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Carbon dioxide and water vapor exchange in a warm temperate grassland

Abstract Grasslands cover about 40% of the ice-free global terrestrial surface, but their contribution to local and regional water and carbon fluxes and sensitivity to climatic perturbations such as drought remains uncertain. Here, we assess the direction and magnitude of net ecosystem carbon exchange (NEE) and its components, ecosystem carbon assimilation (A_c) and ecosystem respiration (R_E), in a southeastern United States grassland ecosystem subject to periodic drought and harvest using a combination of eddy-covariance measurements and model calculations. We modeled A_c and evapotranspiration (ET) using a big-leaf canopy scheme in conjunction with ecophysiological and radiative transfer principles, and applied the model to assess the sensitivity of NEE and ET to soil moisture dynamics and rapid excursions in leaf area index (LAI) following grass harvesting. Model results closely match eddy-covariance flux estimations on daily, and longer, time steps. Both model calculations and eddy-covariance estimates suggest that the grassland became a net source of carbon to the atmosphere immediately following the harvest, but a rapid recovery in LAI maintained a marginal carbon sink during summer. However, when integrated over the year, this grassland ecosystem was a net C source (97 g C m^{-2} a^{-1}) due to a minor imbalance between large A_c (−1,202 g C m^{-2} a^{-1}) and R_E (1,299 g C m^{-2} a^{-1}) fluxes. Mild drought conditions during the measurement period resulted in many instances of low soil moisture ($\theta < 0.2$ m^{3}m^{-3}), which influenced A_c and thereby NEE by decreasing stomatal conductance. For this experiment, low θ had minor impact on R_E. Thus, stomatal limitations to A_c were the primary reason that this grassland was a net C source. In the absence of soil moisture limitations, model calculations suggest a net C sink of −65 g C m^{-2} a^{-1} assuming the LAI dynamics and physiological properties are unaltered. These results, and the results of other studies, suggest that perturbations to the hydrologic cycle are key determinants of C cycling in grassland ecosystems.

Keywords Net ecosystem exchange · Ecosystem modeling · Evapotranspiration · Eddy-covariance · Grassland ecosystems

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Introduction

Understanding the mechanisms that control ecosystem carbon balance is a critical research priority given the sensitivity of the carbon cycle to the biogeochemical and hydrologic cycles of the terrestrial biosphere (Sarmiento and Wofsy 1999; Houghton et al. 2001). Long-term CO_2 and H_2O flux monitoring initiatives such as FLUXNET have arisen to understand how environmental variables drive carbon cycling in ecosystems across the globe (Baldocchi et al. 2001). However, most long-term CO_2 flux research focuses on forests, with a consequent shortage of CO_2 flux data for grassland ecosystems worldwide (Falge et al. 2001a, 2001b; Valentini et al. 2000; Baldocchi et al. 2001). In addition, many studies and summaries of grassland C dynamics historically concentrated on net primary productivity (NPP), not on net ecosystem exchange of carbon (NEE) (e.g., Long et al. 1992; Scurlock et al. 2002).

Forested ecosystems in the southeastern United States are characterized by long, warm, and mesic growing seasons that favor high carbon assimilation rates (Clark et

al. 1999; Baldocchi and Wilson 2001; Oren et al. 2001; Wilson and Baldocchi 2001). The grassland under study here is typical of abandoned agricultural sites in the southeastern United States, and is warmer and wetter than most grassland ecosystems. Grassland ecosystems comprise approximately 40.5% of the Earth's terrestrial land area, excluding areas of permanent ice (White et al. 2000). Large uncertainties remain in resolving whether grassland ecosystems function as CO_2 sources or sinks (Ojima et al. 1993; Parton et al. 1993; Baldocchi et al. 2001): annual grassland NEE estimates based on eddy-covariance measurements and Bowen Ratio Energy Balance techniques vary from a net source of $+400$ g C m^{-2} a^{-1} to a net sink of -800 g C m^{-2} a^{-1} (Table 1). This uncertainty is primarily attributable to the sensitivity of grasslands to interannual variability in climate and associated biomass dynamics (Knapp and Smith 2001; Meyers 2001; Flanagan et al. 2002; Jackson et al. 2002; Scurlock et al. 2002), and incomplete understanding of the regulation of ecosystem respiration (Raich and Potter 1995; Knapp et al. 1998; Wagai et al. 1998).

The objective of this investigation is to assess the magnitude and direction of NEE and its components (A_c and R_E) in a southeastern United States warm-temperate grassland ecosystem, and to assess NEE and ET responses to episodic droughts and harvests. To this end, we use a big-leaf process-based model that combines ecophysiological and radiative transfer principles. The model is calibrated with both leaf-level gas exchange and ecosystem-level eddy-covariance measurements from an abandoned agricultural field at the Duke Forest C-H_2O Research Site near Durham, N. C. The model is then used to conduct a sensitivity analysis to drought and leaf area perturbations, and results are evaluated with respect to grassland water and carbon balance studies to date.

Methods

Model

Net ecosystem carbon exchange (NEE) is defined as the difference between ecosystem carbon assimilation (A_c) and ecosystem respiration (R_E).

$$NEE = A_c + R_E \tag{1}$$

We adopt the micrometeorological convention in which fluxes from the biosphere to the atmosphere are positive. We employed the biochemical photosynthesis model of Farquhar et al. (1980) as given in Appendix A to compute leaf-level assimilation (A_n) for C_3 grass species, and coupled A_n to a big-leaf canopy scheme (Kim and Verma 1991) to scale from leaf to canopy. Grassland foliage is concentrated in short canopy heights, and the big-leaf approximation can be used to scale photosynthesis from leaf to canopy to a first approximation (Kim and Verma 1991) using:

$$A_c \approx A_n \times (f_{LAI} \times LAI) \tag{2}$$

where LAI is leaf area index (m^{2}m^{-2}) and f_{LAI} is the fraction of LAI that absorbs incident photosynthetically active radiation (PAR).

Here, f_{LAI} is modeled after Campbell and Norman (1998):

$$f_{LAI} = \exp\left(-K_b(\psi) \times LAI\right) \tag{3}$$

where K_b, the light extinction coefficient, is a function of the sun zenith angle ψ. K_b is estimated from the Campbell and Norman (1998) model with a leaf angle distribution parameter (x) of 0.7, appropriate for erect grass leaves.

A_n is related to stomatal conductance to CO_2 (g_s) using a variant on Fick's law (e.g., Cowan 1977):

$$A_n = g_s \times C_a \left(\frac{C_i}{C_a} - 1\right) \tag{4}$$

where C_i is the CO_2 concentration in the intercellular spaces in the leaf and C_a is the ambient atmospheric CO_2 concentration (~385 ppm). Numerous empirical and semi-empirical models for g_s and bulk canopy conductance (g_c) have been proposed (e.g., Leuning 1995; Katul et al. 2000), with the simplest being a variant on the Jarvis (1976) model, given by:

$$g_c = g_{ref}(PAR) \times f_1(VPD) \times f_2(\theta)$$
$$= (f_{LAI}LAI) \times g_s \tag{5}$$

where g_{ref} is the conductance at a reference vapor pressure deficit (VPD) of 1 kPa for well-watered conditions (Oren et al. 1999), $f_1(VPD)$ is a reduction function for vapor pressure deficit and $f_2(\theta)$ is a reduction function for soil moisture. The function g_{ref} is assumed to vary with PAR and was determined from eddy-covariance measured water vapor flux when $\theta > \theta_R$, where θ is the volumetric root-zone soil moisture content and θ_R is the soil moisture content at which g_c is limited.

The function $f_1(VPD)$ is given by Oren et al. (1999):

$$f_1(VPD) = 1 - m \times \ln(VPD_i) \tag{6}$$

where i is PAR level (Appendix B) and the sensitivity parameter m (~0.5–0.6) is determined in Appendix B using the boundary line analysis proposed by Oren et al. (1999).

A standard soil moisture reduction function of the form:

$$f_2(\theta) = \begin{cases} 1 & ; \frac{\theta}{\theta_R} > 1 \\ \left(1 - \left(\frac{\theta_R - \theta}{\theta_R}\right)^{\nu}\right) & ; \frac{\theta}{\theta_R} \leq 1 \end{cases} \tag{7}$$

was chosen to account for drought effects on canopy conductance (Campbell and Norman 1998). Following nonlinear optimization using the Gauss-Newton algorithm (Dennis 1977), $\nu=0.6$ and $\theta_R=0.20$. The θ_R is consistent with an earlier modeling study by Lai and Katul (2000) in which actual and potential evapotranspiration were shown to diverge at $\theta_R=0.19$ for the same grassland.

To measure and model night-time respiration, we used a different approach than the standard methodology of only accepting data if the friction velocity (u_*) exceeds a certain threshold, u_{*t}. Commonly, u_{*t} is taken to be between 0.1 and 0.2 m s^{-1} (Goulden et al. 1996; Aubinet et al. 2000; Barford et al. 2001). Our respiration model is based on night-time CO_2 eddy-covariance measurements collected for both $u_* > 0.12$ m s^{-1} and for near-neutral atmospheric stability conditions ($|(z-d)/L| < 0.1$, see Appendix C). Here, z is instrument height (3.0 m), L is the Obukhov length (Brutsaert 1982 p65), and h and d are the mean canopy height and zero-plane displacement (~2/3 h), respectively. The addition of the atmospheric stability constraint to the usual night-time friction velocity threshold ensures that the flow is a fully developed turbulent flow that is near-neutral and not "contaminated" by large-scale phenomena such as gravity waves or meandering, and is critical for constraining the night-time flux footprint (see Appendix C). In fact, from Appendix C, accepting u_{*t} as the only threshold with no atmospheric stability consideration can

Table 1 Annual and growing season/summer net ecosystem carbon exchange (NEE), annual ecosystem carbon assimilation (A_c), annual ecosystem respiration (R_E), and maximum daily NEE and A_c reported from various grassland and sagebrush ecosystems. The sign follows the micrometeorological convention that positive fluxes are from the biosphere to the atmosphere. All measurements are made by eddy-covariance or Bowen ratio energy balance (BREB)[a]. Measurements obtained using BREB are *italicized*. Saigusa et al. (1998) employ an aerodynamic method similar to BREB

Site	Ecosystem type	Year	NEE (g C m^{-2} a^{-1})	Growing season (summer) NEE (g C m^{-2} season^{-1})	A_c (g C m^{-2} a^{-1})	R_E (g C m^{-2} a^{-1})	Max NEE (g C m^{-2} day^{-1})	Max A_c (g C m^{-2} day^{-1})	References
Matador, SK, Canada	*Mixed-grass prairie*	*1970*					*-2.7*	*-4.9*	*Ripley and Saugier (1974, 1978)*
		1971					*-4.1*		*Redmann (1978)*
Lethbridge, AL, Canada	Moist mixed grassland	1998	-109		-373	264	-5.0	-9	Flanagan et al. (2002)
		1999	-21		-287	267	-3.2	-5.5	
		2000	+18		-272	290	-2.4	-4.5	
Mandan, N.D., USA	*Northern mixed grass prairie*	*1995*	*-118*	*-147 [b]*			*—*		*Frank et al. (2001)*
		1996	*-85*	*-113 [b][-108]*			*-4.9*		*Frank and Dugas (2001)*
		1997	*-55*	*-85 [b][-78]*			*-4.6*		
		1998	*—*	*-49 [b]*			*-3.7*		
		1999	*-34 [c]*	*-129 [b]*			*-4.9*		
Dubois, Idaho, USA	*Sagebrush-steppe*	*1996*	*-100 (average)*	*-77 [d]*					*Gilmanov et al. (2003a)*
		1997		*-112 [d]*					
		1998		*-203 [d]*					
		1999		*-301 [d]*					
Manhattan, Kan., USA	*Tallgrass prairie*	*1996*					*-2.2*	*-9.5*	*Ham and Knapp (1998)*
Jasper Ridge, Calif., USA	Serpentine grassland	7/90–7/91	-133				-1.9		Valentini et al. (1995)
Shidler, Okla., USA	Tallgrass prairie	1987		-205 [e]			-7.6		Kim and Verma (1991)
		1989	-318 to -383 [f]	-68 [e]					Kim et al. (1992)
Ponca, Okla., USA	Tallgrass Prairie	1997	-274 [g]	-446	-812 [h]	538 [i]	-9.5		Suyker and Verma (2001)
		1998	-46 [g]	-204	-548 [h]	502 [i]	-7.5		Suyker et al. (2003)
		1999	-124 [g]	-300	-634 [h]	510 [i]	-8.5		
Woodward, Okla., USA	*Mixed grass prairie*	*1995*	*-97 [-101]*	*-118*			*-4.9*		*Sims and Bradford (2001)[j]*
		1996	*+46 [+19]*	*-13*			*-3.3*		*[Frank et al. (2001)]*
		1997	*-159 [-179]*	*-199*			*-5.5*		
Woodward, Okla., USA	*Sagebrush/mixed grassland*	*1995*	*-55*	*-74*			*-2.7*		*Sims and Bradford (2001)*
		1996	*+9*	*+31*			*-2.2*		
		1997	*+27*	*+26*			*-4.6*		
Chickasha, Okla., USA	Mixed-grass rangeland	1995		-196 [k]			-4.5		Meyers (2001)[k]
		1996		-41 [k]			-4		[Falge et al. (2001a)]
		1997	+41 to +150 [f]	-188 [k]			-5		
		1998	+419 to +521	+155 [k]			-1		

Table 1 (continued)

Site	Ecosystem type	Year	NEE (g C m^{-2} a^{-1})	Growing season (summer) NEE (g C m^{-2} season^{-1})	A_c (g C m^{-2} a^{-1})	R_E (g C m^{-2} a^{-1})	Max NEE (g C m^{-2} day^{-1})	Max A_c (g C m^{-2} day^{-1})	References
Temple, Tex., USA	*Tallgrass prairie*	*1993*	*−50* [l]				−5		*Dugas et al. (1999)*
		1994	*−80*				−6.5		*Frank et al. (2001)*
		1995	*−772*	*−831*					
		1996	*−223*	*−286*					
		1997	*−386*	*−476*					
Temple, Tex., USA	*Cynodon dactylon*	*1993*	*+100*				−3		*Dugas et al. (1999)*
		1994	*−800*				−14		
Walnut Gulch Watershed, Ariz., USA (Lucky Hills)	*Mixed shrub*	*1997*	*+130*				−0.8		*Emmerich (2003)*
		1998	*+140*				−2.7		
		1999	*+155*				−2.7		
		2000	*+150*				−2.7		
Walnut Gulch Watershed, Ariz., USA (Kendall)	*Mixed grass*	*1997*	*+130*				−3.8		*Emmerich (2003)*
		1998	*+210*				−4.6		
		1999	*+110*				−5.5		
		2000	*+60*				−3.8		
Shortandy, Kazakhstan	*Shortgrass steppe*	*1998–2001*			*−357 to −534*				*Gilmanov et al. (2003b)*
Kasbegi range, Georgia	*Pasture*	*1996*					−2.1	−2.5	*Tappeiner and Cernusca (1996)*
	Wet meadow						−5.3	−5.9	
	Hay						−5.9	−7.0	
	Tall herb						−8.5	−9.1	
Tsukuba, Japan	*Grass field*	*1993*					−12.5		*Saigusa et al. (1998)*
		1994					−14.2		
Rodonia, Brazil	C$_4$ *pasture*	*5/93*					−1.9 [m]	−8.0 [m]	*Grace et al. (1998)*
Mackenzie Basin, NZ	*Tussock grassland*	*1998–1999*	*+97*				−1.9	−3.9	*Hunt et al. (2002)*
Duke Forest, N.C., USA	*Mixed-grass field*	*4/00–4/01*	*+97*	*+23* [n] (*−2* [k])	*−1,202*	*1,299*	−2.8	−7.6	*Present study*

Table 1 (continued)

Site	Ecosystem type	Year	NEE (g C m^{-2} a^{-1})	Growing season (summer) NEE (g C m^{-2} season^{-1})	A_c (g C m^{-2} a^{-1})	R_E (g C m^{-2} a^{-1})	Max NEE (g C m^{-2} day^{-1})	Max A_c (g C m^{-2} day^{-1})	References
Duke Forest, N.C., USA	Mixed-grass field	4/00–4/01	−65	−179 ^{n}(−94^k)	−1,356	1,291			Modeled annual C flux without θ limitations

[a]BREB systems can be employed at sites in which gradient measurements are conducted in the atmospheric surface layer (e.g., Dugas et al. 1999). The technique has several limitations: (1) errors due to spatially variable soil heat flux, (2) the assumption that eddy-diffusivities for heat, water vapor, and CO_2 are equal, and (3) unreliability when LE is small. Despite these limitations the method still offers a valuable estimate of long-term fluxes when data is properly post-processed (Brustaert 1982)

[b]April 24 to October 26

[c]−57 g C m^{-2} a^{-1} when soil flux, not BREB, is used to measure dormant-season fluxes

[d]Length of growing season varies between 105 and 140 days

[e]May–October 1987, June–August 1989

[f]Value depends on gapfilling and u^* correction, see Falge et al. (2001a)

[g]NEE ~0 g C m^{-2} a^{-1} when prescribed prairie burn is included

[h]Daytime NEE

[i]Night-time NEE

[j]Bracketed values are from Sims and Bradford (2001). Different respiration values are used for estimates of annual fluxes

[k]30 May to 28 August

[l]Burned prior to growing season

[m]Net daily flux for an 11-day period in May 1993

[n]11 April to 6 December

give flux source areas in excess of 5 km, an order of magnitude larger than the dimensions of our field.

Ecosystem respiration was modeled as a function of temperature with the widely used van't Hoff (1898) equation:

$$R_{E} = (R_{10})(Q_{10})^{(T-10)/10} \qquad (8)$$

where R_{10} is the reference respiration rate at 10°C and Q_{10} is the ecosystem respiration sensitivity to temperature. From regression analysis on night-time fluxes of the entire data set, we computed an effective Q_{10} of 1.55 and R_{10} of 2.54 µmol CO_2 m^{-2}s^{-1}. All model parameters are summarized in Table 2.

Seasonal variations in respiration parameters may be important components of the error in annual C budget estimates generated from eddy-covariance measurements that Goulden et al. (1996) termed "sampling uncertainty". There is evidence that ecosystem Q_{10} and R_{10} vary throughout the course of a year, but also that single annual respiration parameters may be sufficient to calculate annual R_E estimates (Janssens and Pilegaard 2003). To test this observation using eddy-covariance measurements, we estimate annual fluxes using both annually averaged and seasonally generated Q_{10} and R_{10} parameters (Tables 2, 3). To quantify respiration parameters that vary throughout the course of the year, Q_{10} and R_{10} are calculated for summer (May–August) and winter (November–February) per unit leaf area, and the actual Q_{10} and R_{10} are generated using a simple interpolation:

$$\begin{aligned} Q_{10} = &(Q_{10,w} - Q_{10,s}) \\ &\times \left(\frac{LAI - LAI_{min}}{LAI_{min} - LAI_{max}} \right) + Q_{10,w} \end{aligned} \qquad (9)$$

where $Q_{10,w}$ and $Q_{10,s}$ are Q_{10} values calculated for winter and summer, respectively, and LAI_{max} and LAI_{min} are maximum and minimum measured LAI. The interpolation for R_{10} follows the same model.

R_E was unrelated to soil moisture for the mild drought conditions encountered during the measurement period. We tested whether the residuals from equation 8 (i.e., the difference between measured and modeled R_E fluxes) depend on soil moisture and found weak correlation (r^2=0.09). Other studies have also shown an insignificant relationship between respiration and soil moisture (Fang and Moncreiff 2001), and this observation appears to hold for the mild drought encountered here though a stronger dependence on soil moisture may result from more severe droughts.

During the study period, the grass was cut on 29 June 2001, necessitating a dynamic LAI growth model immediately following this perturbation. We chose a mathematical model whose canonical form resembles a logistic growth equation. Such a model is approximated by a sequence of cubic splines to the four discrete LAI measurements (Fig. 1). The cubic spline technique to fit discrete data is described in Press et al. (1992 p108).

To calibrate our conductance model and to explore water fluxes from the canopy, we modeled latent heat exchange (LE) as:

$$LE = L_v \times 1.6g_c \times VPD \qquad (10)$$

where L_v is the latent heat of vaporization of water, and the 1.6 factor is needed to correct canopy conductance for differences in binary diffusivity between CO_2 and H_2O.

In the analysis, A_c is computed as the difference between NEE and modeled R_E for daytime runs. R_E is the eddy-covariance-measured NEE value at night when $u_*>0.12$ m s^{-1} and $|(z-d)/L|<0.1$, and is modeled R_E at all other times. Daily, seasonal, and annual sums of fluxes are called "estimates" because they depend on both directly measured fluxes and model results (e.g., equation 8) that fill gaps in the data record.

Table 2 Model parameters were measured via gas exchange or estimated from eddy-covariance through nonlinear optimization or boundary-line analysis (BLA). Parameters not directly measured are taken from the cited literature

Parameter	Description	Value	Units	Source
Photosynthesis				
Vc_{max}	Maximum Rubisco carboxylation capacity	81.3	µmol CO_2 m^{-2}s^{-1}	Gas exhange measurements taken during the growing season
α	Leaf absorptivity for PAR	0.83	mol mol^{-1}	Campbell and Norman (1998)
e_m	Maximum quantum efficiency	0.08	—	Campbell and Norman (1998)
C_i/C_a	Mean ratio of intercellular to ambient CO_2	0.75	—	Gas exhange measurements taken during the growing season
[O_2]	Oxygen mole fraction (mmol mol^{-1})	210	mmol mol^{-1}	Campbell and Norman (1998)
τ	Ratio describing CO_2/O_2 partitioning by Rubisco	1.3	—	Campbell and Norman (1998)
K_{c25}	Michaelis constant for CO_2 fixation	300	µmol mol^{-1}	Campbell and Norman (1998)
γ	K_c parameter	0.074	—	
$K_{O2, 25}$	Michaelis constant for O_2 inhibition	300	mmol mol^{-1}	Campbell and Norman (1998)
γ	K_{O2} parameter	0.018	—	
x	Leaf angle distribution parameter	0.7	—	Campbell and Norman (1998)
Canopy conductance				
ν	Soil parameter	0.6	—	Nonlinear optimization
θ_R	Moisture content below which g_c is reduced	0.2	m^{3}m^{-3}	Nonlinear optimization and Lai and Katul (2000)
m	Sensitivity of canopy conductance to VPD	0.6	—	Eddy-covariance measured LE using BLA. Oren et al. (1999)
Respiration				
R_{10}	Scale parameter	2.54	µmol m^{-2}s^{-1}	Eddy-covariance measurements for $u_*>0.12$ m s^{-1} and $|(z-d)/L|<0.1$
Q_{10}	Slope parameter	1.55	—	Same as R_{10}

Table 3 Modeled and estimated annual carbon and water budgets in a southeastern United States grassland. 'Modeled—no drought' refers to the modeling analysis where soil moisture was parameterized to have no influence on stomatal conductance

Variable	Estimated: single annual respiration paramters	Estimated: seasonal respiration paramters	Modeled	Modeled—no drought	Modeled—drought, no harvest	Modeled—no drought, no harvest
ET (mm a^{-1})	568	568	547	738	570	767
A_c (g C $m^{-2}a^{-1}$)	−1,202	−1,304	−1,207	−1,356	−1,230	−1,381
R_E (g C m^{-2} a^{-1})	1,299	1,433	1,291	1,291	1,291	1,291
NEE (g C m^{-2} a^{-1})	97	129	84	−65	61	−90
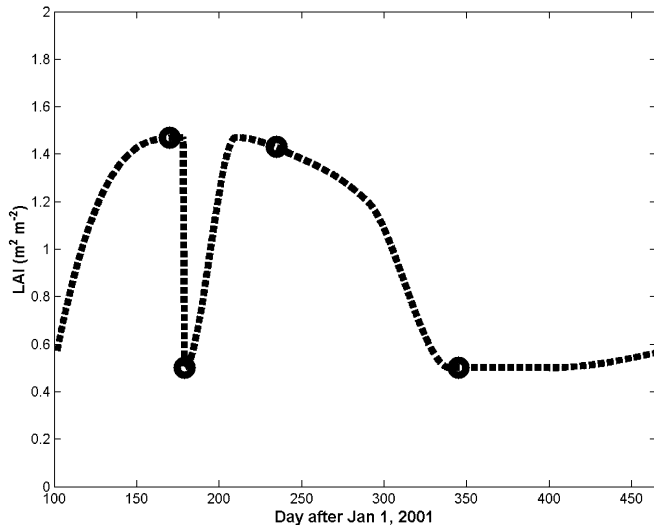
Fig. 1 Modeled leaf area index (LAI) from 11 April 2001 to 11 April 2002. LAI measurements are shown as *large circles*

Measurements

The experimental site is a grass-covered field in the Blackwood Division of the Duke Forest in Orange County, near Durham, North Carolina (35.971°N, 79.09°W, elevation 163 m). The long-term mean annual temperature and precipitation are 15.5°C and 1,145 mm, respectively. The field is approximately 480×305 m, dominated by the C_3 grass *Festuca arundinaria* Shreb., and surrounded by loblolly pine (*Pinus taeda* L.) forest. The vegetation includes minor components of C_3 herbs and the C_4 grass *Schizachyrium scoparium* (Michx.) Nash, not considered here. The site was burned in 1979 and is mowed annually during the summer for hay according to local practices. For this investigation, we consider data collected between 11 April 2001 and 11 April 2002.

Scalar fluxes were measured using an eddy-covariance system comprised of a triaxial sonic anemometer (CSAT3, Campbell Scientific, Logan, Utah) and an open-path gas analyzer (LI-7500, Li-Cor, Lincoln, Neb.), positioned 3.0 m above the canopy. The gas analyzer was tilted 35° from the vertical to avoid direct sunlight contamination and to minimize water accumulation on the absorbing lens surface. The LI-7500 was separated from the CSAT3 by 10 cm, a distance comparable to the sonic path averaging length. The time series of all three velocity components, temperature, and scalar concentrations were sampled using a 23X data logger (Campbell Scientific, Logan, Utah) at 10 Hz. All covariances were then computed over a 30-minute period using the procedures described in Katul et al. (1997). The Webb-Pearman-Leuning correction (Webb et al. 1980) was subsequently applied to the computed scalar covariances.

The tower was located in the middle of the field with approximately 250 m fetch to the southwest, the predominant direction of flow during summer. The peak of the source weight function (x_p) describes the peak of the maximum source area that

contributes to fluxes, and was estimated using the footprint model in Hsieh et al. (2000) to be smaller than 150 m (at z=3 m) for most stability runs, except for stable conditions (Appendix C). The source weight function describes the relative scalar flux contribution to a measurement location for various scalar source areas upwind. The term "footprint" is the distance at which 90% of the scalar flux contributes to the measurement location as determined from the integrated source weight function. R_E data collected during stable atmospheric conditions at night or when x_p exceeded the size of the field were discarded and replaced with the output of the Q_{10} respiration function.

PAR, air temperature (T_a), relative air humidity (RH), net radiation (R_{net}) and θ were sampled every second and averaged every half-hour. R_{net} was measured with a Fritschen-type net radiometer (Q7, REBS, Seattle, WA) and incident PAR with a quantum sensor (LI-190SA Li-Cor, Lincoln, NE). T_a and RH were measured with a HMP35C temperature/RH probe (Campbell Scientific, Logan, Utah). θ was measured using ThetaProbe soil moisture sensors Type ML1 (Delta-T Devices, Cambridge, UK) positioned at 10 cm and 25 cm depths at six locations north and south of the eddy-covariance tower, and at a depth of 10 cm at locations east and west of the tower.

Gas exchange measurements were used to estimate the apparent maximum rubisco carboxylation capacity (Vc_{max}) and were performed in May, June and August 2001 using an open-flow LI-6400 portable photosynthesis system (Li-Cor, Lincoln, Neb.). For leaf-level photosynthesis, Vc_{max} was directly fitted to in situ responses of A_n to CO_2 supply under controlled conditions (following the approach of Medlyn et al. 2002). The response of A_n to intercellular CO_2 concentration (C_i) was measured in the field within 50 m of the tower in mid-morning on sunny days by controlling chamber conditions to light saturation (1,800 µmol m^{-2} s^{-1} quantum flux density) and 29–32°C leaf temperature with VPD=1.8 kPa for 9–10 different C_i steps. Vc_{max} was then fitted to the initial slope comprising at least five C_i levels <250 µmol mol^{-1}, with r^2 exceeding 98% (Table 2).

We calculated LAI from PAR transmission data collected along three 50 m transects in a 120° swath to the south of the eddy-covariance tower. The PAR transmission data were measured with an 80-sensor series of quantum sensors (AccuPAR model PAR-80 Ceptometer, Decagon Instruments, Pullman, Wash.) and used to calculate gap fractions, which were inverted to provide LAI estimates after Norman and Campbell (1989). Time series of environmental drivers for the measurement period 11 April 2001 to 11 April 2002 are presented in Fig. 2.

The eddy-covariance methodology is prone to missing data points that can occur due to precipitation, extreme weather events, sensor malfunction, or power outage. Raw flux data coverage for this site over the period of examination (11 April 2001 to 11 April 2002) was 92.9% (16,281 of 17,520 potential data points). After filtering out night-time CO_2 flux data using the criteria in Appendix C, 45.1% of potential CO_2 flux data points remain. A variety of methods exist to 'gapfill' missing CO_2 and LE data, as summarized in Falge et al. (2001a, 2001b). NEE data gaps when PAR exceeded the light compensation point (213 µmol photons m^{-2} s^{-1}) were filled by fitting a nonlinear regression of measured CO_2 flux about PAR and replacing missing data points with the results of the regression (Fig. 3a). NEE data gaps for night-time and low PAR periods were filled using the Q_{10} respiration equation. Gaps in the LE record were

Fig. 2 Time series of maximum daily measurements for key ecophysiological drivers from 11 April 2001 to 11 April 2002: **a** photosynthetically active radiation (PAR), **b** R_{net}, **c** maximum and minimum T_a, **d** vapor pressure deficit, and **e** volumetric soil moisture content (θ). Measured data are *black points*; *gray points* indicate gapfilled data. The point at which soil moisture limits conductance ($\theta=0.2$ m^{3}m^{-3}) is indicated by a *dashed line*
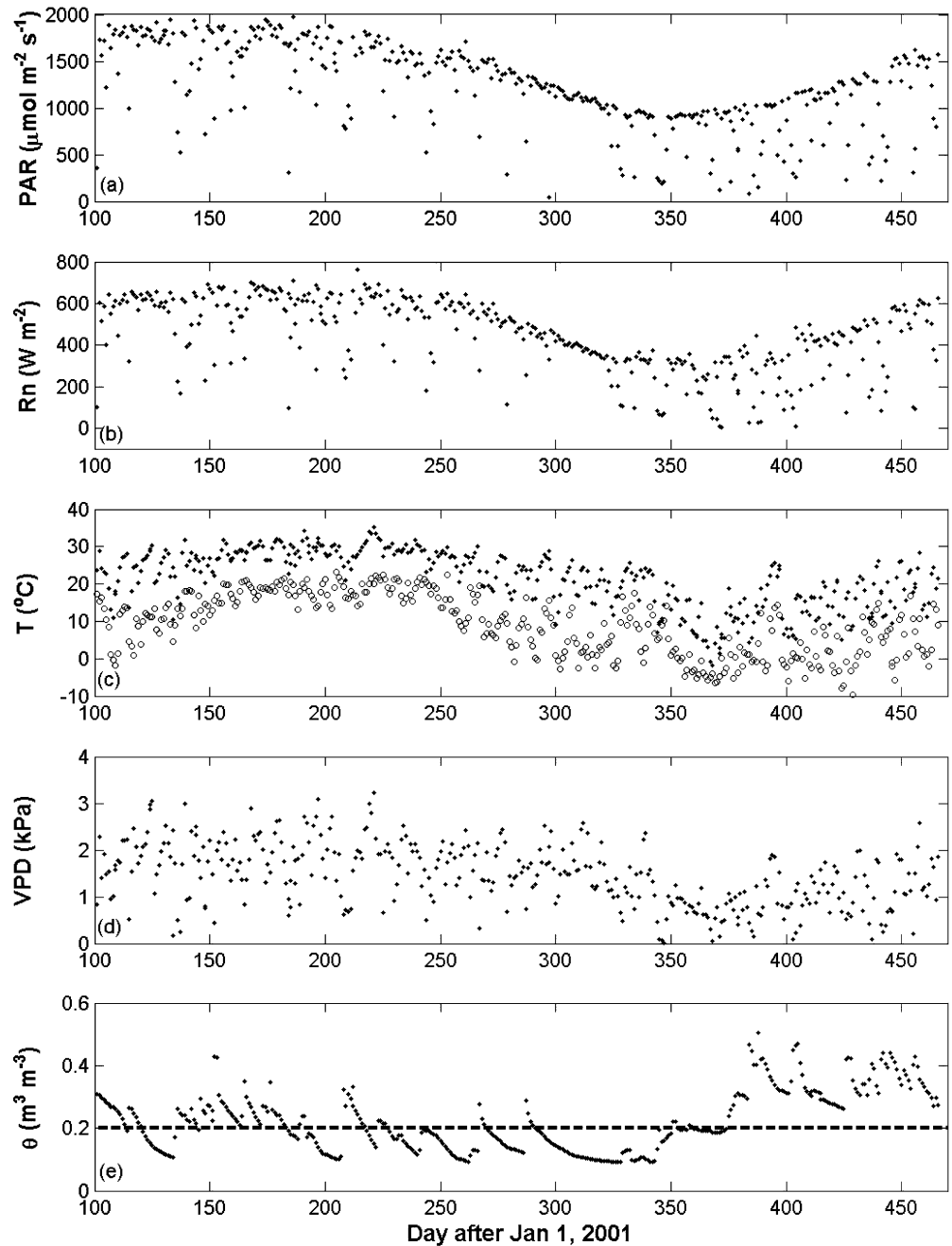
filled by fitting a linear regression of LE about R_{net} (Fig. 3b), and replacing missing data points with the results of the regression (Brutsaert and Sugita 1992).

Temporal data coverage for PAR was 87.5%, for R_{net} 87.0%, for RH and T_a 80.5% and for θ 67.6%. To gapfill missing environmental data, a linear relationship was derived between measured data points at the grass site and adjacent pine and hardwood eddy-covariance tower sites under identical climatic and edaphic conditions. Missing data were gapfilled with the results of the regression.

Results and discussion

To address the study objectives, we first discuss estimated and modeled ET and NEE and compare these results with other studies. We then proceed to assess the impact of

harvesting on ET and NEE and summarize the contributions of this study to current understanding of grassland water and carbon cycling.

Evapotranspiration

Maximum estimated daily evapotranspiration (ET, 4.1 mm day^{-1}) is within the range of values estimated for other grasslands based on eddy-covariance, which range from ~3 mm day^{-1} to 5.5 mm day^{-1} (Ripley and Saugier 1978; Meyers 2001; Dugas et al. 1999; Hunt et al. 2002; Wever et al. 2002). Values estimated by other methods range from 4.2 mm day^{-1} to 6.2 mm day^{-1} as summarized by Kelliher

Fig. 3 a The relationship between net ecosystem carbon exchange (NEE) and PAR for the one-year measurement record. The solid nonlinear regression line is used to estimate NEE for PAR above the C compensation point (PAR=213 μmol m^{-2} s^{-1}) for gaps in the measurement record. **b** Latent heat exchange (LE) plotted against net radiation (R_{net}). The solid linear regression line is used to estimate LE for gaps in the measurement record
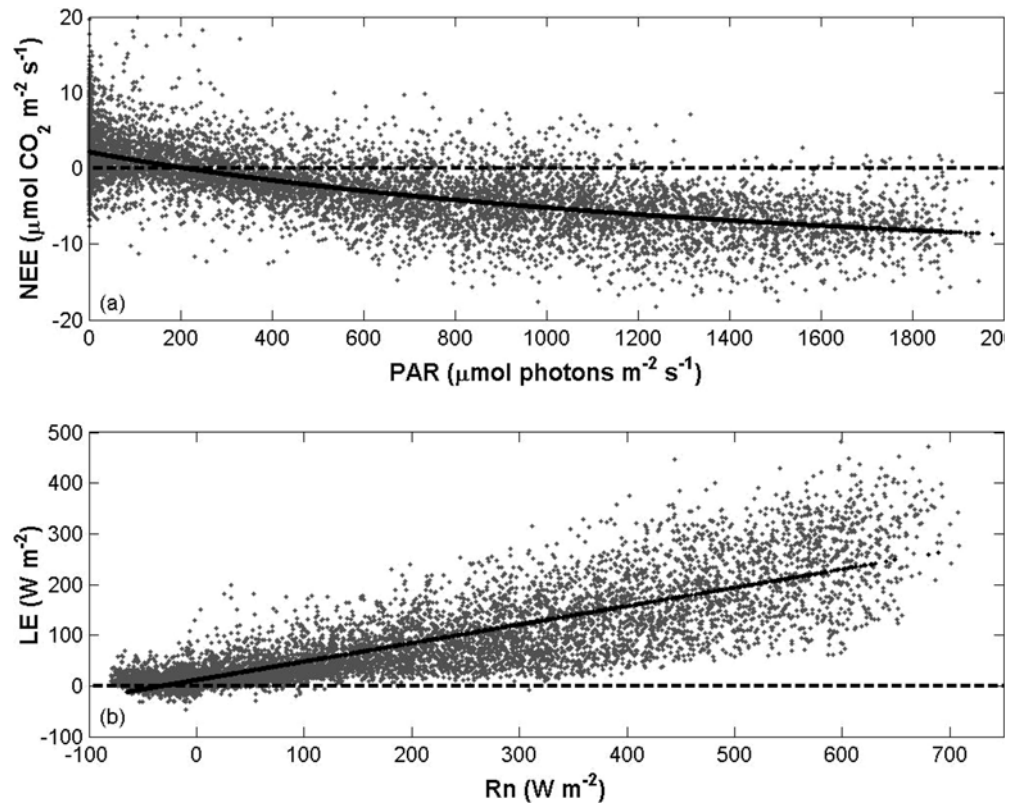

et al. (1993). We repeated the model analysis assuming that soil moisture does not limit conductance for the entire record, yet retaining the same T_a and VPD for a 'drought-free' scenario. In the absence of soil moisture limitations, modeled maximum daily ET is 5.3 mm, near the maximum of eddy-covariance estimated values for grasses (5.5 mm in Dugas et al. 1999).

Total summer evapotranspiration [ET$_s$, for day of year (DOY) 150–240 based on Meyers (2001)] was 239.2 mm. Our value is close to ET$_s$ over an Oklahoma rangeland during three non-drought seasons (1995–1997), which averaged ~253 mm (Meyers 2001); ET$_s$ in southeastern United States grassland during a dry year resembled ET$_s$ during average precipitation years over the United States Great Plains.

Annual precipitation (P_a) for the measurement period 11 April 2001 to 11 April 2002 was 821.5 mm. This is 72% of the long-term average of 1,145 mm, indicating mild drought conditions. Annual evapotranspiration (ET$_a$) for the study period was 568 mm, slightly more than modeled ET$_a$ (547 mm; Fig. 4; Table 3). ET$_a$ represented 69.1% of P_a, which is intermediate between published ET$_a$/P_a for grasslands that range from <50% to over 100% (Meyers 2001; Paz et al. 1996; Bellot et al. 1999; Nouvellon et al. 2000; Everson 2001; Wever et al. 2002). ET$_a$/P_a here is consistent with a natural grassland catchment in Natal Drakensberg, South Africa during two low precipitation years (~70%; Everson 2001), and two mixed-grassland sites in northwestern Spain during a low precipitation year (~69%; Paz et al. 1996), suggesting similarities in the

water balance of warm-temperate/Mediterranean grassland ecosystems during dry years.

Soil moisture limited g_c (meaning $\theta < \theta_R$, θ_R=0.2 m^{3}m^{-3}) 52% of the time for the entire year and 66% of the time during non-winter periods (Figs. 5a, b). We consider non-winter periods to be DOY 101–340, when A_c is not seasonally suppressed by dead vegetation. Re-parameterizing the model to simulate the 'drought-free' scenario results in modeled ET$_a$ of 738 mm or ET$_a$/P_a of 89.9% (Table 3). The drought-free modeled ET$_a$/P_a is consistent
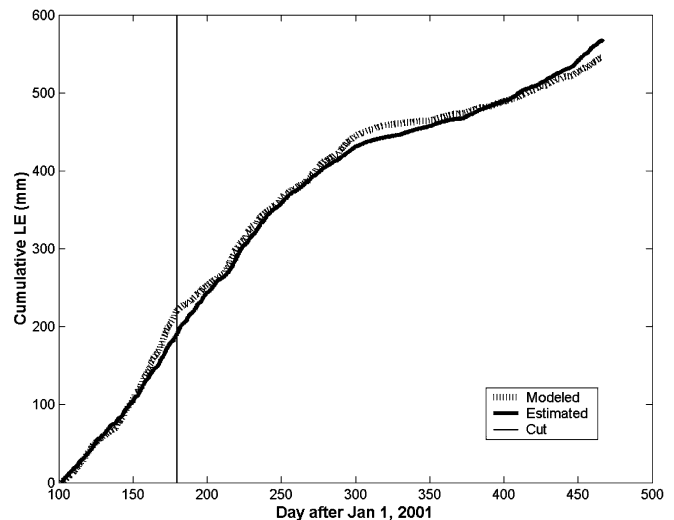
Fig. 4 Estimated and modeled cumulative annual evapotranspiration

with eddy-covariance and Bowen Ratio Energy Balance studies in grasslands during years with normal to above-average precipitation, although infiltration and soil storage and lower VPD during very wet years decrease this ratio (Meyers 2001; Nouvellon et al. 2000; Wever et al. 2002). Eddy-covariance studies are typically performed on flat terrain. Thus, surface runoff is a small component of the water budget and is not likely to affect the water balance.

Net ecosystem exchange

Maximum daily A_c (-7.6 g C m^{-2}day^{-1}) is at the upper end of the range of reported values for other grasslands (-2.5 g C m^{-2}day^{-1} to -9.1 g C m^{-2}day^{-1}; Table 1). Maximum daily NEE was low because of high daily R_E but comparable to other studies with drought impacts (Table 1). High maximum daily A_c and low maximum daily NEE suggest that the magnitude of R_E played a major role in determining the magnitude of net fluxes during both drought and non-drought periods.

Previous studies have demonstrated that R_E decreases with θ (e.g., Reichstein et al. 2002). However, in our study, the magnitude of R_E was primarily dependent on temperature and was insensitive to θ for the measurement period, consistent with Fang and Moncreiff (2001). Perhaps a more prolonged drought, especially when coupled with high temperatures, would generate a stronger dependence of R_E on θ.
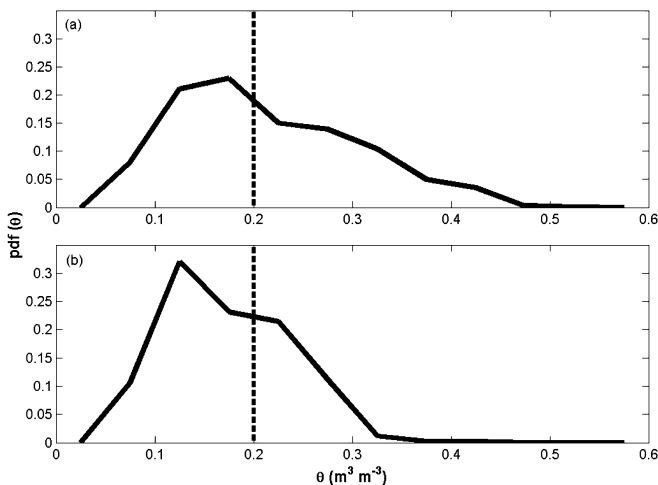
Positive NEE throughout non-winter periods indicated a net return of CO_2 to the atmosphere during this time (Table 1). However, model results show that, in a drought-free year with no soil moisture limitation on conductance, growing season NEE in our grassland is comparable to other studies (Table 1). NEE is near zero during summer, in contrast to a south-central United States rangeland

Fig. 5 a Probability density function (pdf) of measured root-zone soil moisture content (θ) from 11 April 2001 to 10 April 2002. $\theta < \theta_R$ for 52% of the year. The dotted line indicates the point at which θ suppresses canopy conductance. **b** pdf of soil moisture content (θ) measurements for non-winter periods (11 April 2001 to 6 December 2002, defined as the period when A_c is not suppressed). $\theta < \theta_R$ for 66% of the season

which experienced negative net C fluxes except in the case of severe drought (Meyers 2001). Model results suggest that even in the absence of drought, summer C fluxes in our grassland only approach 50% of summer values observed by Meyers (2001) (Table 1), indicating that our grassland is unable to sequester appreciable C during the summer. In the absence of drought, growing season NEE values approach those of other grasslands not because of a large summertime sink, but because of a longer growing season in the southeastern United States.

Annual NEE ($+97$ g C m^{-2} a^{-1}) was an order of magnitude smaller than estimated annual A_c ($-1,202$ g C m^{-2} a^{-1}) and R_E ($+1,299$ g C m^{-2} a^{-1}; Tables 1, 3; Fig. 6). Annual A_c and R_E were 1.5 times larger and over 2.4 times larger, respectively, than other grasslands (Table 1). These large fluxes reflect the longer growing season in the southeast United States that is warmer and wetter than in the grassland biome. These annual flux estimates were generated using static respiration parameters for the entire year (Tables 2, 3). The "effective" Q_{10} for the entire year, 1.55, is at the low end of previously reported values for ecosystems (Raich and Schlesinger 1992; Kirschbaum 2000). Q_{10} estimates are highly dependent on the reference temperature used (Lloyd and Taylor 1994; Tjoelker et al. 2001), whether air or soil temperatures are employed in the calculations, and how the data is pooled or ensemble-averaged.
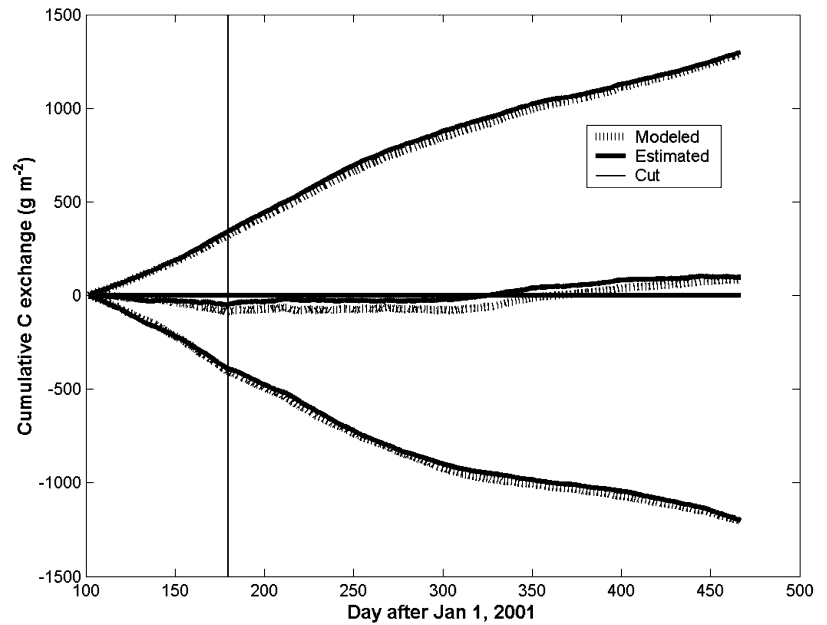
Flux estimates using respiration parameters that are scaled by leaf area resulted in $A_c = -1,304$ g C m^{-2} a^{-1} (i.e., 102 g C m^{-2} a^{-1} more negative) and increased R_E to 1,433 g C m^{-2} a^{-1} (i.e., 134 g C m^{-2} a^{-1} more positive) for a modified NEE estimate of 129 g C m^{-2} a^{-1} (Table 3). Despite the large variation in LAI, the annual exchange rates appear to be robust to seasonally dynamic leaf-area scaled respiration parameters. A chamber-based study of belowground respiration by Janssens and Pilegaard (2003) suggested that single annual respiration parameters are adequate for estimating annual belowground respiration. In this eddy-covariance-based study, the magnitude of annual NEE was impacted little by varying respiration parameters throughout the year, although component fluxes (A_c and R_E) increased in magnitude by over 100 g C m^{-2} a^{-1}.

Modeled A_c, R_E, and NEE with and without soil moisture limitations on g_c are contrasted in Table 3. Estimated and modeled A_c, R_E, and NEE are presented in Fig. 6 as cumulative carbon exchange throughout the measurement period. Root mean square error between modeled and estimated NEE is 0.057 g C m^{-2} a^{-1}. Estimated annual NEE represents a non-trivial C flux to the atmosphere compared to many other grassland eddy-covariance studies (Table 1; but see Falge et al. 2001a). Model calculations suggest that this grassland ecosystem switches from a net annual C source to a net annual C sink depending on soil moisture conditions (Table 3). A_c increases when soil moisture limitations are removed due to g_c enhancement, while R_E is insensitive to θ under mild drought and does not change in the 'drought-free' model analysis since no soil moisture limitation was employed.

Fig. 6 Estimated and modeled cumulative A_n (negative fluxes), R_E (positive fluxes), and NEE


The sign shift observed in drought-free modeled NEE is consistent with results from a northern Great Plains mixed grassland (Flanagan et al. 2002), a southern Great Plains rangeland (Frank et al. 2001), and a southern Great Plains tallgrass prairie (Suyker et al. 2003) (Table 1). In all three studies, the sign shift or increase in NEE sink strength was attributed to an increase in A_c and not a reduction in annual R_E, consistent with our model calculations (Table 3). These studies, although limited in number, suggest that NEE variability is driven by drought impacts on assimilation and subsequent growth (Knapp and Smith 2001). This contrasts with observations made across a range of European forests, which found that R_E, not A_c, was the primary contributor of variation in the carbon balance across sites (Valentini et al. 2000).

Positive annual NEE values commonly occur as a result of drought (Table 1), highlighting the strong coupling of the carbon and water cycles in grasslands and further suggesting that perturbations in the hydrologic cycle disrupts the C balance in grasslands (e.g., Knapp and Smith 2001). However, even in the absence of soil moisture limitations, NEE modeled for our site is low compared to the range of non-drought annual grassland NEE (Tables 1, 3), further suggesting that this southeastern United States grassland is unable to sequester large amounts of carbon under the management protocol (i.e., mowing) required to check woody encroachment.

Our grassland was a net daily C sink before the harvest on DOY 179 (28 June 2001; Fig. 7), but became a net source immediately thereafter due to the combined impacts of low LAI (Fig. 1) and low θ (Figs. 2, 5). Unlike Bremer et al. (1998) and Bremer and Ham (2002), we found little reduction in R_E after harvesting. Leaf biomass is a small component of the total respiring biomass, and leaf area is able to quickly respond to mechanical destruction to balance R_E within days (Dugas et al. 1999). Thus, the grassland turned into a net daily

sink (on a 24-h basis) as soon as 6 days after harvesting (Fig. 7). These results are similar to a harvested Bermudagrass [*Cynodon dactylon* (L.)] field (Dugas et al. 1999). In the *C. dactylon* field, negative daily C fluxes were nearly restored 5 days after the cut, and fully restored after 11 days. In both harvesting studies, restoration of negative daily NEE was impelled by the rapid recovery of LAI after the cut (Fig. 1; see also Dugas et al. 1999). However, perturbations on longer time scales, such as drought or nutrient limitation, may have long-lasting effects on LAI and NEE (Meyers 2001; Flanagan et al. 2002).

To evaluate the effect of the management protocol on NEE, we re-parameterized the model to simulate a
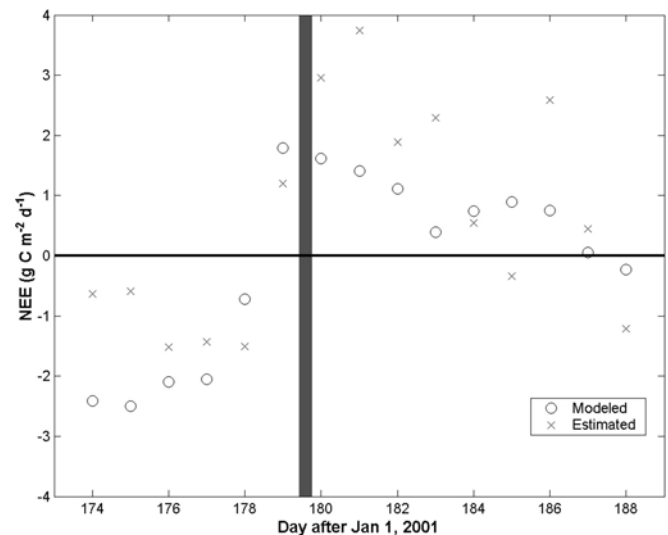
Fig. 7 Comparison between estimated (*points*) and modeled (*circles*) daily NEE estimates before and after grass harvesting. The vertical shaded line represents the duration of the tractor harvest and is omitted from the record

scenario without a harvest. In these simulations, the physiological properties (leaf and respiration parameters) and maximum LAI were not modified after the harvest. Under these idealized conditions, harvesting had a weak and transient effect on NEE fluxes at seasonal and annual time scales, increasing annual NEE by an additional ~ -24 g C m^{-2} a^{-1} for both drought and non-drought scenarios (Table 3). Thus, the model sensitivity analysis suggests that attempting to manage for C sequestration by ending the annual harvest over the course of the measurement period would have resulted in little additional C sequestration. In reality, harvesting impacts other processes, including nutrient content and physiological properties, community composition, and soil compaction and below-ground dynamics, all of which are likely to impact both A_c and R_E, but whose effects cannot be assessed with our approach.

It has been suggested that grasslands in warmer and wetter climates will act as a large carbon sink in the future to help mitigate greenhouse warming (Ojima et al. 1993). Although the low estimated and modeled potential C sink strength for this grassland does not support this notion, more long-term monitoring must be undertaken before the role of warm, moist grasslands in C sequestration is ascertained (e.g., Miranda et al. 1997; Wilsey et al. 2002).

The emerging picture of net ecosystem C cycling in grassland ecosystems based on this study and similar ones (Table 1) suggests a characteristic NEE that is close to zero —but comprised of large assimilatory and respiratory fluxes—that can readily switch between C source and sink depending primarily on hydrologic perturbations (Kim et al. 1992; Bruce et al. 1999; Frank et al. 2001; Flanagan et al. 2002). A recent study has suggested that future changes in elevated atmospheric CO_2 can have an adverse effect on grass ecosystem NPP when combined with other likely global changes including increased N deposition, temperature, and precipitation (Shaw et al. 2002). Another study has suggested that past increases in atmospheric CO_2 have played a more important role in C sequestration in grasslands than will projected future CO_2 enrichment (Gill et al. 2002). Thus, if future increases in atmospheric CO_2 may have little effect on future grassland NEE dynamics, the effects of global changes on the variability in the hydrological cycle (Vörösmarty and Sahagian 2000; Jackson et al. 2001; Houghton et al. 2001; Rosenzweig et al. 2002) may be the key driver of future NEE responses in grasslands.

Conclusions

This study investigated ET and the direction and magnitude of NEE and its components (A_c and R_E) in a southeastern grassland ecosystem under drought, under simulated drought-free conditions, and with rapid changes in LAI through harvesting.

We found that the relationship between annual ET and annual precipitation was similar to drought-impacted warm-temperate and Mediterranean grasslands, and that

'drought-free' modeled ET resembled North American Great Plains grassland ecosystems studied during non-drought years. The impact of soil moisture limitation on g_c and consequently A_c, and not on the variability of R_E, was the dominant control on NEE at time scales from days to seasons during a year with mild drought. This contrasts with results from eddy-covariance studies in European forests, which have suggested that variability in R_E exerts dominant control on C exchange (Valentini et al. 2000). Low soil moisture ($0.1 < \theta < 0.2$) reduced stomatal conductance for over half of the year, resulting in a grass ecosystem that was a net source of CO_2. In the absence of soil moisture limitations, model calculations suggest that this grassland ecosystem would become a small net annual C sink. The synthesis of results on grassland studies further implies that interannual variability in NEE is large (Table 1), and additional sources of climatic and hydrologic sensitivity should be explored (Knapp and Smith 2001) to improve predictability of grassland ecosystem C cycling for the future.

Appendix A: leaf-level assimilation model

According to Farquhar et al. (1980), as later modified by Collatz et al. (1991) and Campbell and Norman (1998), the net photosynthetic rate at the leaf scale depends on light, CO_2 concentration, and leaf temperature (T_l) and can be described as:

$$A_n = \min \begin{pmatrix} J_E \\ J_C \end{pmatrix} - R_d$$

where J_E and J_C are the assimilation rates restricted by light-driven electron transport processes and ribulose bisphosphate (RuBP) carboxylase-oxygenase activity (Rubisco), respectively, and R_d is dark respiration. For leaf-level processes we adopt the ecophysiological convention of positive fluxes into the leaf. When these fluxes are scaled to the canopy we revert to the micrometeorological convention. J_E is given by:

$$J_E = \alpha \times e_m \times Q_p \times \frac{\overline{C_i} - \Gamma_*}{\overline{C_i} + 2\Gamma_*}$$

where α is the leaf absorptivity [not to be confused with the apparent quantum efficiency (α_a)] for photosyntheti-

cally active radiation (PAR), e_m is the maximum quantum efficiency for leaf CO_2 uptake, Q_p is PAR irradiance on the leaf, and $\overline{C_i}$ is the mean intercellular CO_2 concentration. The values of all parameters are listed in Table 3. The photosynthetic CO_2 compensation point, Γ_*, is given by:

$$\Gamma_* = \frac{[O_2]}{2\tau}$$

where $[O_2]$ is the oxygen concentration in air (210 mmol mol^{-1}), and τ is a ratio of kinetic parameters describing the partitioning of RuBP to the carboxylase or oxygenase reactions of Rubisco. J_c is computed from

$$J_c = \frac{Vc_{max}(\overline{C_i} - \Gamma_*)}{\overline{C_i} + K_c(1 + [O_2]/K_{O_2})}$$

where Vc_{max} is the maximum catalytic capacity of Rubisco per unit leaf area (µmol m^{-2}s^{-1}), and K_c and K_{O_2} are the Michaelis constants for CO_2 fixation and O_2 inhibition with respect to CO_2, respectively. J_c increases linearly with increasing $\overline{C_i}$, but approaches a maximum under a high CO_2 concentration state rarely encountered under present conditions, though likely under future climate scenarios.

Temperature dependence of kinetic variables is computed following the equations in Campbell and Norman (1998). Five kinetic parameters are needed to adjust for temperature: K_c, K_{O_2}, τ, Vc_{max} and R_d. For the first two parameters, a modified exponential temperature function of the form:

$$k = k_{25} \times \exp[\gamma(T_L - 25)]$$

is employed, where k is defined at the leaf surface temperature or T_l, k_{25} is the value of the parameter at 25°C, and γ is the temperature coefficient for that parameter. τ is assumed to be 1.3.

Vc_{max} and R_d are adjusted by:

$$Vc_{max} = \frac{Vc_{max,25} \exp[.088(T_L - 25)]}{1 + \exp[.29(T_L - 41)]}$$

and

$$R_d = \frac{R_{d,25} \exp[.069(T_L - 25)]}{1 + \exp[1.3(T_L - 55)]}$$

where $Vc_{max,\,25}$ and $R_{d,\,25}$ are values of Vc_{max} and R_d at 25°C, respectively (Campbell and Norman 1998).

Following Collatz et al. (1991), the dark respiration rate at 25°C ($R_{d,\,25}$) can be estimated using

$$R_{d,25} = 0.015 \times Vc_{max,25}$$

Appendix B: the boundary line analysis

Stomatal conductance was modeled according to Oren et al. (1999), with the parameters m and g_{ref} generated from a boundary line analysis. The boundary line analysis sorts the measured conductance data into 10 bins characterized by increasing mean light levels. A logarithmic function relating conductance to VPD is generated for each light level (i) using data points falling above the mean plus one standard deviation, after removing outliers at each light level. The function is given by:

$$g_{s,i} = a_i \times \ln(VPD_i) + b_i$$

where i=1–10 (for ten light levels). The slope (a_i) and intercept (b_i) for each i were computed via regression analysis, and the parameter m is the ratio of these two vectors:

$$m = \frac{a}{b}$$

in this study, m=0.64, which is consistent with the theoretical value of m=0.6 from Oren et al. (1999). We use the latter value in the model.

The parameter g_{ref} is a light-dependent function derived from fitting the intercept vector b as a logarithmic function of PAR. Here, we found that g_{ref} is

$$g_{ref} = 0.0922 \times \log(PAR) \\ - 0.3985 \; \mu\text{mol m}^{-2} \text{ s}^{-1}$$

Appendix C: night-time atmospheric stability considerations

Correcting night-time eddy-covariance fluxes under conditions of low u_* with respiration models parameterized using night-time fluxes with high u_* is standard eddy-covariance methodology (Goulden et al. 1996; Aubinet et al. 2000; Falge et al. 2001a). We conducted a sensitivity analysis on the annual NEE estimate by varying u_{*t} between 0 and 0.3, and found that NEE did not vary appreciably for u_{*t} between 0.12 and 0.18. Hence, we first filtered the data with u_{*t}=0.12 m s^{-1}. NEE is highly sensitive to the u_* threshold value chosen (u_{*t}; Barford et al. 2001), but the exclusive use of u_{*t} has not been examined, and we propose additional meteorological constraints to filters used for night-time eddy-covariance data. Namely, we propose two additional constraints that only accept fluxes when atmospheric stability conditions are near-neutral and when the peak of the source-weight function (x_p) lies within the dimensions of the study site

272

Fig. 8a–c The effect of u_* and atmospheric stability on the calculated night-time CO_2 flux footprint. The measurement tower is at the center of the polar plot. Radial lines represent wind directions (0°=North) and concentric lines represent radial distances from tower (m). **a** Points represent footprint distances from the tower for all night-time 30-minute runs. **b** same as **a** but implementing the friction velocity threshold (i.e., selecting only runs with $u_*>u_{*t}$, $u_{*t}=0.12$). **c** Same as **a** but implementing both friction velocity and atmospheric stability thresholds (i.e., selecting runs with $u_*>0.12$ and $|(z-d)/L|<\varsigma_n$, $\varsigma_n=0.1$)
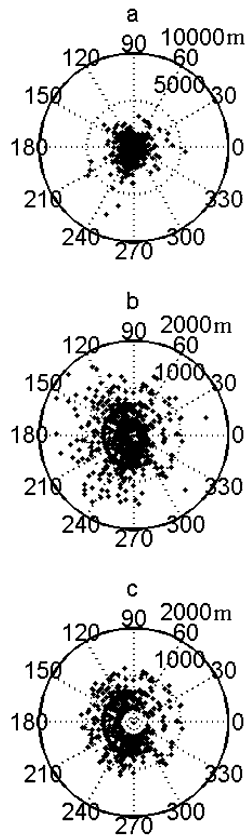
(here 150 m). The atmospheric stability parameter in the atmospheric surface layer is defined as $\varsigma=(z-d)/L$, and near-neutral conditions are defined as $|\varsigma|<0.1$. We define the near-neutral atmospheric stability threshold of 0.1 to be ς_n.

The importance of adding ς_n, to model night-time respiration is illustrated by considering the flux footprint at night for all atmospheric conditions, which exceeds 5 km (Fig. 8a). Adding u_{*t} alone results in a flux footprint that exceeds 2 km, an order of magnitude larger than the dimensions of our field (Fig. 8b). Filtering with both u_{*t} and ς_n (Fig. 8c) reduces the night-time flux footprint to ~1,000 m, which still exceeds field dimensions, so we further filter night-time flux measurements when the peak of the source-weight function (x_p) exceeds 150 m, guaranteeing that measured night-time fluxes originate from our field in a probabilistic sense.

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