2013

CO₂ uptake and ecophysiological parameters of the grain crops of midcontinent North America: Estimates from flux tower measurements

Tagir G. Gilmanov
South Dakota State University, tagir.gilmanov@sdsstate.edu

Bruce K. Wylie
USGS EROS, wylie@usgs.gov

Larry L. Tieszen
USGS EROS, llt@sio.midco.net

Tilden P. Meyers
NOAA/Air Resources Laboratory, Tilden.Meyers@noaa.gov

Vern S. Baron
Lacombe Research Centre, vern.baron@agr.gc.ca

See next page for additional authors

Follow this and additional works at: <https://digitalcommons.unl.edu/biosysengfacpub>

Gilmanov, Tagir G.; Wylie, Bruce K.; Tieszen, Larry L.; Meyers, Tilden P.; Baron, Vern S.; Bernacchi, Carl J.; Billesbach, David P.; Burba, George G.; Fischer, Marc L.; Glenn, Aaron J.; Hanan, Niall P.; Hatfield, Jerry L.; Heuer, Mark W.; Hollinger, Steven E.; Howard, Daniel M.; Matamala, Roser; Prueger, John H.; Tenuta, Mario; and Young, David G., "CO₂ uptake and ecophysiological parameters of the grain crops of midcontinent North America: Estimates from flux tower measurements" (2013). *Biological Systems Engineering: Papers and Publications*. 298.
<https://digitalcommons.unl.edu/biosysengfacpub/298>

This Article is brought to you for free and open access by the Biological Systems Engineering at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Biological Systems Engineering: Papers and Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Authors

Tagir G. Gilmanov, Bruce K. Wylie, Larry L. Tieszen, Tilden P. Meyers, Vern S. Baron, Carl J. Bernacchi, David P. Billesbach, George G. Burba, Marc L. Fischer, Aaron J. Glenn, Niall P. Hanan, Jerry L. Hatfield, Mark W. Heuer, Steven E. Hollinger, Daniel M. Howard, Roser Matamala, John H. Prueger, Mario Tenuta, and David G. Young

CO₂ uptake and ecophysiological parameters of the grain crops of midcontinent North America: Estimates from flux tower measurements

Tagir G. Gilmanov^{a,*}, Bruce K. Wylie^b, Larry L. Tieszen^b, Tilden P. Meyers^c, Vern S. Baron^d, Carl J. Bernacchi^e, David P. Billesbach^f, George G. Burba^g, Marc L. Fischer^h, Aaron J. Glennⁱ, Niall P. Hanan^j, Jerry L. Hatfield^k, Mark W. Heuer^{c,l}, Steven E. Hollinger^m, Daniel M. Howardⁿ, Roser Matamala^o, John H. Prueger^p, Mario Tenuta^q, David G. Young^r

^a Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA

^b USGS EROS, Sioux Falls, SD 57198, USA

^c NOAA/Air Resources Laboratory, Atmospheric Turbulence and Diffusion Division, 456 South Illinois Avenue, Oak Ridge, TN 37830, USA

^d Forage Physiology, Forage and Beef Systems and Grazing, Lacombe Research Centre, 6000 C&E Trail, Lacombe, AB T4L 1W1, Canada

^e USDA-ARS Photosynthesis Research Unit and Department of Plant Biology, University of Illinois, 1201W. Gregory Drive, Urbana, IL 61801, USA

^f Biological Systems Engineering Department, 157 L.W. Chase Hall, Univ. of Nebraska, Lincoln, NE 68583-0726, USA

^g Advanced R&D, LI-COR Biosciences, Lincoln, NE 68504, USA

^h Sustainable Energy Systems Group, Environmental Energy Technologies Division, E.O. Lawrence Berkeley National Laboratory MS 90K-125 1 Cyclotron Rd., Berkeley, CA 94720, USA

ⁱ Science and technology Branch, Agriculture and Food Canada, Brandon, MB R7A 5Y3, Canada

^j Geographic Information Science Center, South Dakota State University, Box 506B, Brookings, SD 57007, USA

^k National Laboratory for Agriculture and the Environment, 2110 University Blvd, Ames, IA 50011, USA

^l Oak Ridge Associated Universities, Oak Ridge, TN 37830, USA

^m Center for Atmospheric Science, Illinois State Water Survey, Prairie Research Institute, University of Illinois, Champaign, IL 61820, USA

ⁿ Stinger Ghaffarian Technologies, US Geological Survey Earth Resources Observation and Science (EROS) Center 47914 252nd Street, Sioux Falls, SD 57198, USA

^o Argonne National Laboratory, Biosciences Division, Building 203, 9700 S. Cass Avenue, Argonne, IL 60439, USA

^p National Laboratory for Agriculture and the Environment, Soil, Water, and Air Resources Research Unit, 2110 University Boulevard, Ames, IA 50011-3120, USA

^q Canada Research Chair in Applied Soil Ecology, Department of Soil Science, University of Manitoba 13 Freedman Crescent, Winnipeg, MB R3T 2N2, Canada

^r Agriculture and Agri-Food Canada, Crop & Soils Research Section, 6000 C and E Trail Lacombe, AB T4L 1W1, Canada

ARTICLE INFO

Article history:

Received 21 July 2012

Received in revised form

24 September 2012

Accepted 25 September 2012

Available online 17 December 2012

Keywords:

Net CO₂ exchange partitioning

Gross photosynthesis

VPD limitation of photosynthesis

CO₂ sink

Maize

Wheat

ABSTRACT

We analyzed net CO₂ exchange data from 13 flux tower sites with 27 site-years of measurements over maize and wheat fields across midcontinent North America. A numerically robust “light-soil temperature–VPD”-based method was used to partition the data into photosynthetic assimilation and ecosystem respiration components. Year-round ecosystem-scale ecophysiological parameters of apparent quantum yield, photosynthetic capacity, convexity of the light response, respiration rate parameters, ecological light-use efficiency, and the curvature of the VPD-response of photosynthesis for maize and wheat crops were numerically identified and interpolated/extrapolated. This allowed us to gap-fill CO₂ exchange components and calculate annual totals and budgets. VPD-limitation of photosynthesis was systematically observed in grain crops of the region (occurring from 20 to 120 days during the growing season, depending on site and year), determined by the VPD regime and the numerical value of the curvature parameter of the photosynthesis–VPD-response, σ_{VPD} . In 78% of the 27 site-years of observations, annual gross photosynthesis in these crops significantly exceeded ecosystem respiration, resulting in a net ecosystem production of up to 2100 g CO₂ m^{−2} year^{−1}. The measurement-based photosynthesis, respiration, and net ecosystem production data, as well as the estimates of the ecophysiological parameters, provide an empirical basis for parameterization and validation of mechanistic models of grain crop production in this economically and ecologically important region of North America.

© 2012 Elsevier B.V. All rights reserved.

* Corresponding author.

E-mail addresses: tagir.gilmanov@sdstate.edu (T.G. Gilmanov), wylie@usgs.gov (B.K. Wylie), llt@sio.midco.net (L.L. Tieszen), tilden.meyers@noaa.gov (T.P. Meyers), vern.baron@agr.gc.ca (V.S. Baron), bernacch@illinois.edu (C.J. Bernacchi), dbillesbach1@unl.edu (D.P. Billesbach), george.burba@licor.com (G.G. Burba), mlfischer@lbl.gov (M.L. Fischer), aaron.glenn@agr.gc.ca (A.J. Glenn), niall.hanan@sdstate.edu (N.P. Hanan), jerry.hatfield@ars.usda.gov (J.L. Hatfield), mark.heuer@noaa.gov (M.W. Heuer), hoboinc87@comcast.net (S.E. Hollinger), dhoward@usgs.gov (D.M. Howard), matamala@anl.gov (R. Matamala), john.prueger@ars.usda.gov (J.H. Prueger), mario.tenuta@ad.umanitoba.ca (M. Tenuta), david.young@agr.gc.ca (D.G. Young).

1. Introduction

In the framework of traditional IPCC methodology, with its emphasis on terminal sequestration in compartments with long carbon residence time (“enhanced sinks”), agricultural lands are considered to be nearly carbon-neutral or weak sources for atmospheric CO₂: “Despite large annual exchanges of CO₂ between the atmosphere and agricultural lands, the net flux is estimated to be approximately balanced, with CO₂ emissions around 0.04 GtCO₂/year only” (Smith et al., 2007). Given the large net annual CO₂ uptake on agricultural fields, materialized in the form of harvested biomass, such a conclusion can be reached only by combining actual fields where agricultural crops are grown with locations to which the harvested biomass is laterally transported for processing and eventual metabolism (crop processing and animal production facilities, human settlements, etc.). This interpretation, based mostly on organic matter inventory data, offers a biased picture of biogeochemical pathways of agricultural carbon, particularly of the actual role of crop fields in the local and regional cycling of carbon. This picture is in contrast to the latest results from the other three methods: (i) long-term continuous CO₂ exchange measurements at flux tower stations on croplands, (ii) high-resolution remote sensing observations, and (iii) inverse atmospheric CO₂ modeling. These other studies demonstrated that many, though not all, agroecosystems take up considerably more CO₂ from the atmosphere through photosynthetic assimilation than is returned by respiration and abiotic oxidation. Thus, in terms of atmospheric exchange, these systems are strong – though temporary and local – sinks for atmospheric CO₂ (Xiao et al., 2008, 2010; Ceschia et al., 2010; Crevoisier et al., 2010; Gilmanov et al., 2010; Hayes et al., 2012). The net sink exists in increased soil organic matter, in harvestable and transportable plant material, or in other plant material (e.g., litter or residue). The currently available higher-resolution measurement and modeling techniques make it possible to differentiate local CO₂ sinks at crop production fields from local (and usually more concentrated) CO₂ sources where harvested biomass is utilized (West et al., 2010).

Grain crops (mostly maize, *Zea mays* L., and wheat, *Triticum aestivum* L.) in the United States and Canada represent two of the largest ecosystems in temperate North America. The high productivity and spatial extent of these ecosystems, occupying 20% of the total cropland area of the United States and Canada, make them a dominant factor in shaping the carbon balance of the Great Plains. Specific management decisions can lead to wide fluctuations in these ecosystems, releasing carbon to the atmosphere (C sources) or taking up carbon (C sinks). Recent studies have analyzed atmospheric CO₂ exchange processes and their carbon budget implications for grain crops of the region (Hollinger et al., 2005; Baker and Griffis, 2005; Verma et al., 2005; Bernacchi et al., 2006; Coulter et al., 2006; Fischer et al., 2007; Matamala et al., 2008; Glenn et al., 2010; Hernandez-Ramirez et al., 2011; Suyker and Verma, 2012). These studies used various methods based on either direct integration of net CO₂ exchange data (F) or modeled key components of the ecosystem carbon budget.

Partitioning of the flux tower measurements (F) into gross photosynthesis (P_g) and ecosystem respiration (R_e) components was recognized as a crucial part of post-processing and application of the flux tower data (Falge et al., 2001; Gilmanov et al., 2003b; Reichstein et al., 2005). Historically, the methods of estimating P_g and R_e from flux tower measurements of net CO₂ exchange were based on either using nighttime measurements to estimate daytime respiration (Wofsy et al., 1993; Goulden et al., 1996), or estimation of daytime respiration from daytime measurements (Hanan et al., 2002; Gilmanov et al., 2003b; Stoy et al., 2006). As substantial differences in the nighttime and daytime respiration rates were documented (Gilmanov et al., 2005; Wohlfahrt et al., 2005),

light-response-based methods became the preferred tool for partitioning tower CO₂ fluxes into P_g and R_e components (Gilmanov et al., 2007, 2010; Beer et al., 2010). Recently, Lasslop et al. (2010) proposed the partitioning algorithm where global radiation (Q_g), air temperature (T_a), and vapor pressure deficit (VPD) are used as empirical predictors of the daytime CO₂ exchange. Nevertheless, the authors indicated problems with numerical convergence of their calculation scheme. The high correlation between air temperature and VPD at sub-hourly time steps, leading to multicollinearity and unstable estimates of the light-response parameters, may have caused the problems. The problems became particularly significant for non-forest ecosystems where a substantial part of the metabolically active biomass is located belowground and the ecosystem metabolism at the sub-hourly scale is driven by soil temperature rather than air temperature.

Recently in a paradigm-changing paper summarizing flux tower measurements on the croplands of Europe, Ceschia et al. (2010) established that most crops behaved as atmospheric sinks, while the average carbon budget of the ecosystems is negative, corresponding to a carbon loss. Along the same line of research, our paper is devoted to synthesis of flux tower observations in the croplands of the midcontinent North America that is long overdue. We propose a unified approach based on partitioning of the flux tower data into photosynthesis and respiration components using a standardized “light-soil temperature-VPD response” method. Standardizing the fluxes from measurements of CO₂ exchange over grain-based cropland will allow better comparisons of fluxes throughout the Great Plains.

2. Materials and methods

Measurements of net CO₂ exchange were compiled from grain crops flux tower stations throughout the Great Plains, representing a wide geographical range (Fig. 1, Table 1).

Flux towers in the data set cover a wide range of climatic conditions with mean annual temperatures from 1.5 to 18.3 °C, annual precipitation totals from 180 to 1200 mm, growing season (5 °C base) from 179 to 357 days, and growing degree days from 1400 to 4900 (Table 1). Flux stations in the data set represent a variety of ecoregions (Fig. 1). Eleven of the 13 sites in the data set have eddy-covariance (EC) instrumentation with measurements following the Ameriflux protocol (Meyers, 2001; Meyers and Hollinger, 2004), while at the site near Lacombe, Alberta, the Bowen ratio–energy balance (BREB) technique (Dugas et al., 1997, 1999) was used, and at the Trace Gas Manitoba site the flux/gradient (FG) micrometeorological technique (Glenn et al., 2010) was used.

2.1. Partitioning of the net CO₂ flux data into photosynthesis and respiration

Net CO₂ fluxes, F , provided by terrestrial flux tower measurements represented the difference between two fundamental processes of gross photosynthesis P_g and ecosystem respiration R_e :

$$F = P_g - R_e. \quad (1)$$

We used the ecophysiological notations *sensu* Thornley and Johnson (2000) when P_g and R_e were considered as positive scalar variables combined in the right-hand side of the balance equations according to contribution of the processes they denote. In general, drivers of photosynthesis and respiration at the crop level are not always the same, and the patterns of P_g and R_e response to a given driver are not identical (Thornley and Johnson, 2000). Therefore, partitioning of F into photosynthesis P_g and respiration R_e was recognized as a necessary part of flux tower data processing. In the past, partitioning was usually based on estimation of daytime respiration from nighttime fluxes (Goulden et al., 1996), but more

Fig. 1. Location of the crop flux towers across the midcontinent region of North America.

Table 1

Location, crops, and climatic conditions of the study sites.

Site	Crop	Latitude (°)	Longitude (°)	Elevation (m)	Year	MAT (°C)	PCPN _{hyd} (mm year ⁻¹)	Gr.Season (T ≥ 5 °C) (days)	T _{sums} (deg. day)	Principal investigator
Lacombe crop, Alberta	Spring wheat	52.4317	-113.8125	870	2007	3.67	546	179	1390	Baron, V.S.
Trace Gas Manitoba	Maize	49.6453	-97.1579	235	2006	4.68	293	181	2017	Tenuta, M.
Trace Gas Manitoba	Spring wheat	49.6453	-97.1579	235	2008	1.51	423	181	2540	Tenuta, M.
Rosemount conventional, Minnesota	Maize	44.7143	-93.0898	260	2005	8.16	700	221	2622	Baker, J.M.
Rosemount conventional, Minnesota	Maize	44.7143	-93.0898	260	2007	7.654	647	217	2618	Baker, J.M.
Lennox, South Dakota	Maize	43.2408	-96.9020	386	2008	6.784	565	202	2385	Meyers, T.P.
Lennox, South Dakota	Maize	43.2408	-96.9020	386	2009	6.776	572	207	2177	Meyers, T.P.
Lennox, South Dakota	Maize	43.2408	-96.9020	386	2010	8.08	921	228	2679	Meyers, T.P.
Lennox, South Dakota	Maize	43.2408	-96.9020	386	2011	7.98	559	213	2495	Meyers, T.P.
Brooks Field-10, Iowa	Maize	41.9749	-93.6914	319	2007	9.53	803	229	3011	Prueger, J.H.
Ames, Iowa	Maize	41.7200	-93.4100	300	2003	9.00	667	224	2681	Prueger, J.H.
Mead irrigated continuous, Nebraska	Maize	41.1650	-96.4766	361	2002	10.81	829	236	2875	Verma, S.B.
Mead irrigated rotation, Nebraska	Maize	41.1649	-96.4701	362	2003	10.14	836	237	2899	Verma, S.B.
Curtis Ranch, Colorado	Winter wheat	40.7345	-104.3013	1526	2005	8.89	276	223	2270	Hanan, N.P.
Curtis Ranch, Colorado	Millet	40.7345	-104.3013	1526	2006	9.27	183	234	2423	Hanan, N.P.
Fermi-Agricultural, Illinois	Maize	41.8593	-88.2227	225	2006	10.3	662	237	2636	Matamala, R.
Bondville, Illinois	Maize	40.0061	-88.2919	219	1997	10.22	721	242	2731	Meyers, T.P.
Bondville, Illinois	Maize	40.0061	-88.2919	219	1999	11.51	859	251	3064	Meyers, T.P.
Bondville, Illinois	Maize	40.0061	-88.2919	219	2001	11.72	609	258	3127	Meyers, T.P.
Bondville, Illinois	Maize	40.0061	-88.2919	219	2003	10.88	807	250	2998	Meyers, T.P.
Ponca City, Oklahoma	Winter wheat	36.7667	-97.1333	310	1998	14.91	910	277	3990	Verma, S.B.
Ponca City, Oklahoma	Winter wheat	36.7667	-97.1333	310	1999	15.61	1202	312	3491	Verma, S.B.
Lamont ARM main, Oklahoma	Winter wheat	36.6053	-97.4891	329	2003	18.26	669	357	4862	Fisher, M.L.
Lamont ARM main, Oklahoma	Winter wheat	36.6058	-97.4888	314	2004	14.66	804	300	3884	Fisher, M.L.
Lamont ARM main, Oklahoma	Maize	36.6058	-97.4888	314	2005	15.66	663	311	3939	Fisher, M.L.
Lamont ARM main, Oklahoma	Winter wheat	36.6058	-97.4888	314	2006	16.46	590	313	4385	Fisher, M.L.
Lamont ARM main, Oklahoma	Winter wheat	36.6053	-97.4891	329	2007	15.14	932	287	4124	Fisher, M.L.

recently derivation of daytime respiration from daytime flux measurements has become more popular (Hanan et al., 2002; Gilmanov et al., 2003b, 2005, 2007, 2010; Lasslop et al., 2010). A key premise used in partitioning algorithms based on daylight measurements is that the decrease of F is directly associated with the increase in R_e , which, in turn, is closely related to temperature. The problem is that the decrease in F may also be caused by decreasing photosynthesis P_g , due to water stress. A number of methods to incorporate water stress were proposed (e.g., Gilmanov et al., 2003a; Lasslop et al., 2010). In this study, a physiologically based approach incorporating combined effects of photosynthetically active radiation (Q), soil temperature (T_s), and vapor pressure deficit (VPD) is described.

2.2. Light–soil temperature–VPD–response of the ecosystem-scale CO_2 exchange

CO_2 exchange data in a wide range of grassland and crop ecosystems can be partitioned in the following functional form:

$$F(Q, T_s, VPD) = P_g(Q, VPD) - R_e(T_s), \quad (2)$$

provided that the net flux F , incident photosynthetically active radiation Q , soil temperature T_s , and vapor pressure deficit VPD come from 30-min data on each single day. This assumption excludes the need to introduce factors that slowly change within a day such as soil water content, soil nutrient concentrations, and leaf area. We used soil temperature (T_s) instead of air temperature (T_a) in Eq. (2) based on the current understanding that soil respiration is a significant part of ecosystem respiration in non-forested ecosystems (Arkebauer et al., 2009). In addition, the use of T_s reduced multicollinearity among factors–predictors of the total flux F because it was less correlated than T_a to VPD. For example, meteorological data for the winter wheat crop of the Lamont ARM main site, 2007, showed the range $[-0.3, 0.9]$ for the cross correlation function of T_a and VPD, $\rho_{T_a, VPD}(\tau)$, and the more narrow range $[-0.1, 0.75]$ for the cross correlation of T_s and VPD, $\rho_{T_s, VPD}(\tau)$. Similarly, for the maize crop of the Trace Gas Manitoba site, 2006, corresponding ranges were $[-0.35, 0.85]$ and $[-0.25, 0.75]$. In both cases, cross correlation function $\rho_{T_s, VPD}(\tau)$ lagged approximately 2 h behind the $\rho_{T_a, VPD}(\tau)$. This clearly indicated stronger collinearity of the $\{T_a, VPD\}$ pair of variables compared to $\{T_s, VPD\}$, justifying the choice of the top-soil temperature as a complementary driver to Q and VPD in a CO_2 exchange model.

A popular approach to describe photosynthetic light response was to use the rectangular hyperbolic equation (Baly, 1935; Tamiya, 1951) or the Mitscherlich-type equation (Mitscherlich, 1909; Webb et al., 1974). The key parameters of these equations are: α , the initial slope (apparent quantum yield), and A_{max} , the asymptote (photosynthetic capacity) of the light-response curve. To incorporate VPD-limitation, these equations were multiplied by a normalized factor $\varphi(VPD)$, describing inhibition of photosynthesis by vapor pressure deficit (Lasslop et al., 2010). Unfortunately, these equations were unable to describe light-response curves of varying convexity, including the ramp-type Blackman function (Blackman 1905). This led to significant biases in parameter estimates, particularly for C_4 plants such as maize, which often demonstrate Blackman-type response to light. To allow variation of the convexity of the light-response at the canopy level we used a modification of the nonrectangular hyperbolic light-response function with convexity parameter θ (Prioul and Chartier, 1977; Thornley and Johnson, 2000):

$$P_g(Q, VPD; \alpha, A_{max}, \theta, \sigma_{VPD}) = \frac{\varphi(VPD; VPD_{cr}, \sigma_{VPD})}{2\theta} \times (\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max}\theta Q}) \quad (3)$$

Fig. 2. VPD-response functions of gross photosynthesis with $VPD_{cr} = 1$ kPa and various values of the curvature parameter $\sigma_{VPD} = 1, 2, 4, 7$ and 10 kPa.

$$\varphi(VPD, VPD_{cr}, \sigma_{VPD}) = \begin{cases} 1, & VPD \leq VPD_{cr} \\ \exp\left(-\left(\frac{VPD - VPD_{cr}}{\sigma_{VPD}}\right)^2\right), & VPD > VPD_{cr} \end{cases}, \quad (4)$$

where the normalized VPD-response function $\varphi(VPD; VPD_{cr}, \sigma_{VPD})$ depends on two parameters: the critical value of VPD_{cr} , below which water deficit does not affect photosynthesis ($\varphi = 1$ for $VPD \leq VPD_{cr}$), and the curvature parameter σ_{VPD} ($1 \leq \sigma_{VPD} \leq 30$) with lower values describing a strong water-stress effect, and higher values describing a weak effect (Fig. 2). Generally speaking, the values of the VPD_{cr} parameter may vary between crops and ecosystems. However, following El-Sharkaway et al. (1984) and Lasslop et al. (2010) at this early stage of analysis we accepted a general value $VPD_{cr} = 1$ kPa and considered a one-parametric VPD-response function in the form $\varphi(VPD; \sigma_{VPD}) = \varphi(VPD; 1, \sigma_{VPD})$ (Fig. 2).

Looking at the $\varphi(VPD; \sigma_{VPD})$ curves on Fig. 2 with various σ_{VPD} values, one may notice that for VPD values in the range $4 \text{ kPa} \leq VPD \leq 5 \text{ kPa}$, typical for maximum daily VPD on hot summer days, φ values corresponding to $\sigma_{VPD} = 4$ kPa are close to 0.5. Thus, $\sigma_{VPD} = 4$ might be considered a threshold parameter value, analogous to the Michaelis-Menten constant in the rectangular hyperbolic model, as it describes the situation of 50% reduction of photosynthesis due to VPD limitation (see also Fig. 7 below).

Because soil respiration is not closely linked to VPD, it was possible to describe ecosystem respiration using only a temperature-dependent term $R_e(T_s)$. Following Thornley and Johnson (2000), we described $R_e(T_s)$ according to Van't-Hoff's equation in its exponential form:

$$R_e(T_s; r_0, k_T) = r_0 \exp(k_T T_s), \quad (5)$$

where $r_0 = R_e(0)$ and k_T is the temperature sensitivity coefficient. Thus we modeled net CO_2 exchange (F ; eq. (2)) as the combination of Eqs. (3)–(5):

$$F(Q, T_s, VPD; \alpha, A_{max}, \theta, r_0, k_T, \sigma_{VPD}) = \frac{\varphi(VPD; VPD_{cr}, \sigma_{VPD})}{2\theta} \times \left(\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max}\theta Q} \right) - r_0 \exp(k_T T_s) \quad (6)$$

The detailed formulas for estimation of the diurnal ($0 \leq \tau \leq 24$) terms of gross photosynthesis, $P_g(\tau, t)$, and ecosystem respiration,

$R_e(\tau, t)$, for any day, t , with missing fluxes, as well as for calculation of the daily and annual totals of photosynthesis, respiration, and net ecosystem production, are presented in the Appendix 1.

2.3. Estimation of the parameters

We numerically estimated the parameters α , $A_{\max}$, θ , σ_{VPD} , r_0 , and k_T of the function (Eq. (6)) for every day of the growing season with available Q , T_s , VPD, and F data. This was achieved through identification of the best-fit parameter values $\{\alpha, A_{\max}, \theta, \sigma_{\text{VPD}}, r_0, k_T\}$ for every day's $\{Q(i), T_s(i), \text{VPD}(i), F(i), i=1, 2, \dots, n\}$ data set of $n \leq 48$ records with a 30-min time step using the optimization tools of the *Mathematica* system (Wolfram Research, 2011). While respiration term in equations (5) and (6) formally depends only on soil temperature, T_s , it should be noticed, that because during the growing season parameters of these equations (including respiration-related r_0 and k_T) are estimated separately for every day, their numerical values implicitly reflect dependence of respiration on other factors, such as soil water content, W_s , which do not substantially vary within a day, but may differ from day to day. The day-specific r_0 values were different for days with different W_s , meaning that our modeling procedure provided respiration estimates reflecting changes in soil water content. Outside the growing season in the absence of photosynthesis, the ecosystem respiration $R_e(T_s; r_0, k_T)$ was approximated by fitting parameters r_0 and k_T (Eq. (5)) using the data for moving windows of, typically, 9-day width. Though in this case no other factors were explicitly introduced as respiration predictors, the error associated to the 9-day window would have been minimized by (i) low fluxes and (ii) low W_s changes in frozen soils.

2.4. VPD limitation of photosynthesis

Estimated σ_{VPD} values typically lie in the interval from 1.5 to 16 kPa, the lower range characterizing strong VPD effect (rapid decrease of F with VPD increasing to values higher than 1 kPa), while higher values of σ_{VPD} describe functions $\varphi(\text{VPD}; \sigma_{\text{VPD}})$ which decrease only gradually with increasing VPD (Fig. 2).

Occasionally, on days with low temperature amplitude and low VPD, the parameter estimation procedure for eq. (6) generated insignificant estimates of the temperature- and VPD-effect parameters r_0 , k_T and σ_{VPD} . In such cases, a nonrectangular hyperbolic light-response function (Rabinowitch, 1951) was used:

$$F(Q; \alpha, A_{\max}, \theta, r_0) = \left(\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max} \theta Q} \right) - r_0, \quad (7)$$

which usually resulted in significant estimates of parameters, as illustrated by the data from the maize field near Lennox, DOY 204, 2010 (Fig. 3, Table 2).

Thus, the VPD factor in Eq. (6) affects photosynthesis through stomata control and water balance, while the topsoil temperature is directly related to soil respiration, providing an additional factor-predictor of ecosystem CO_2 exchange, complementary to Q and VPD, and potentially leading to more robust estimates of light-response parameters.

2.5. Model performance

The optimization analysis to estimate the parameters in Eqs. (6) and (7) converged for most of the 27 site-years sub-hourly (30 min or 20 min time step) datasets. However, the percent convergence is not known because of the inhomogeneity and construction history of the database. The overall pattern of convergence of parameter

Fig. 3. Light-response function of the maize field near Lennox, SD, DOY 204, 2010 described by a Blackman-type function fitted by eq. (7) with parameters shown in Table 2.

estimates may be illustrated by the following examples. For the maize crop of the Lennox site 2009, the full set of eq. (6) parameters was estimated for 111 days, while the reduced eq. (7) was applied on 11 days. For the maize crop of the Bondville site 2003, eq. (6) was used for 157 days, while eq. (7) for 42 days. And for the winter wheat–soybeans double crop at the Lamont ARM main site 2007, parameters of eq. (6) were estimated for 164 days, and eq. (7) was used for 147 days. A note of caution is appropriate at this point: not every set of parameters generated by the fitting procedure will necessarily be physiologically or ecologically acceptable, typical examples being too high α or k_T or too low σ_{VPD} values. It is the researcher's responsibility to make the final decision of which parameter sets to apply.

The case of significant limitation of daytime CO_2 exchange through both increase of ecosystem respiration due to high daytime temperatures and suppression of photosynthesis due to VPD-stress was illustrated by fitting the model (Eq. (6)) to the tower flux data from the Trace Gas Manitoba maize site for DOY 199, 2006 (Fig. 4). The simple (Q, F) scatter plot on panel A shows considerable decrease of the CO_2 uptake in the afternoon period compared to morning; fitting by the nonrectangular hyperbolic model (Eq. (7)) provided $\text{SE} = 0.14 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $R^2 = 0.86$ ($n = 42$). The surface on panel B describes the relationship of the CO_2 flux to both light Q and soil temperature T_s calculated by eq. (6), assuming that the VPD argument is fixed at the average daily vapor pressure deficit value, VPD_{avg} . The red dots showing flux values calculated as functions of all the three arguments, Q , T_s , and VPD, lie closer to the blue dots (actual flux values) than the $F(Q, T_s)_{\text{VPD}=\text{VPD}_{\text{avg}}}$ surface, emphasizing additional effect of actual VPD values compared to the average daily VPD_{avg} . Deviation of the red dots from the surface and their proximity to the blue dots (actual flux measurements) are particularly pronounced in afternoon hours (left part of the panel B) where the actual VPD values were particularly high (maximum VPD for DOY 199 was 2.6 kPa). The overall goodness of fit of model (Eq. (6)) in this case (Table 4) shows lower errors and higher R^2 than the simple light-response function, with particular significance of the VPD factor (t -value 5.48, p -value < 0.0001).

2.6. Ecological light-use efficiency

Light-use efficiency characteristics are often used as important tools of comparative ecological analysis (Turner et al., 2003; Bradford et al., 2005). From a number of coefficients we selected the coefficient of gross ecological light-use efficiency, LUE, defined as a

Table 2

Numerical values and the goodness-of-fit characteristics of the parameters of nonrectangular hyperbolic equation (7) for day 204, 2010 at the Lennox maize site ($n=43$; $SE=0.10 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $R^2=0.97$).

Parameter	α ($\text{mg CO}_2 \text{ mol}^{-1}$)	$A_{\max}$ ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	θ ratio	r_0 ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
Value	0.00099	1.4116	1.0	0.2248
St. error	0.000035	0.0846	0.0012	0.0231
t-value	28.31	16.69	857.7	9.734
p-value	<0.0001	<0.0001	<0.0001	<0.0001

Table 3

Numerical values and the goodness-of-fit of the parameters of equation (6) for day 199, 2006 at the Trace Gas Manitoba maize site ($n=42$; $SE=0.10 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $R^2=0.94$).

Parameter	α ($\text{mg CO}_2 \text{ mol}^{-1}$)	$A_{\max}$ ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	θ ratio	r_0 ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	k_T ($^{\circ}\text{C}^{-1}$)	σ_{VPD} (kPa)
Value	0.00152	1.74	0.80	0.065	0.069	2.48
St. error	0.00023	0.49	0.32	0.035	0.025	0.45
t-value	6.51	3.53	2.49	1.84	2.80	5.48
p-value	<0.0001	0.0012	0.0176	0.0747	0.0082	<0.0001

ratio of daily gross photosynthesis P_g to daily income of photosynthetically active radiation Q (Cooper, 1970; Gilmanov et al., 2005):

$$\text{LUE} = \frac{P_g}{Q}. \quad (8)$$

While the coefficient of apparent quantum yield, α , characterizes potential physiological light-use efficiency, LUE is a measure of ecologically realized photosynthetic productivity, making comparison of the α and LUE values an important tool of comparative ecological analysis.

3. Results and discussion

3.1. Magnitude and dynamics of ecophysiological parameters

Parameters estimated by flux partitioning demonstrated seasonal and year-to-year patterns highly important for understanding, gap-filling, predictive modeling, and scaling-up of the whole-ecosystem CO_2 exchange. Considerable day-to-day variability and the patterns of seasonal dynamics made mean annual or seasonal values of the ecophysiological parameters not appropriate for comparative purposes. The maximum values of parameters were more useful as often they characterized situations when the effects of other factors were less pronounced. Along with daily values (e.g., daily maxima), which most fully express ecophysiological potential of the crop, but exhibit stochastic variability (most often evident in daily estimates of α and LUE), we found it necessary to calculate a 7-day averages of parameters and their errors, which provided more consistent and comparable results. As an example, panels on Fig. 5 show dynamics of the eco-physiological parameters

of maize at the Lennox site during the 2008–2011 measurement period. They demonstrated both the overall seasonal patterns and the intra-seasonal fluctuations, e.g., mid-summer decrease of photosynthesis and respiration parameters reflecting soil moisture limitation.

Table 4 summarizes estimated values of the absolute daily maxima and the maximum of the mean weekly values of ecophysiological parameters of grain crops of the region. As expected from plant water availability, the maximum values were observed in the most productive regions of the Corn Belt (Illinois-Iowa-Nebraska), while the lowest parameters of both the CO_2 uptake with photosynthesis and its release with respiration were demonstrated by the water-stressed marginal crops of the short grass ecoregion of the High Plains (Colorado). Overall, the maximum values of the ecophysiological parameters of the croplands of midcontinent North America (Table 4) matched or exceeded the corresponding global maxima outlined in Gilmanov et al. (2010), emphasizing the global significance of this megaregion for agricultural production of the world.

Comparison of the parameters for wheat and maize showed that the mean of the maximum mean weekly apparent quantum yield for wheat, $\alpha_{\max, \text{wk}, \text{wheat}} = 26.92 \text{ mmol mol}^{-1}$ was significantly lower ($p=0.0001$) than $\alpha_{\max, \text{wk}, \text{maize}} = 39.10 \text{ mmol mol}^{-1}$ for maize. Coefficients of light-use efficiency followed the same pattern, with $\text{LUE}_{\max, \text{wk}, \text{wheat}} = 20.84 \text{ mmol mol}^{-1}$ lower ($p=0.0006$) than $\text{LUE}_{\max, \text{wk}, \text{maize}} = 33.65 \text{ mmol mol}^{-1}$. Particularly large was the difference between mean photosynthetic capacities of the wheat (C_3 type) and maize (C_4 type) crops: $A_{\max, \text{wk}, \text{wheat}} = 1.34 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $A_{\max, \text{wk}, \text{maize}} = 2.54 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, with the difference significant at the $p<0.0001$

Fig. 4. Light-response (A) and light-soil temperature-VPD-response (B) functions of the maize crop at the Trace Gas Manitoba site, DOY 199, 2006. Parameters for (B) fitted by eq. (6) are presented in Table 3.

Table 4

Maximum values of the daily (max) and mean weekly (max,wk) estimates of the major eco-physiological parameters of the grain crops of midcontinent North America.

Site	Crop	Year	$\alpha_{\max}$ (mol mol ⁻¹)	$\alpha_{\max, \text{wk}}$	$A_{\max}$ (mg CO ₂ m ⁻² s ⁻¹)	$A_{\max, \text{wk}}$	$r_{\text{day}, \max}$ (mg CO ₂ m ⁻² s ⁻¹)	$r_{\text{day}, \max, \text{wk}}$ (mol mol ⁻¹)	LUE _{max}	LUE _{max, wk}	D _{VPD} (days)
Lacombe, Alberta	Spring wheat	2007	37.6	24.58	2.14	1.30	0.355	0.234	29.96	19.29	77
Trace Gas Manitoba	Maize	2006	39.8	27.07	2.03	1.63	0.380	0.292	23.45	19.01	47
Trace Gas Manitoba	Spring wheat	2008	50.4	37.33	2.44	2.02	0.370	0.251	42.07	31.29	23
Rosemount conventional, Minnesota	Maize	2005	61.0	46.30	3.20	2.90	0.450	0.438	50.56	39.78	–
Rosemount conventional, Minnesota	Maize	2007	53.5	38.93	3.43	3.03	0.605	0.438	56.27	37.57	28
Lennox, South Dakota	Maize	2008	35.3	35.10	2.20	2.17	0.366	0.298	34.03	32.22	–
Lennox, South Dakota	Maize	2009	40.4	33.97	2.79	2.14	0.312	0.241	39.34	32.07	56
Lennox, South Dakota	Maize	2010	45.5	34.82	2.32	1.95	0.388	0.315	45.05	29.70	35
Lennox, South Dakota	Maize	2011	38.4	30.62	2.60	2.04	0.334	0.247	36.81	29.28	54
Brooks Field-10, Iowa	Maize	2007	56.8	44.68	3.25	2.92	0.798	0.560	47.94	40.14	58
Ames, Iowa	Maize	2003	47.5	37.52	2.70	2.58	0.602	0.426	44.98	32.51	34
Mead irrigated continuous, Nebraska	Maize	2002	52.2	40.92	3.80	3.43	0.535	0.451	51.50	40.00	31
Mead irrigated rotation, Nebraska	Maize	2003	64.4	49.79	3.87	3.63	0.549	0.490	60.54	46.29	42
Curtis Ranch, Colorado	Millet	2005	22.2	12.63	0.99	0.68	0.117	0.087	11.12	9.46	88
Curtis Ranch, Colorado	Winter wheat	2006	26.5	18.43	0.67	0.49	0.239	0.197	14.14	7.39	52
Fermi-Agricultura, Illinois	Maize	2006	48.7	41.19	3.32	3.09	0.725	0.634	43.73	37.80	42
Bondville, Illinois	Maize	1997	57.7	45.87	2.80	2.72	0.427	0.236	55.21	38.37	–
Bondville, Illinois	Maize	1999	53.7	47.43	3.50	3.17	0.456	0.330	50.02	42.66	–
Bondville, Illinois	Maize	2001	47.7	42.51	2.78	2.42	0.358	0.330	37.24	32.70	–
Bondville, Illinois	Maize	2003	61.9	50.30	4.30	3.95	1.142	0.432	52.50	44.53	68
Ponca City, Oklahoma	Winter wheat	1998	32.0	23.14	1.60	1.46	0.272	0.229	29.78	19.78	–
Ponca City, Oklahoma	Winter wheat	1999	46.0	28.72	2.20	1.87	0.373	0.272	35.93	30.99	–
Lamont ARM main, Oklahoma	Winter wheat	2003	35.0	22.27	1.50	0.97	0.241	0.192	25.98	16.45	70
Lamont ARM main, Oklahoma	Winter wheat	2004	40.1	25.40	1.40	1.30	0.325	0.257	32.11	19.56	42
Lamont ARM main, Oklahoma	Maize	2005	35.3	27.79	1.00	0.76	0.336	0.254	20.47	8.23	111
Lamont ARM main, Oklahoma	Winter wheat	2006	38.4	27.15	1.48	1.05	0.293	0.185	24.25	18.16	133
Lamont ARM main, Oklahoma	Winter wheat	2007	49.8	35.25	1.89	1.60	0.311	0.209	33.52	24.64	63

Fig. 5. Seasonal and year-to-year dynamics of major ecosystem-scale eco-physiological parameters of the maize field near Lennox, SD, during 2008–2011 period: (A) apparent quantum yield, α ; (B) photosynthetic capacity, $A_{\max}$; (C) ecological light-use efficiency, LUE; (D) average day-time ecosystem respiration rate, r_{day} . Dots—mean weekly parameter values; error bars—standard errors of the means.

level. As might be expected, the respiration rate of wheat $r_{\text{day,max,wk,wheat}} = 0.23 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was also substantially lower ($p < 0.0001$) than of maize $r_{\text{day,max,wk,maize}} = 0.37 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

These values represent the first generalization of the tower-based ecosystem-scale light-response and productivity parameters of the grain crops of North America. Overall, their interrelationships agree with the leaf- and plant-scale parameters for maize and wheat obtained earlier in physiological studies (Good and Bell, 1980; Schmitt and Edwards, 1981; Long and Drake, 1992; Long et al., 1993). Processing of data from additional sites and years will certainly allow further stratification with respect to management practice, e.g., irrigated vs. non-irrigated, till vs. no-till, continuous culture vs. rotation, etc.

3.2. Grain crops as local sinks for atmospheric CO_2

The data in Table 5 describe the daily maxima and the annual totals of photosynthetic production, respiration, and net CO_2 exchange for all site-years in our study. Maximum daily rates of both photosynthetic assimilation ($110 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and ecosystem respiration ($64 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) were achieved on intensively managed maize fields of Illinois, followed by maize crops of Iowa and Nebraska. The lowest levels of CO_2 exchange ($P_{g,\max}$ $16\text{--}22 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ and $R_{e,\max}$ $10\text{--}20 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) were observed on the wheat and millet fields of Colorado. Overall, the average maximum daily gross photosynthesis in maize crops ($81.8 \pm 5.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) was significantly higher ($P < 0.0001$) than in wheat crops ($45.5 \pm 5.1 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). The average maximum daily ecosystem respiration in maize fields ($42.0 \pm 3.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) was also higher ($P < 0.0005$) than in wheat crops ($25.8 \pm 1.6 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), but not to such an extent as for photosynthesis. As a result, maximum daily net ecosystem production of the maize crops ($54.7 \pm 3.9 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) remained significantly ($P \leq 0.001$) higher than that for wheat ($32.0 \pm 1.6 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$).

To evaluate the CO_2 sink/source performance of the grain agroecosystems, a plot of annual respiration against gross primary production was considered as shown in Fig. 6. Of the 27 points describing the site-years of the data set, only 6 are located on or

above the 1:1 line; the rest (particularly for maize crops) lie significantly below the 1:1 line, with a maximum deviation of GPP from RE greater than $2100 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$, indicating strong sink activity of the agroecosystem. The advantage of the GPP-RE diagram is that along with the GPP and RE it implicitly shows the $\text{NEP} = \text{GPP} - \text{RE}$ data, which may be represented as the horizontal distance from the diagonal to the (GPP, RE) point. For example, for point A, describing the winter wheat crop of the Ponca City site in Oklahoma in the year 1998 characterized by strong water stress (Burba and Verma, 2005), $\text{NEP} = 1583 - 2289 = -706 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ is negative (the arrow pointing to the left in Fig. 6). For point B, corresponding to the maize crop of the Bondville site in Illinois, which in 2003

Fig. 6. Total annual ecosystem respiration (RE) of grain crops plotted against their annual gross primary production (GPP).

Table 5The daily maxima and the annual totals of photosynthetic production, respiration, and net CO₂ exchange for the site-years of the study.

Site	Crop	Year	Gr.Season ($T \geq 5^{\circ}\text{C}$)	$P_{g\max}$ ($\text{gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$)	$R_{\max}$ ($\text{gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$)	$\text{NEP}_{\max}$ ($\text{gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$)	GPP ($\text{gCO}_2 \text{ m}^{-2} \text{ year}^{-1}$)	RE ($\text{gCO}_2 \text{ m}^{-2} \text{ year}^{-1}$)	NEP ($\text{gCO}_2 \text{ m}^{-2} \text{ year}^{-1}$)
Lacombe, Alberta	Spring wheat	2007	179	49.4	29.2	42.9	2405	2541	−135
Trace Gas Manitoba	Maize	2006	181	56.0	30.4	34.0	2686	2308	379
Trace Gas Manitoba	Spring wheat	2008	181	78.6	30.3	58.2	2337	1498	839
Rosemount conventional, Minnesota	Maize	2005	221	90.7	50.2	56.0	5597	3612	1984
Rosemount conventional, Minnesota	Maize	2007	217	93.3	52.8	55.1	4630	3662	968
Lennox, South Dakota	Maize	2008	202	71.8	27.5	52.0	3155	2131	1024
Lennox, South Dakota	Maize	2009	207	66.7	26.6	47.9	3561	2191	1370
Lennox, South Dakota	Maize	2010	228	65.7	29.9	46.4	3320	2875	445
Lennox, South Dakota	Maize	2011	213	63.3	29.3	37.8	2982	2446	536
Brooks Field-10, Iowa	Maize	2007	229	94.3	64.3	51.7	4940	4017	924
Ames, Iowa	Maize	2003	224	75.6	48.4	63.3	4708	3349	1360
Mead irrigated continuous, Nebraska	Maize	2002	236	96.4	44.7	62.1	5883	4256	1627
Mead irrigated rotation, Nebraska	Maize	2003	237	109.7	47.0	67.7	6967	4960	2008
Curtis Ranch, Colorado	Millet	2006	234	16.2	9.9	11.2	1058	1099	−41
Curtis Ranch, Colorado	Winter wheat	2005	223	21.81	20.4	11.0	1390	1433	−43
Fermi-Agricultural, Illinois	Maize	2006	237	101.4	61.1	61.9	4979	3899	1080
Bondville, Illinois	Maize	1997	242	85.5	30.0	55.2	4140	2947	1193
Bondville, Illinois	Maize	1999	251	94.1	37.6	77.0	5256	3356	1900
Bondville, Illinois	Maize	2001	258	71.9	30.7	49.7	4404	3125	1278
Bondville, Illinois	Maize	2003	250	109.7	64.1	80.6	5485	3377	2108
Ponca City, Oklahoma	Winter wheat	1998	277	40.5	23.0	32.3	1583	2289	−706
Ponca City, Oklahoma	Winter wheat	1999	312	54.6	31.7	35.8	2829	2679	150
Lamont ARM main, Oklahoma	Winter wheat	2003	357	39.3	17.5	26.9	2199	2032	167
Lamont ARM main, Oklahoma	Winter wheat	2004	300	38.5	25.2	26.9	3118	2648	469
Lamont ARM main, Oklahoma	Maize	2005	311	26.3	26.7	14.7	1973	2246	−273
Lamont ARM main, Oklahoma	Winter wheat	2006	313	39.8	28.2	24.7	2297	2451	−154
Lamont ARM main, Oklahoma	Winter wheat	2007	287	46.51	26.7	29.3	3375	2917	459

achieved the highest NEP of $5485-3377=2108\text{ g CO}_2\text{ m}^{-2}\text{ year}^{-1}$, the arrow is directed to the right. Notice that of the 15 maize site-years only one (point C) lies to the left of the main diagonal, because it [(GPP,RE)=(1973, 2246)] represents a failed maize crop at the ARM main site near Lamont, Oklahoma in 2005.

The results in Fig. 6 support the conclusions of earlier generalizations from flux tower measurements in other regions of the world (Gilmanov et al., 2007, 2010; Ceschia et al., 2010) that highly productive crops and intensively managed grasslands are strong local CO_2 sinks. This conclusion, based on flux tower data analysis (Fig. 6) is also supported by the remote sensing and inverse atmospheric CO_2 modeling. For example, MODIS-based modeling by Potter et al. (2007) demonstrated that in years with different meteorological conditions agriculture-intensive regions of the midcontinent United States were moderate to strong annual sinks for atmospheric CO_2 , and many of them remained sinks even in dry years such as 2002 (Potter et al., 2007, Fig. 8). Xiao et al. (2008, 2011) also used remote sensing and modeling methods to show that at a per unit area scale, pre-harvest CO_2 sink intensity of croplands is close to that of deciduous forests (maximum mean 8-day NEP estimated as $18\text{ g CO}_2\text{ m}^{-2}\text{ d}^{-1}$ for croplands and 19.4 for deciduous forests—Fig. 11(a) in Xiao et al., 2008). Absolute numbers also reveal the significant role of croplands as CO_2 sink: they take up from the atmosphere $0.58\text{ pg C year}^{-1}$, or 48% of the total U.S. annual NEP of $1.21\text{ pg C year}^{-1}$ (Xiao et al., 2011). Using the estimate of the cropland area provided by Xiao et al. (2008, Fig. 11 (b)), we obtained the NEP estimate of $\sim 1100\text{ g CO}_2\text{ m}^{-2}\text{ year}^{-1}$, which was even higher than the median of NEP estimates in our Table 5, which equal $881\text{ g CO}_2\text{ m}^{-2}\text{ year}^{-1}$. The data obtained using the atmospheric CO_2 modeling technique has also revealed the dominant role of agroecosystems as atmospheric CO_2 sinks in the United States. Deciduous forests are traditionally considered major players in the CO_2 sink performance of the U.S. ecosystem because of forest regrowth (Houghton and Hackler, 2000). However, Crevoisier et al. (2010), based on the detailed accounting of the CO_2 concentrations, sources, and sinks for the control volume of atmosphere over North America, established that the Midwest states dominated by agricultural land use account for 52% of the North American land CO_2 sink. This percentage far surpasses the southeastern region (22%), which is heavy with deciduous forests.

Finally, in the most recent review of the issue combining inventory, modeling, and atmospheric inversions methods, Hayes et al. (2012) recognized U.S. croplands as net carbon sinks with the strength of $264.32\text{ Tg C year}^{-1}$, which on a per unit area basis is equal to approximately $715\text{ g CO}_2\text{ m}^{-2}\text{ year}^{-1}$. This number is consistent with NEP median of $881\text{ g CO}_2\text{ m}^{-2}\text{ year}^{-1}$ found in this study, taking into account the dominance of maize in our data set and the fact that these estimates were obtained using totally different methodology.

Occasionally, a skeptical attitude toward recognizing the strong atmospheric CO_2 sink activity of agroecosystems was justified by referring to lateral transport of harvested NEP (Dobermann et al., 2006; Aubinet et al., 2009) and the limited potential of croplands to serve as terminal sinks for atmospheric CO_2 (Fissore et al., 2010). These approaches however did not account for the need to develop tools and methods to manage agroecosystems and predict their response to environmental change. There were a number of attempts to take into account harvesting using the concept of the net biome production (NBP), originally developed to be applied at regional and higher levels (Schulze and Heimann, 1998), to the level of individual site-ecosystems (e.g., Aubinet et al., 2009; Kutsch et al., 2010). As pointed out by Randerson et al. (2002), such attempts were linked with a number of ambiguities and, in our opinion, may inadvertently lead to double-counting of ecosystem fluxes.

Indeed, a significant part of the net production of the agroecosystem will be laterally removed from the field with the harvested biomass (in some cases with wind and water erosion as well) that may be exported to other countries (crops are one of the largest exports in the U.S. and Canada). In certain cases, the net result of agricultural practices might even lead to a negative carbon balance of the field (e.g., resulting in depletion of the soil organic matter reserve). Comprehensive analysis, also taking into consideration inputs of organic matter to the field, is no doubt required in such cases and the concept of the net ecosystem carbon balance (NECB, sensu Chapin et al., 2006) is the most appropriate tool for the task. Smith et al. (2010) have recently summarized the methods to adequately assess the NECB of agroecosystems, and West et al. (2010) presented an attempt to summarize NECB for croplands of the United States. Unfortunately, for most of the flux tower sites the data to construct NECB remained incomplete. Nevertheless, for adequate understanding of the actual biogeochemical pathways of carbon it should be realized that even croplands with negative net carbon balance may and actually are acting as strong local sinks for atmospheric CO_2 , as demonstrated by flux tower, remote sensing, and inverse modeling data. In this context, it seems appropriate to remember the paper by Körner (2003) who emphasized the disproportionately low representation of the CO_2 sources, in particular, strong, though short-term sources, like fires, in carbon cycling monitoring systems. Of course, this is still true, but does not eliminate the need to identify strong CO_2 sinks.

3.3. σ_{VPD} distribution as a measure of crop water stress

More detailed accounting of the intra-seasonal control of temperature and moisture conditions on the CO_2 exchange of agroecosystems may be obtained by looking into the distribution of the parameter σ_{VPD} characterizing the curvature of the response of photosynthesis to vapor pressure deficit (Fig. 2). A comprehensive description of the VPD-limitation of photosynthesis at the crop level is provided by a cumulative distribution function of the σ_{VPD} parameter. Fig. 7 illustrates two typical cases. The maize crop in southeastern South Dakota at the Lennox site, 2009 season (Fig. 7A), is moderately limited by the drought, with the total number of days with drought limitation being only 68, and the number of days with strong limitation ($\sigma_{VPD} < 4$) equal to 56. In contrast, the maize crop in north-central Oklahoma at the ARM main site, 2005 season (Fig. 7B), experienced significant water stress during 117 days of the season, with the number of days with drought limitation ($\sigma_{VPD} < 4$) achieving 104. As a result, gross primary production of this maize crop was extremely low, only $1973\text{ g CO}_2\text{ m}^{-2}\text{ year}^{-1}$. To facilitate comparison among sites and years, and using the $\sigma_{VPD} = 4\text{ kPa}$ value as a threshold indicating strong VPD limitation, we suggest the D_{VPD} parameter defined as a number of days of the growing season for which $VPD > 1\text{ kPa}$ and the curvature parameter $\sigma_{VPD} < 4\text{ kPa}$ (Fig. 7).

Reflecting the north-south climatic gradient, the D_{VPD} parameter values range from 23 in Manitoba to 133 in Oklahoma (Tables 1 and 4), parabolically increasing with decreasing latitude (LAT), as described by the regression equation:

$$D_{VPD} = 1135 + 0.511\text{ LAT} - 47.37\text{ LAT}^2. \\ (R^2 = 0.40, p\text{ - value} = 0.013) \quad (9)$$

As might be expected, the data in Tables 1 and 4 also show a strong linear trend of increasing D_{VPD} with mean annual temperature (MAT):

$$D_{VPD} = 22.83 + 3.45\text{ MAT}. \quad (R^2 = 0.29; p\text{ - value} = 0.014) \quad (10)$$

These trends indicate potential value of the D_{VPD} parameter as a tool for comparative analysis of partitioned flux tower data

Fig. 7. Cumulative distribution functions of the daily VPD-response curvature parameter values, σ_{VPD} , for: A – maize crop at the Lennox site, 2009, and B – maize crop at the ARM main site, 2005.

sets serving as a water stress characteristic complementary to the traditionally used atmospheric precipitation.

4. Conclusions

1. Modification of the classical non-rectangular hyperbolic model for crop CO_2 exchange by incorporating the VPD-limiting factor (Eq. (6)) serves as a flexible tool for identification of major eco-physiological parameters of grain crop ecosystems at the stand level.
2. Statistical distribution of the curvature parameter of the photosynthesis VPD-response, σ_{VPD} , provided characteristics of crop productivity conditions complementary to rainfall. The D_{VPD} parameter (number of days when $\text{VPD} > 1$ kPa and $\sigma_{VPD} < 4$ kPa) varied from 20 to 130 from higher to lower latitudes and may be used for comparison of growth conditions.
3. Major stand-scale ecophysiological parameters (apparent quantum yield, photosynthetic capacity, daily ecosystem respiration rate, ecological light-use efficiency) were significantly higher for maize crops than for wheat crops. These parameters exhibited distinct patterns of seasonal and yearly dynamics, which should be taken into account when used in process-based models.
4. Contrary to the earlier assessments of agricultural crops as carbon-neutral or even CO_2 sources for the atmosphere, our empirically based study demonstrated that contemporary highly-productive grain crops of midcontinent North America take-up with photosynthesis considerably more atmospheric CO_2 than release with ecosystem respiration. This surplus carbon may be subsequently returned to the atmosphere during crop processing and use, but this usually takes place geographically far from the production fields, thus establishing the fields as strong local sinks for atmospheric CO_2 .

Acknowledgements

This work was performed under USGS contract G10PC00044 and funding was provided by the USGS Geographic Analysis and Monitoring program. This work was also supported in part by the grant from the South Dakota Corn Utilization Council. Measurements at the US-ARM site were supported by the Office of Biological and Environmental Research of the U.S. Department of Energy under contract DE-AC02-05CH11231 as part of the Atmospheric Radiation Measurement Program. We thank Ameriflux database supervisor Dr. Thomas Boden and Ameriflux contributors Drs. J. Baker, T. Griffis, A. Suyker, and S. Verma for assistance with the data needs of this project.

Appendix A.

A.1. Gap filling and calculation of production and respiration totals

For every calendar day, t ($t = 1, 2, \dots, 365$), and every time within the day, τ , ($0 \leq \tau \leq 24$) for which the measurement of the net CO_2 flux, $F(\tau, t)$, is available, gross photosynthesis $P_g(\tau, t)$ was calculated as:

$$P_g(\tau, t) = F(\tau, t) + R_e(\tau, t), \quad (\text{A1})$$

where

$$R_e(\tau, t) = \begin{cases} r_0 \text{Exp}(k_T T_s(\tau, t)), & \text{if eq.(6) was used for day } t \\ r_0, & \text{if eq.(7) was used for day } t \end{cases} \quad (\text{A2})$$

The gap-filling procedure for the days and diurnal times with fluxes unavailable had two options, (i) and (ii), described below. Let the set of calendar day numbers $T_p = \{t_j, j = 1, 2, \dots, n\}$ denote the list of all n days for which at least some flux measurements were available and the parameter estimation procedure has for every day $t_j \in T_p$ produced appropriate of parameters $\alpha(t_j), A_{\max}(t_j), \theta(t_j), r_0(t_j), k_T(t_j), \sigma_{VPD}(t_j)$. Let $\Pi = \{\alpha(t_j), A_{\max}(t_j), \theta(t_j), r_0(t_j), k_T(t_j), \sigma_{VPD}(t_j), j = 1, 2, \dots, n\}$ denote the $6 \times n$ -dimensional time series of available parameter values generated by the fitting routine applied to data days listed in T_p . For example, if the measurement period was from April 15 (DOY 105) to September 15 (258), but parameter estimates were not available for 5 days from July 26 (207) to August 1 (213), the set T_p will consist of $n = 149$ numbers listed in $T_p = \{105, 106, \dots, 205, 206, 214, 215, \dots, 257, 258\}$ (note that days 207 to 213 are missing in T_p).

(i). There may be (and usually were) days t for which for at least some τ within a day fluxes $F(\tau, t)$ were missing, though it was still possible to estimate all the parameters $\alpha(t), A_{\max}(t), \theta(t), r_0(t), k_T(t), \sigma_{VPD}(t)$ (thus, $t \in T_p$). For those τ , photosynthesis and respiration were estimated as:

$$P_g(\tau, t) = \frac{\varphi(\text{VPD}(\tau, t); 1, \sigma_{VPD}(t))}{2\theta(t)} \times \quad (\text{A3})$$

$$\left(\alpha(t) Q(\tau, t) + A_{\max}(t) - \sqrt{(\alpha(t) Q(\tau, t) + A_{\max}(t))^2 - 4\alpha(t) A_{\max}(t) \theta(t) Q(\tau, t)} \right) \quad (\text{A4})$$

and the missing fluxes calculated as:

$$F(\tau, t) = P_g(\tau, t) - R_e(\tau, t), \quad (\text{A5})$$

where $\text{VPD}(\tau, t)$, $Q(\tau, t)$ and $T_s(\tau, t)$ describe the diurnal course of vapor pressure deficit, photosynthetically active radiation and soil temperature during day t .

(ii). This option describes any day t_m (m standing for “missing”) not included in T_p (e.g., $t_m = 207$ to 213 in the example

above). Parameter estimates $\{\alpha(t_m), A_{\max}(t_m), \theta(t_m), r_0(t_m), k_T(t_m), \sigma_{VPD}(t_m)\}$ for these days would be obtained by the smooth interpolation of the time series Π of available parameters. Note, that for some times τ during day t_m , flux values $F(\tau, t_m)$ may be available from measurements (though the data did not permit estimation of all the parameters). For these t_m respiration term was calculated as:

$$R_e(\tau, t_m) = \begin{cases} r_0(t_m) \text{Exp}(k_T(t_m) T_s(\tau, t_m)), & \text{if eq.(6) was used for day } t_m \\ r_0(t_m) & \text{if eq.(7) was used for day } t_m \end{cases} \quad (\text{A6})$$

and photosynthesis estimated as:

$$P_g(\tau, t_m) = F(\tau, t_m) + R_e(\tau, t_m). \quad (\text{A7})$$

Eventually, for those times τ on day t_m with missing flux values photosynthesis, respiration, and net flux were estimated using interpolated parameters as:

$$P_g(\tau, t_m) = \frac{\varphi(\text{VPD}(\tau, t_m); 1, \sigma_{\text{VPD}}(t_m))}{2\theta(t_m)} \times \left(\alpha(t_m) Q(\tau, t_m) + A_{\max}(t_m) - \sqrt{(\alpha(t_m) Q(\tau, t_m) + A_{\max}(t_m))^2 - 4\alpha(t_m) A_{\max}(t_m) \theta(t_m) Q(\tau, t_m)} \right) \quad (\text{A8})$$

$$R_e(\tau, t_m) = r_0(t_m) \text{Exp}(k_T(t_m) T_s(\tau, t_m)), \quad (\text{A9})$$

$$F(\tau, t_m) = P_g(\tau, t_m) - R_e(\tau, t_m). \quad (\text{A10})$$

Daily totals of gross photosynthesis, $P_g(t)$, daytime ecosystem respiration, $R_{\text{day}}(t)$, and night-time ecosystem respiration, $R_{\text{night}}(t)$ were obtained by numerical integration of corresponding functions $P_g(\tau, t)$ and $R_e(\tau, t)$ in equations (A1) to (A10) over diurnal variable τ running, respectively, through light and dark periods of each calendar day t . The total 24-hour ecosystem respiration $R_e(t)$, and the net 24-hour ecosystem CO_2 exchange, $F(t)$, were calculated as:

$$R_e(t) = R_{\text{day}}(t) + R_{\text{night}}(t) \quad (\text{A11})$$

$$F(t) = P_g(t) - R_e(t) \quad (\text{A12})$$

Finally, annual totals of gross primary production, GPP, ecosystem respiration, RE, and net ecosystem production, NEP, were calculated as sums of the daily values $P_g(t)$, $R_e(t)$, and $F(t)$ over the whole year ($t = 1, 2, \dots, 365$).

Appendix B.

List of symbols

Latin symbols

$A_{\max}$	maximum gross photosynthetic assimilation ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
D_{VPD}	number of days with the σ_{VPD} parameter less than 4 kPa and maximum daily vapor pressure deficit higher than 1 kPa.
F	net CO_2 flux ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
GPP	annual gross primary production ($\text{g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$)
k_T	coefficient in the exponent for respiration temperature dependence ($^{\circ}\text{C}^{-1}$)
LUE	gross ecological light-use efficiency ($\text{mmol CO}_2 (\text{mol incident quanta})^{-1}$)
MAT	mean annual temperature ($^{\circ}\text{C}$)
NEP	net ecosystem production ($\text{g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$)
P_{day}	daytime integral of the net ecosystem CO_2 flux ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
P_g	gross photosynthetic assimilation ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
PCPN _{hyd}	atmospheric precipitation of the hydrologic year (mm year^{-1})

Q	incoming photosynthetically active radiation ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$; $\text{mol quanta m}^{-2} \text{ d}^{-1}$)
Q_g	incoming global radiation
R^2	coefficient of determination (dimensionless)
r_{day}	daytime ecosystem respiration rate ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
R_{day}	daytime ecosystem respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
R_e	ecosystem respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
RE	annual total ecosystem respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$)
RH	air relative humidity (%)
R_{night}	night-time ecosystem respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
R_{net}	net radiation (W m^{-2} ; $\text{MJ m}^{-2} \text{ d}^{-1}$)
r_0	ecosystem respiration rate at temperature $T_s = 0^{\circ}\text{C}$ ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
R_{night}	night-time ecosystem respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
SE	standard error (various units)
t	calendar day
T_a	air temperature ($^{\circ}\text{C}$)
t_m	calendar day with missing estimate of parameters
T_p	series of days with available parameter estimates
T_s	soil temperature (typically, at 5 cm depth) ($^{\circ}\text{C}$)
$T_{\text{sum}5}$	annual sum of mean daily temperatures above 5°C (degree days)
VPD	vapor pressure deficit (kPa)
VPD _{cr}	critical value of vapor pressure deficit (kPa)
W_s	soil water content, $\text{m}^3 \text{ m}^{-3}$

Greek symbols

α	apparent quantum yield of gross photosynthetic assimilation ($\text{mmol CO}_2 \text{ mol quanta}^{-1}$; $\text{mg CO}_2 \mu\text{mol quanta}^{-1}$)
α_{wk}	weekly mean of the apparent quantum yield of gross photosynthetic assimilation ($\text{mmol CO}_2 \text{ mol quanta}^{-1}$)
θ	convexity coefficient of the light-response equation (dimensionless)
Π	time series of parameter estimates
$\rho_{x,y}$	cross correlation function of variables x and y
$\sigma, \sigma_{\text{VPD}}$	curvature (standard deviation) parameter of the truncated Gaussian function for photosynthesis VPD response
τ	diurnal time ($0 \leq \tau \leq 24 \text{ h}$; $0 \leq \tau \leq 1 \text{ d}$)
φ	VPD response function

References

- Arkebauer, T.J., Walter-Shea, E.A., Mesarch, M.A., Suyker, A.E., Verma, S.B., 2009. Scaling up of CO_2 fluxes from leaf to canopy in maize-based agroecosystems. *Agric. Forest Meteorol.* 149, 2110–2119.
- Aubinet, M., Moureaux, C., Bodson, B., Dufranne, D., Heinesch, B., Suleau, M., Vancutsem, F., Vilret, A., 2009. Carbon sequestration by a crop over a 4-year sugar beet/winter wheat/seed potato/winter wheat rotation cycle. *Agric. Forest Meteorol.* 149, 407–418.
- Baker, J.M., Griffis, T.J., 2005. Examining strategies to improve the carbon balance of corn/bean agriculture using eddy covariance and mass balance techniques. *Agric. Forest Meteorol.* 128, 163–177.
- Baly, E.C.C., 1935. The kinetics of photosynthesis. *Proc. R. Soc. Lond. Ser. B* 117, 218–239.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W., Rouspard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I., Papale, D., 2010. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science* 329, 834–838.
- Bernacchi, C.J., Hollinger, S.E., Meyers, T., 2006. Corrigendum: The conversion of the corn/soybean ecosystem to no-till agriculture may result in a carbon sink. *Global Change Biol.* 12, 1585–1586.
- Bradford, J.B., Hicke, J.A., Lauenroth, W.K., 2005. The relative importance of light-use efficiency modifications from environmental conditions and cultivation for estimation of large-scale net primary productivity. *Remote Sens. Environ.* 96, 246–255.
- Burba, G.G., Verma, S.B., 2005. Seasonal and interannual variability in evapotranspiration of native tallgrass prairie and cultivated wheat ecosystems. *Agric. Forest Meteorol.* 135, 190–201.
- Ceschia, E., Béziat, P., Dejoux, J.F., Aubinet, M., Bernhofer, C., Bodson, B., Buchmann, N., Carrara, A., Cellier, P., Tommasi, P.D., Elbers, J.A., Eugster, W., Grünwald, T.,

- Jacobs, C.M.J., Jans, W.W.P., Jones, M., Kutsch, W., Lanigan, G., Magliulo, E., Marloie, O., Moors, E.J., Moureaux, C., Olisio, A., Osborne, B., Sanz, M.J., Saunders, M., Smith, P., Soegaard, H., Wattenbach, M., 2010. Management effects on net ecosystem carbon and GHG budgets at European crop sites. *Agriculture, Ecosystems and Environment* 139, 363–383.
- Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., Clark, D.A., Harmon, M.E., Schimel, D.S., Valentini, R., Wirth, C., Aber, J.D., Cole, J.J., Goulden, M.L., Harden, J.W., Heimann, M., Howarth, R.W., Matson, P.A., McGuire, A.D., Melillo, J.M., Mooney, H.A., Neff, J.C., Houghton, R.A., Pace, M.L., Ryan, M.G., Running, S.W., Sala, O.E., Schlesinger, W.H., Schulze, E.-D., 2006. Reconciling Carbon-cycle Concepts, Terminology, and Methods. *Ecosystems* 9, 1041–1050.
- Cooper, J.P., 1970. Potential production and energy conversion in temperate and tropical grasses. *Herbage Abstr.* 40, 1–13.
- Coulter, R.L., Klazura, G.E., Martin, T.J., Lucas, J.D., Pekour, M.S., Cook, D.R., 2006. Surface energy and carbon dioxide fluxes above different vegetation types within ABLE. *Agric. Forest Meteorol.* 136, 147–158.
- Crevoisier, C., Sweeney, C., Gloore, M., Sarmiento, J.L., Tans, P.P., 2010. Regional US carbon sinks from three-dimensional atmospheric CO₂ sampling. *PNAS* 107, 18348–18353.
- Dobermann, A., Walters, D.T., Baker, J.M., 2006. Comment on “Carbon budget of mature no-till ecosystem in North Central Region of the United States”. *Agric. Forest Meteorol.* 136, 83–84.
- Dugas, W.A., Heuer, M.L., Mayeux, H.S., 1999. Carbon dioxide fluxes over bermudagrass, native prairie, and sorghum. *Agric. Forest Meteorol.* 93, 121–139.
- Dugas, W.A., Reicosky, D.C., Kiniry, J.R., 1997. Chamber and micrometeorological measurements for CO₂ and H₂O fluxes for three C₄ grasses. *Agric. Forest Meteorol.* 83, 113–133.
- El-Sharkawy, M.A., Cook, J.H., Held, A.A., 1984. Water use efficiency of Cassava. II. Differing sensitivity of stomata to air humidity in Cassava and other warm-climate species. *Crop Sci.* 24, 503–507.
- Falge, E., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N.O., Katul, G., Keronen, P., Kowalski, A., Chun Ta, L., Law, B.E., Meyers, T., Moncrieff, J., Moors, E., Munger, J.W., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., Wofsy, S., Baldocchi, D., Olson, R., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. Forest Meteorol.* 107, 43–69.
- Fischer, M.L., Billesbach, D.P., Berry, J.A., Riley, W.J., Torn, M.S., 2007. Spatiotemporal variations in growing season exchanges of CO₂, H₂O, and sensible heat in agricultural fields of the Southern Great Plains. *Earth Int.* 11, Paper No. 17.
- Fissore, C., Espeleta, J., Nater, E.A., Hobbie, S.E., Reich, P.B., 2010. Limited potential for terrestrial carbon sequestration to offset fossil-fuel emissions in the upper midwestern US. *Front. Ecol. Environ.* 8, 409–413.
- Gilmanov, T.G., Aires, L., Bellelli, L., Barcza, Z., Baron, V.S., Beringer, J., Billesbach, D., Bonal, D., Bradford, J., Ceschia, E., Cook, D., Corradi, C., Frank, A., Gianelle, D., Gimeno, C., Gruenwald, T., Guo, H., Hanan, N., Haszpra, L., Heilman, J., Jacobs, A., Johnson, D.A., Kiely, G., Li, S., Magliulo, V., Moors, E., Nagy, Z., Naszyrov, M., Owensby, C., Pinter, K., Pio3, C., Reichstein, M., Sanz, M.J., Scott, R., Soussana, J.-F., Svejcar, T., Tuba, Z., Zhou, G., 2010. Productivity, Respiration, and Light-Response Parameters of World Grassland and Agro-Ecosystems Derived From Flux-Tower Measurements. *Rangeland Ecol. Manag.* 63, 16–39.
- Gilmanov, T.G., Johnson, D.A., Saliendra, N.Z., 2003a. Growing season CO₂ fluxes in a sagebrush-steppe ecosystem in Idaho: Bowen ratio/energy balance measurements and modeling. *Basic Appl. Ecol.* 4, 167–183.
- Gilmanov, T.G., Soussana, J.F., Aires, L., Allard, V., Ammann, C., Balzarolo, M., Barcza, Z., Bernhofer, C., Campbell, C.L., Cernusca, A., Cescatti, A., Clifton-Brown, J., Dirks, B.O.M., Dore, S., Eugster, W., Fuhrer, J., Gimeno, C., Gruenwald, T., Haszpra, L., Hensen, A., Ibrom, A., Jacobs, A.F.G., Jones, M.B., Lanigan, G., Laurila, T., Lohila, A., Manca, G., Marcollo, B., Nagy, Z., Pilegaard, K., Pinter, K., Pio, C., Raschi, A., Rogiers, N., Sanz, M.J., Stefani, P., Sutton, M., Tuba, Z., Valentini, R., Williams, M.L., Wohlfahrt, G., 2007. Partitioning European grassland net ecosystem CO₂ exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agric. Ecosyst. Environ.* 121, 93–120.
- 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 CO₂ 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, 271–292.
- Gilmanov, T.G., Verma, S.B., Sims, P.L., Meyers, T.P., Bradford, J.A., Burba, G.G., Suyker, A.E., 2003. Gross primary production and light response parameters of four Southern Plains ecosystems estimated using long-term CO₂-flux tower measurements – art. no. 1071. *Global Biogeochemical Cycles* 17, <http://dx.doi.org/10.1029/2002GB002023>, 002003.
- Glenn, A.J., Amiro, B.D., Tenuta, M., Steward, S.E., Wagner-Riddle, C., 2010. Carbon dioxide exchange in a northern prairie cropland system over three years. *Agric. Forest Meteorol.* 150, 908–918.
- Good, N.E., Bell, D.H., 1980. Photosynthesis, plant productivity and crop yield. In: Carlson, P.S. (Ed.), *The Biology of Crop Productivity*. Academic Press, New York, pp. 3–51.
- Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and critical evaluation of accuracy. *Global Change Biol.* 2, 169–182.
- Hanan, N.P., Suyker, A., Walter-Shea, E.A., Burba, G., Verma, S.B., Berry, J.A., 2002. Inversion of net ecosystem CO₂ flux measurements for estimation of canopy PAR absorption. *Global Change Biol.* 8, 563–574.
- Hayes, D.J., Turner, D.P., Stinson, G., McGuire, A.D., Wei, Y., West, T.O., Heath, L.S., DeJong, B., McConkey, B.G., Birdsey, R.A., Kurz, W.A., Jacobson, A.R., Hutzinger, D.N., Pan, Y., Post, W.M., Cook, R.B., 2012. Reconciling estimates of the contemporary North American carbon balance among terrestrial biosphere models, atmospheric inversions, and a new approach for estimating net ecosystem exchange from inventory-based data. *Global Change Biol.* 18, 1282–1299.
- Hernandez-Ramirez, G., Hatfield, J.L., Parkin, T.B., Sauer, T.J., Prueger, J.H., 2011. Carbon dioxide fluxes in corn-soybean rotation in the midwestern U.S.: Inter- and intra-annual variations, and biophysical controls. *Agric. Forest Meteorol.* 151, 1831–1842.
- Hollinger, S.E., Bernacchi, C.J., Meyers, T.P., 2005. Carbon budget of mature no-till ecosystem in North Central Region of the United States. *Agric. Forest Meteorol.* 130, 59–69.
- Houghton, R.A., Hackler, J.L., 2000. Changes in terrestrial carbon storage in the United States 1. The roles of agriculture and forestry. *Global Ecol. Biogeogr.* 9, 125–144.
- Körner, C., 2003. Slow in, rapid out—carbon flux studies and Kyoto target. *Science* 300, 1242–1243.
- Kutsch, W.L., Aubinet, M., Buchmann, N., Smith, P., Osborne, B., Eugster, W., Wattenbach, M., Schimpf, M., Schulze, E.D., Tomelleri, E., Ceschia, E., Bernhofer, C., Béziat, P., Carrara, A., Tommasi, P.D., Grünwald, T., Jones, M., Magliulo, V., Marloie, O., Moureaux, C., Olisio, A., Sanz, M.J., Saunders, M., Sogaard, H., Ziegler, W., 2010. The net biome production of full crop rotations in Europe. *Agric. Ecosyst. Environ.* 139, 336–345.
- Lasslop, G., Reichstein, M., Papale, D., Richardson, A.D., Arneth, A., Barr, A., Stoy, P., Wohlfahrt, G., 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Global Change Biol.* 16, 187–208.
- Long, S.P., Drake, B.G., 1992. Photosynthetic CO₂ assimilation and rising atmospheric CO₂ concentrations. In: Baker, N.R., Thomas, H. (Eds.), *Crop Photosynthesis: Spatial and Temporal Determinants*. Elsevier Science Publ. B.V., Amsterdam, pp. 69–103.
- Long, S.P., Postl, W.F., Bolhár-Nordenkamp, H.R., 1993. Quantum yields for CO₂ uptake in C₃ vascular plants of contrasting habitats and taxonomic groupings. *Planta* 189, 226–234.
- Matamala, R., Jastrow, D.J., Miller, R.M., Garten, C., 2008. Temporal changes in the distribution of C and N stocks in a Restored Tallgrass Prairie in the U.S. Midwest. *Ecol. Appl.* 18, 1470–1488.
- Meyers, T.P., 2001. A comparison of summertime water and CO₂ fluxes over rangeland for well watered and drought conditions. *Agric. Forest Meteorol.* 106, 205–214.
- Meyers, T.P., Hollinger, S.E., 2004. An assessment of storage terms in the surface energy balance of maize and soybean. *Agric. Forest Meteorol.* 125, 105–115.
- Mitscherlich, E.A., 1909. Das Gesetz des Minimums und das Gesetz des abnehmenden Bodenfruchtages. *Landwirtschaftliches Jahrbuch der Schweiz* 38, 537–552.
- Potter, C., Klooster, S., Huete, A., Genovesi, V., 2007. Terrestrial carbon sinks for the United States predicted from MODIS Satellite Data and ecosystem modeling. *Earth Int.* 11, 1–21, Paper No. 13.
- Prioul, J.L., Chartier, P., 1977. Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: a critical analysis of the methods used. *Ann. Bot.* 41, 789–800.
- Rabinowitch, E.I., 1951. *Photosynthesis and Related Processes*, vol. 2. Interscience Publishers, Inc, New York, Part 1.
- Randerson, J.T., Chapin, F.S., Harden, J.W., Neff, J.C., Harmon, M.E., 2002. Net ecosystem production: a comprehensive measure of net carbon accumulation by ecosystems. *Ecol. Appl.* 12, 937–947.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Valentini, R., Aubinet, M., Bernhofer, C., Buchmann, N., Falk, M., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Janous, D., Knohl, A., Laurela, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Perrin, D., Pumanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biol.* 11, 1424–1439.
- Schulze, E.-D., Heimann, M., 1998. Carbon and water exchange of terrestrial ecosystems. In: Galloway, N.J., Melillo, J.M. (Eds.), *Asian change in the context of global climate change (Proceedings of the Fourth Scientific Advisory Council Meeting of IGBP in Beijing 1995)*. IGBP Publication, Series 3, pp. 145–161.
- Smith, P., Lanigan, G., Kutsch, W., Buchmann, N., Eugster, W., Aubinet, M., Ceschia, E., Béziat, P., Yeluripati, J., Osborne, B., 2010. Measurements necessary for assessing the net ecosystem carbon budget of croplands. *Agric. Ecosyst. Environ.* 139, 302–315.
- Schmitt, M.R., Edwards, G.E., 1981. Photosynthetic capacity and nitrogen use efficiency of maize, wheat, and rice: a comparison between C₃ and C₄ photosynthesis. *J. Exp. Bot.* 32, 459–466.
- Smith, P., Martino, D., Cai, Z., Gwary, D., Janzen, H., Kumar, P., McCarl, B., Ogle, S., O'Mara, F., Rice, C., Scholes, B., Sirotenko, O., 2007. *Agriculture*. In: Metz, B., Davidson, O.R., Bosch, P.R., Dave, R., Meyer, L.A. (Eds.), *Climate Change 2007: Mitigation. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 497–540.
- Stoy, P.C., Juang, J.Y., Novick, K.A., Uebelherr, J.M., Oren, R., Katul, G.G., Siqueira, M.B.S., 2006. An evaluation of models for partitioning eddy covariance-measured net ecosystem exchange into photosynthesis and respiration. *Agric. Forest Meteorol.* 141, 2–18.

- Suyker, A.E., Verma, S.B., 2012. Gross primary production and ecosystem respiration of irrigated and rainfed maize-soybean cropping systems over 8 years. *Agric. Forest Meteorol.* 165, 12–25.
- Tamiya, H., 1951. Some theoretical notes on the kinetics of algal growth. *Bot. Magaz.* 6, 167–173.
- Thornley, J.H.M., Johnson, I.R., 2000. Plant and crop modelling. In: *A Mathematical Approach to Plant and Crop Physiology*. The Blackburn Press, Caldwell, New Jersey.
- Turner, D.P., Urbanski, S.P., Bremer, D., Wofsy, S., Meyers, T., Gower, S.T., Gregory, M., 2003. A cross-biome comparison of daily light use efficiency for gross primary production. *Global Change Biol.* 9, 383–395.
- Verma, S.B., Walters, D.T., Knops, J.M., Arkebauer, T.J., Suyker, A.E., Burba, G.G., Amos, B., Yang, H., Ginting, D., Hubbard, K.G., Gitelson, A.A., Walter-Shea, E.A., Dobermann, A., Cassman, K.G., 2005. Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems. *Agric. Forest Meteorol.* 131, 77–96.
- Webb, W.L., Newton, M., Starr, D., 1974. Carbon dioxide exchange of *Alnus rubra*: A mathematical model. *Oecologia* 17, 281–291.
- West, T.O., Brandt, C.C., Baskaran, L.M., Hellwinckel, C.M., Mueller, R., Bernacchi, C.J., Bandaru, V., Yang, B., Wilson, B.S., Marland, G., Nelson, R.G., Ugarte, D.G.D.L.T., Post, W.M., 2010. Cropland carbon fluxes in the United States: increasing geospatial resolution of inventory-based carbon accounting. *Ecol. Appl.* 20, 1074–1086.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO₂ in a mid-latitude temperate forest. *Science* 260, 1314–1317.
- Wohlfahrt, G., Newesely, C., Cernusca, A., Bahn, M., Haslwanter, A., 2005. Estimation of daytime ecosystem respiration to determine gross primary production of a mountain meadow. *Agric. Forest Meteorol.* 130, 13–25.
- Wolfram Research, 2011. Wolfram Mathematica portal: <http://www.wolfram.com/>, accessed April 22, 2012.
- Xiao, J., Zhuang, Q., Baldocchi, D.D., Ma, S., Law, B.E., Richardson, A.D., Chen, J., Oren, R., Katul, G.G., Starr, G., Noormets, A., Verma, S.B., Suyker, A.E., Wharton, S., Falk, M., Paw, U.K.T., Wofsy, S.C., Bolstad, P.V., Burns, S.P., Monson, R.K., Cook, D.R., Curtis, P.S., Drake, B.G., Fischer, M.L., Foster, D.R., Gu, L., Hadley, J.L., Hollinger, D.Y., Litvak, M., Martin, T.A., Matamala, R., McNulty, S., Sun, G., Meyers, T.P., Munger, J.W., Oechel, W.C., Schmid, H.P., Scott, R.L., Torn, M.S., 2008. Estimation of net ecosystem carbon exchange for the conterminous United States by combining MODIS and AmeriFlux data. *Agric. Forest Meteorol.* 148, 1827–1847.
- Xiao, J., Zhuang, Q., Law, B.E., Chen, J., Baldocchi, D.D., Cook, D.R., Oren, R., Richardson, A.D., Wharton, S., Ma, S., Martin, T.A., Verma, S.B., Suyker, A.E., Scott, R.L., Monson, R.K., Litvak, M., Hollinger, D.Y., Sun, G., Davis, K.J., Bolstad, P.V., Burns, S.P., Curtis, P.S., Drake, B.G., Falk, M., Fischer, M.L., Foster, D.R., Gu, L., Hadley, J.L., Katul, G.G., Matamala, R., McNulty, S., Meyers, T.P., Munger, J.W., Noormets, A., Oechel, W.C., U., K.T.P., Schmid, H.P., Starr, G., Torn, M.S., Wofsy, S.C., 2010. A continuous measure of gross primary production for the conterminous United States derived from MODIS and AmeriFlux data. *Remote Sens. Environ.* 114, 576–591.
- Xiao, J., Zhuang, Q., Law, B.E., Baldocchi, D.D., Jiquan Chene Richardson, A.D., Melillo, J.M., Davis, K.J., Hollinger, D.Y., Wharton, S., Oren, R., Noormets, A., Fischer, M.L., Verma, S.B., Cook, D.R., Sun, G., McNulty, S., Wofsy, S.C., Bolstad, P.V., Burns, S.P., Curtis, P.S., Drake, B.G., Falk, M., Foster, D.R., Gu, L., Hadley, J.L., Katul, G.G., Litvak, M., Mad, S., Martin, T.A., Matamala, R., Meyer, T.P., Monson, R.K., Munger, J.W., Oechel, W.C., Paw, U.K.T., Schmid, H.P., Scott, R.L., Starr, G., Suyker, A.E., Torn, M.S., 2011. Assessing net ecosystem carbon exchange of U.S. terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations. *Agric. Forest Meteorol.* 151, 60–69.