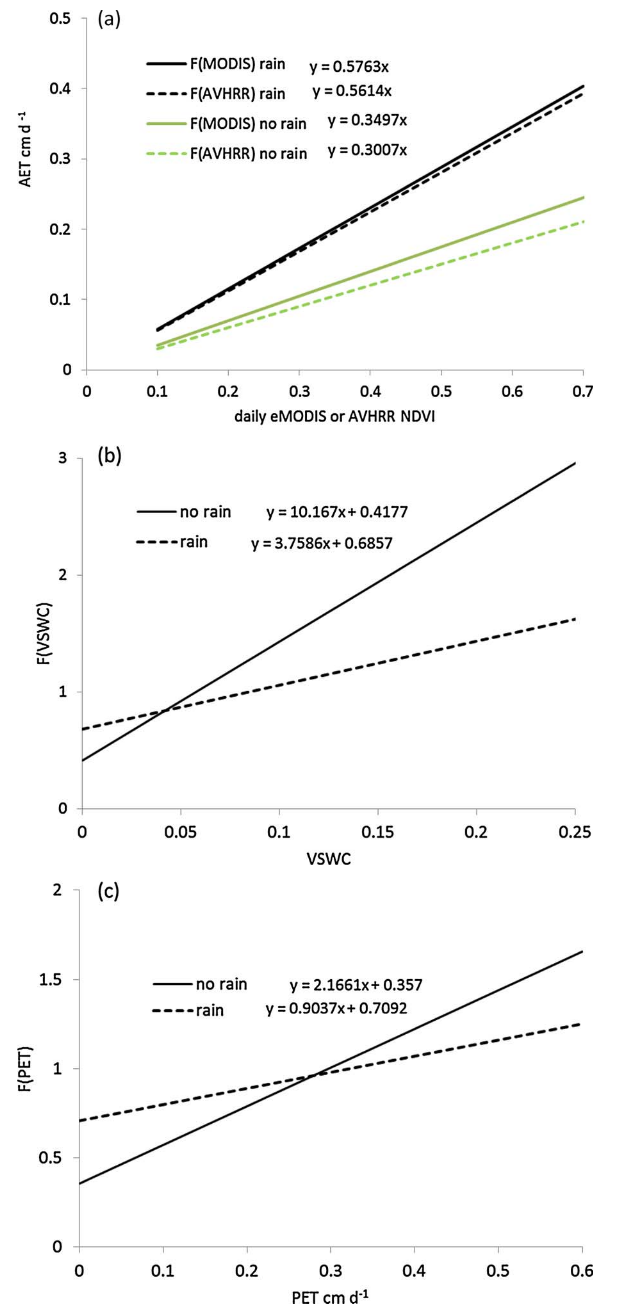

Fig. 6. Best fitting linear equations representing the response of actual evapotranspiration (AET) to NDVI (a) and the impacts of volumetric soil water content (VSWC) (b) and potential evapotranspiration (PET) (c) on AET. Daily NDVI values for both eMODIS and AVHRR were inferred by linearly interpolating between days with consecutive observations.

Table 1
Net ecosystem exchange (NEE) of C predicted from NDVI and volumetric soil water content (VSWC, 0–15 cm depth) for shortgrass steppe during the growing season.

		eMODIS		AVHRR	
	Model	R^2 day	R^2 night	R^2 day	R^2 night
rain days	NEE = F(NDVI)	0.41	0.15	0.28	0.12
rain days	NEE = F(NDVI)*F (VSWC)	0.44	0.15	0.35	0.12
non-rain days	NEE = F(NDVI)	0.60	0.29	0.37	0.15
non-rain days	NEE = F(NDVI)*F (VSWC)	0.70	0.40	0.58	0.36

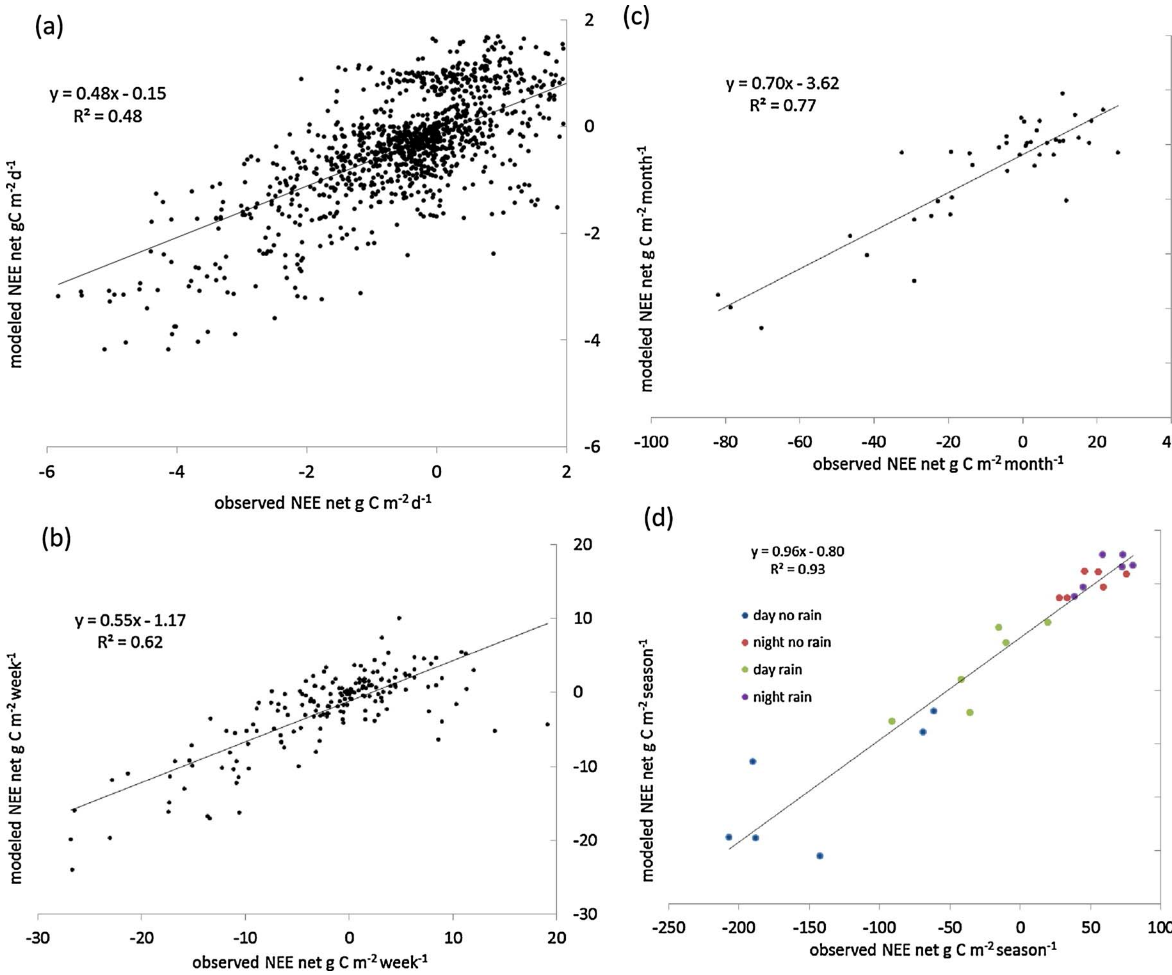

Fig. 7. Modeled (based on eMODIS NDVI) vs. observed net ecosystem carbon exchange (NEE) aggregated to daily (a), weekly (b), monthly (c), and growing season (d) time periods for shortgrass steppe.

observations). This is a crude test, but provides some indication of model performance because GPP is correlated with NPP (e.g., Hao et al., 2013, 2017).

Similar to NEE, NDVI was the dominant driver for AET during both rain and non-rain days, with a higher portion of variability explained on non-rain days. eMODIS NDVI performed better than AVHRR NDVI (Table 2). Unlike NEE, a driver involving temperature (PET) was correlated with AET and including PET improved model fit (Table 2). Like NEE, the overall model showed better correlations with observed AET when aggregated to longer time scales (Fig. 9). Models based on eMODIS and AVHRR also performed well at the daily scale ($n = 1199$) with independent data from different pastures, with the eMODIS model doing slightly better ($R^2 = 0.64$) than AVHRR ($R^2 = 0.60$). Using the eMODIS model, coefficients improved to 0.78, and 0.83 at the weekly and monthly scales, respectively.

We applied the model to isolate rain induced respiration and see if this influences seasonal NEE. We found that the portion of modeled respiration that was due to rain events was close to 50% on average and ranged from about 40–60%. Furthermore, there were moderate correlations ($R^2 = 0.51$ for eMODIS and 0.44 for AVHRR) between the portion of total respiration due to rain events and NEE with NEE becoming more negative (greater sink) as this portion decreased. Using actual weather, the average portion of total respiration associated with rainfall events was 47% for the AVHRR model and 52% for the eMODIS model; these portions decreased to 41% for AVHRR and 46% for eMODIS when using the modified weather file with precipitation aggregated to single weekly events. Using the modified weather file also increased net carbon uptake by on average 38 g C m^{-2} per season for AVHRR and 32 g C m^{-2} per season for eMODIS. These increases were due to both increased plant uptake from higher VSWC and decreased amount of rainfall induced respiration. Note that these results are incomplete because in addition to altering soil water dynamics, concentrating rainfall into large events would also likely impact NDVI, but we could not account for this.

4. Discussion

Simple models based on land surface environmental factors and remotely-sensed data explained a large portion of the variability in NEE and AET patterns for the semiarid shortgrass steppe in Colorado. The major control on both NEE and AET was NDVI which is consistent with previous research showing that NDVI is correlated with plant growth in water-limited, semiarid grasslands (Morgan et al., 2016; Hermance et al., 2015; Zhang et al., 2010). However, the nature of the relationships between NDVI and NEE or AET was influenced by rainfall events. For a given NDVI value, daytime C uptake was higher on non-rain days whereas AET and nighttime C losses were higher on rain days (Fig. 2). Rainfall events stimulate heterotrophic respiration rates (Parton et al., 2012) and respiration (C loss) on rain days often equals or exceeds photosynthesis (C gain) at daily (Fig. 2a) and even sometimes on seasonal (Fig. 8c) time scales. In contrast, on non-rain days seasonal daytime C uptake always exceeds respiration (Fig. 8b) and daily C uptake almost always exceeds respiration (Fig. 2a). Dependence of C flux on precipitation events has been previously observed by Huxman et al.

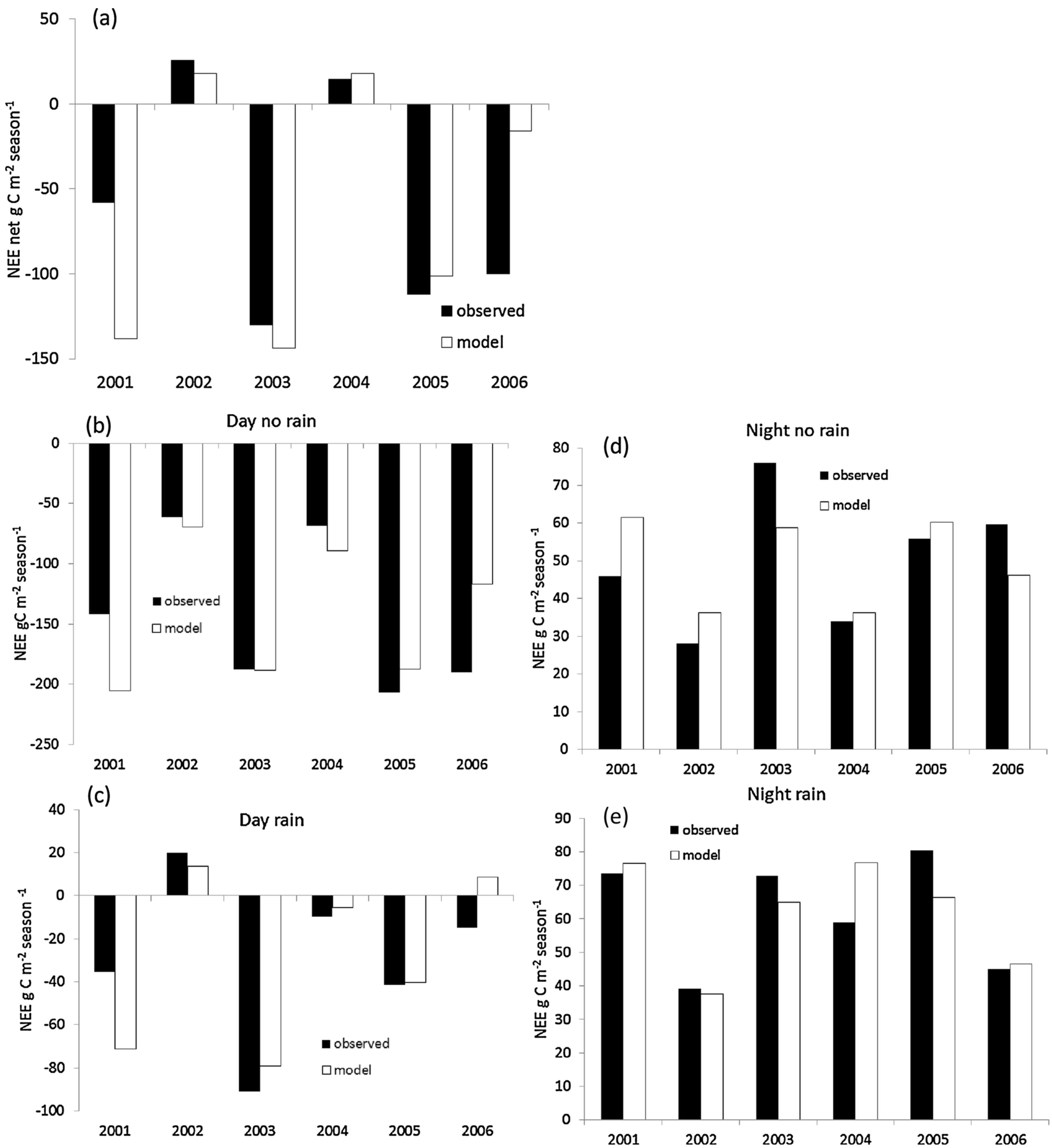

Fig. 8. Seasonal observed and modeled (based on eMODIS NDVI) net ecosystem carbon exchange (NEE) disaggregated to days with no rain (a), days with rain (b), nights with no rain (c) and nights with rain (d) for shortgrass steppe.

Table 2
Actual evapotranspiration (AET) predicted from NDVI, volumetric soil water content (VSWC, 0–15 cm depth), and potential evapotranspiration (PET) for shortgrass steppe during the growing season.

	Model	R^2 eMODIS	R^2 AVHRR
rain days	AET = F(NDVI)	0.50	0.40
rain days	AET = F(NDVI)*F(VSWC)	0.55	0.48
rain days	AET = F(NDVI)*F(VSWC)*F(PET)	0.57	0.52
non-rain days	AET = F(NDVI)	0.52	0.28
non-rain days	AET = F(NDVI)*F(VSWC)	0.64	0.50
non-rain days	AET = F(NDVI)*F(VSWC)*F(PET)	0.72	0.61

(2004) who noted that microbial respiration responds immediately to even very small (2 mm) events. Stimulation of microbial activity by small rain events also helps to explain the pattern that including VSWC in the model improved correlation coefficients during rain days only marginally for daytime NEE and not at all for night-time NEE (Table 1). Our results support prior observations (Huxman et al., 2004) that microbial activity and C loss is stimulated by rainfall events regardless of size; sufficiently large rain events that wet the subsurface soil layers are required to enhance plant growth enough to lead to net C uptake (Parton et al., 2012; Heisler-White et al., 2008).

eMODIS NDVI explained 60% of the variability in daytime NEE on non-rain days whereas AVHRR NDVI explained just 37% (Table 1). There are two related reasons to explain the better performance of

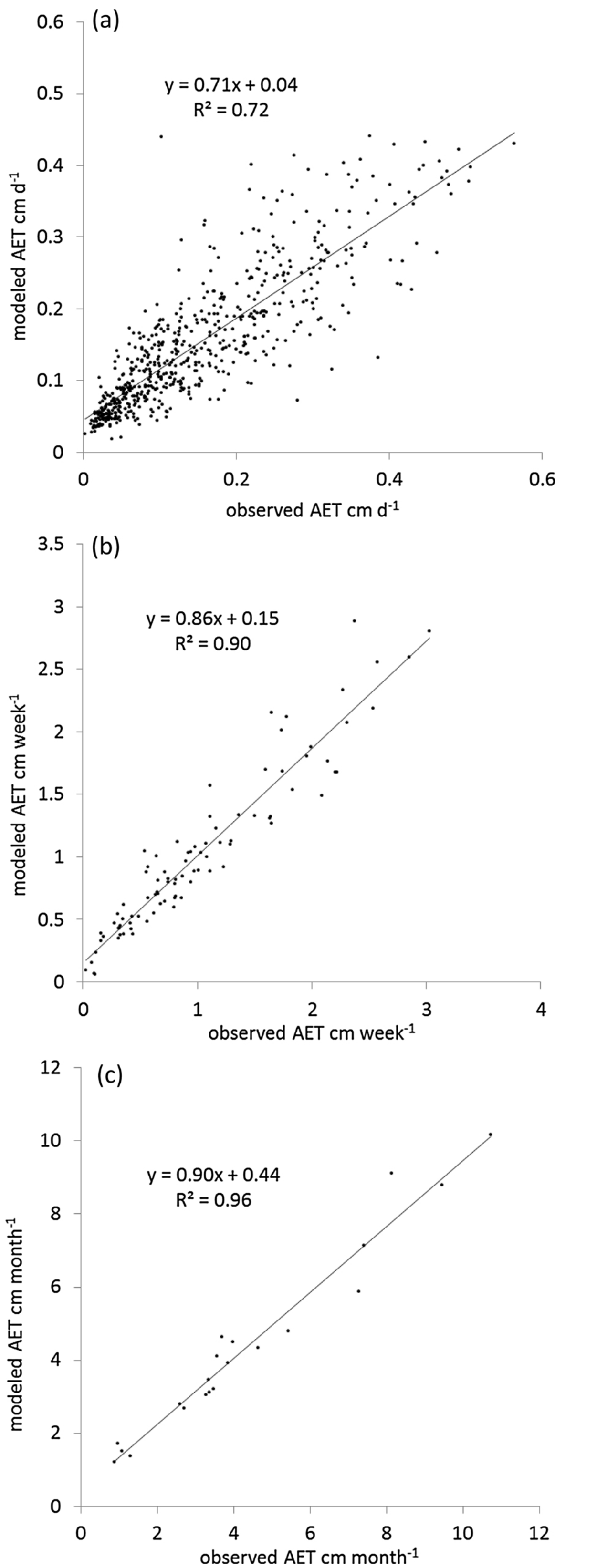

Fig. 9. Modeled (based on eMODIS NDVI) vs. observed actual evapotranspiration (AET) aggregated to daily (a), weekly (b) and monthly (c) time periods for shortgrass steppe.

eMODIS NDVI; eMODIS has higher spatial and temporal resolution than AVHRR and eMODIS integrates mean values within the sampled area whereas AVHRR picks the highest value within the sampled area. Compared to eMODIS, including a soil water multiplier in the model improved model fit to a greater extent when using AVHRR NDVI (Table 1). One reason for this is because AVHRR does not explain as much variance on its own so other variables can have greater influence. Another possible reason is related to AVHRR being less resolved spatially and temporally than eMODIS and including daily pasture level VSWC model inputs could partially compensate for this limitation. Another pattern evident from Fig. 2 and Table 1 is that daytime NEE is more highly correlated with NDVI than nighttime NEE. This may be related to NDVI being a metric of photosynthesis which is often the dominant process driving C flux during the daytime.

Addition of VSWC improved correlations compared to NDVI alone except for nighttime NEE during rain days and the improvements were larger on non-rain than rain days (Table 1). This variance in the sensitivity of NEE to VSWC and the observation that respiration often exceeded C uptake on rain days support previous suggestions that microbes inhabiting surface and near-surface soil layers become hydrated by small rain events that do not appreciably affect autotrophic processes which are more sensitive to environmental conditions in deeper soil layers (Huxman et al., 2004).

NDVI based on eMODIS explained more of the variability in AET compared to AVHRR on rain (50% vs. 40%) and non-rain days (52% vs. 28%). Including multipliers for soil water content and PET significantly improved model results, especially on non-rain days (Table 2). Similar to the NEE, including other factors in the models improved results to a greater extent when using AVHRR compared to eMODIS NDVI. Unlike NEE, including a temperature dependent factor (PET) in the model significantly improved the ability to predict AET. This is likely due to the direct effect of PET on the evaporation component of AET (Parton et al., 1981). Likewise, enhanced evaporation on rain days from water intercepted by biomass, litter, and bare soil likely contributes to the observation that for a given value of NDVI, AET was higher on rain days (Fig. 2c). This is consistent with assumptions in other models that precipitation intercepted by biomass is evaporated (e.g., Zhang and Wegehenkel, 2006).

Our simple eMODIS based model explained close to 50% of the variability in daily NEE which is similar to previous work involving more complex models. For example, an NEE regression tree model for the conterminous United States based on eMODIS surface temperature, enhanced vegetation index, and normalized difference water index explained 53% of the variability in observed NEE (Xiao et al., 2008). Also similar to Xiao et al. (2008), model performance tended to improve as NEE was aggregated to longer time scales (Fig. 7). One reason for the substantial increase in correlation coefficient from 0.48 for NEE at the daily scale to 0.62 for NEE at the weekly scale is that the eMODIS data represent 7 day composite values. The fact that we used linear interpolation to derive daily NDVI values likely contributed to model error at the finer scale. Our simple eMODIS AET model achieved a daily r^2 value of 0.72 for the parameterization data set and correlations improved to 0.90 when aggregated at the weekly scale and to 0.96 at the monthly scale (Fig. 9). Similar to the above for NEE, using linear interpolation to derive daily NDVI values likely contributed to AET model error at the daily scale. For the independent data set, correlation coefficients were 0.64, 0.78, and 0.83 at the daily, weekly, and monthly scales, respectively. For comparison, a more complex model based on radiation, enhanced vegetation index, and diurnal temperature range as an indicator of soil moisture in the top 5 cm layer was able to explain 89–98% of the variability in observed 16 day AET values for sites across the US (Wang and Liang, 2008). These comparisons suggest that our simple models based on readily available remotely sensed and land surface environmental drivers perform as well, or nearly as well, as more complex models.

Although our simple models performed reasonably well, they are limited in that factors such as plant phenology, carbohydrate storage, and soil nitrogen accumulation that can influence NEE and AET were not explicitly included. There is evidence that the response time of peak NDVI to rainfall events in the shortgrass steppe decreases from about two weeks early in the growing season to 12 days in the late growing season, related to physiological traits of C3 vs. C4 grasses (Hermance et al., 2015). In addition, Hermance et al. (2015) suggested that accumulation of soil nitrogen during drought years contributes to higher than expected plant production during the subsequent post drought year. Although such factors were not explicitly represented in our models, they do influence NDVI and so are implicitly included.

To investigate the impacts of precipitation events we ran the NEE models using actual precipitation data and assuming no rain days to isolate the impact of rain induced CO_2 pulses. Our findings suggest that as the portion of seasonal respiration due to rainfall events increases, net carbon uptake tends to decrease. To explore the impact of altered precipitation frequency, we compared long term modeled NEE using actual weather and aggregated rainfall events at a weekly scale during the growing season. This resulted in increased net carbon uptake which provides evidence that the frequency distribution of precipitation is important to C dynamics. This is consistent with previous work in this semiarid grassland showing that increasing event size and decreasing frequency while keeping seasonal rainfall constant increased above ground NPP (Heisler-White et al., 2008). Similarly, Thomey et al. (2011) found that grassland plots in New Mexico receiving a single large rainfall event each month had higher ANPP than plots receiving multiple smaller events. Our results are also similar to those of Jia et al. (2016) who found multiple small rainfall events did not sufficiently wet soil, leading to suppressed plant production and positive annual NEE.

5. Conclusions

Four main conclusions can be drawn from this work: 1) NDVI is a main driver of NEE and AET, with eMODIS NDVI performing better than AVHRR NDVI, 2) daily pasture level VSWC improves modeled NEE, and VSWC and PET improve modeled AET, 3) using separate equations for rain vs. non-rain days improves optimization of model performance, and 4) simple models based on remotely sensed NDVI and weather related environmental factors explained a large portion of the variability in shortgrass steppe NEE and AET, especially when aggregated to weekly and greater time scales. Separating rain vs. non-rain days is the most novel aspect of our modeling approach and provides evidence that enhanced microbial respiration on rain days has a substantial impact on NEE. One implication is that predicted climate changes in the alteration of frequency, intensity, or timing of rainfall events, but not necessarily total annual precipitation, will have substantial effects on NEE. Specifically, small-sized, frequent rainfall events lead to C loss (Munson et al., 2010) whereas larger rainfall events lead to C uptake (Li et al., 2017) and enhanced ANPP (Heisler-White). By including separate relationships for rain vs. non-ran days, our model helps to quantify these impacts and can be applied to project how changes in precipitation patterns will impact NEE in the shortgrass steppe.

Conflicts of interest

None.

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References

Adams, J.M., Faure, H., Faure-Denard, L., McGlade, J.M., Woodward, F.I., 1990. Increases in terrestrial carbon storage from the Last Glacial Maximum to the present. Nature 348, 711–714.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop Evapotranspiration-Guidelines for Computing Crop Water Requirements-FAO Irrigation and Drainage Paper 56, vol. 300 FAO, Rome (9) D05109.

Del Grosso, S.J., Parton, W.J., Mosier, A.R., Holland, E.A., Pendall, E., Schimel, D.S., Ojima, D.S., 2005. Modeling soil CO_2 emissions from ecosystems. Biogeochemistry 73, 71–91.

Del Grosso, S.J., Parton, W., Stohlgren, T., Zheng, D., Bachelet, D., Prince, S., Hibbard Olson, K.R., 2008. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89 (8), 2117–2126.

Dunn, B.H., Smart, A.J., Gates, R.N., Johnson, P.S., Beutler, M.K., Diersen, M.A., Janssen, L.L., 2010. Long-term production and profitability from grazing cattle in the Northern Mixed Grass Prairie. Rangeland Ecol. Manage. 63, 233–242.

Gilmanov, T.G., Tieszen, L.L., Wylie, B.K., Flanagan, L.B., Frank, A.B., Haferkamp, M.R., Meyers, T.P., Morgan, J.A., 2005. Integration of CO_2 flux and remotely-sensed data for primary production and ecosystem respiration analyses in the Northern Great Plains: potential for quantitative spatial extrapolation. Global Ecol. Biogeogr. 14 (3), 271–292.

Hao, Y., Kang, X., Wu, X., Cui, X., Liu, W., Zhang, H., Li, Y., Wang, Y., Xu, Z., Zhao, H., 2013. Is frequency or amount of precipitation more important in controlling CO_2 fluxes in the 30-year-old fenced and the moderately grazed temperate steppe? Agric. Ecosyst. Environ. 171, 63–71.

Hao, Y.B., Zhou, C.T., Liu, W.J., Li, L.F., Kang, X.M., Jiang, L.L., Cui, X.Y., Wang, Y.F., Zhou, X.Q., Xu, C.Y., 2017. Aboveground net primary productivity and carbon balance remain stable under extreme precipitation events in a semiarid steppe ecosystem. Agric. For. Meteorol. 240, 1–9.

Heisler-White, J.L., Knapp, A.K., Kelly, E.F., 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158 (1), 129–140.

Hermance, J.F., Augustine, D.J., Derner, J.D., 2015. Quantifying characteristic growth dynamics in a semi-arid grassland ecosystem by predicting short-term NDVI phenology from daily rainfall: a simple four parameter coupled-reservoir model. Int. J. Remote Sens. 36 (22), 5637–5663. http://dx.doi.org/10.1080/01431161.2015.1103916.

Huang, L., He, B., Chen, A., Wang, H., Liu, J., Lű, A., Chen, Z., 2016. Drought dominates the interannual variability in global terrestrial net primary production by controlling semi-arid ecosystems. Sci. Rep. 6, 24639. http://dx.doi.org/10.1038/srep24639.

Huxman, T.E., Keirith, A., Snyder, D.T., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141 (2), 254–268.

Jenkerson, C.B., Maiersperger, T.K., Schmidt, G.L., 2010. eMODIS: A User-friendly Data Source, U.S. Geol. Surv. Open File Rep., 2010-1055.

Jia, X., Zha, T., Gong, J., Wang, B., Zhang, Y., Wu, B., Qin, S., Peltola, H., 2016. Carbon and water exchange over a temperate semi-arid shrubland during three years of contrasting precipitation and soil moisture patterns. Agric. For. Meteorol. 228, 120–129.

Lauenroth, W.K., 2013. SGS-LTER Standard Production Data: 1983–2008 Annual Aboveground Net Primary Production on the Central Plains Experimental Range, Nunn, Colorado, USA 1983–2008, ARS Study Number 6. (http://hdl.handle.net/10217/81141).

Li, G., Han, H., Du, Y., Hui, D., Xia, J., Niu, S., Li, X., Wan, S., 2017. Effects of warming and increased precipitation on net ecosystem productivity: a long-term manipulative experiment in a semiarid grassland. Agric. For. Meteorol. 232, 359–366.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L., Kazempour, M.K., 1989. Effects of grazing,topography, and precipitation on the structure of a semiarid grassland. Plant Ecol. 80, 11–23.

Morgan, J.A., Parton, W.J., Derner, J.D., Gilmanov, T.G., Smith, D.P., 2016. Importance of early season conditions and grazing on carbon dioxide fluxes in Colorado shortgrass steppe. Rangeland Ecol. Manage. 69 (5), 342–350.

Munson, S.M., Benton, T.J., Lauenroth, W.K., Burke, I.C., 2010. Soil carbon flux following pulse precipitation events in the shortgrass steppe. Ecol. Res. 25 (1), 205–211.

Parton, W.J., Lauenroth, W.K., Smith, F.M., 1981. Water loss from a shortgrass steppe. Agric. Meteorol. 24, 97–109.

Parton, W.J., Morgan, J.A., Smith, D.P., Del Grosso, S.J., Prihodko, L., LeCain, D.R., Kelly, R., Lutz, S., 2012. Impact of precipitation dynamics on net ecosystem productivity. Global Change Biol. 18, 915–927. http://dx.doi.org/10.1111/j.1365-2486.2011.02611.x.

Reynolds, J.F., Smith, D.M., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernandez, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science 316, 847–851.

Thomey, M.L., Collins, S.L., Vargas, R., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens, M.T., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. Global Change Biol. 17 (4), 1505–1515.

Tucker, C.J., Pinzon, J.E., Brown, M.E., Slayback, D.A., Pak, E.W., Mahoney, R., Vermote, E.F., El Saleous, N., 2005. An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. Int. J. Remote Sens. 26 (20), 4485–4498.

Wang, K., Liang, S., 2008. An improved method for estimating global evapotranspiration based on satellite determination of surface net radiation, vegetation index, temperature, and soil moisture. J. Hydrometeorol. 9 (4), 712–727.

Xiao, J., Zhuang, Q., Baldocchi, D.D., Law, B.E., Richardson, A.D., Chen, J., Oren, R., Starr, G., Noormets, A., Ma, S., Verma, S.B., Wharton, S., Wofsy, S.C., Bolstad, P.V., Burns, S.P., Cook, D.R., Curtis, P.S., Drake, B.G., Falk, M., Fischer, M.L., Foster, D.R., Gu, L., Hadley, J.L., Hollinger, D.Y., Katul, G.G., Litvak, M., Martin, T.A., Matamala, R., McNulty, S., Meyers, T.P., Monson, R.K., Munger, J.W., Oechel, W.C., Paw U, K.T., Schmid, H.P., Scott, R.L., Sun, G., Suyker, A.E., Torn, M.S., 2008. Estimation of net ecosystem carbon exchange for the conterminous United States by combining MODIS and AmeriFlux data. Agric. For. Meteorol. 148 (11), 1827–1847.

Zhang, Y., Wegehenkel, M., 2006. Integration of MODIS data into a simple model for the spatial distributed simulation of soil water content and evapotranspiration. Remote Sens. Environ. 104 (4), 393–408.

Zhang, L., Wylie, B.K., Ji, L., Gilmanov, T.G., Tieszen, L.L., 2010. Climate-driven interannual variability in net ecosystem exchange in the northern Great Plains grasslands. Rangeland Ecol. Manage. 63 (1), 40–50.