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1 **Productivity, Respiration, and Light-Response Parameters of World Grassland and**
2 **Agro-Ecosystems Derived From Flux-Tower Measurements**

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5
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14

LIST OF SYMBOLS

Latin symbols

- 1
2
- 3 **Latin symbols**
- 4 A_{max} – maximum gross photosynthetic assimilation ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
- 5 $CumNEE$ – cumulative net ecosystem CO_2 exchange ($\text{g CO}_2 \text{ m}^{-2}$)
- 6 F_c – net CO_2 flux ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 7 GPP – annual gross primary production ($\text{g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$)
- 8 k_T – coefficient in the exponential equation for respiration temperature dependence ($^{\circ}\text{C}^{-1}$)
- 9 L – leaf area index ($\text{m}^2 \text{ m}^{-2}$)
- 10 L_{max} – seasonal maximum leaf area index ($\text{m}^2 \text{ m}^{-2}$)
- 11 P_d – daytime integral of the net ecosystem CO_2 flux ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 12 P_g – gross photosynthetic assimilation ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 13 Q – incoming photosynthetically active radiation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{mol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 14 Q_a – absorbed photosynthetically active radiation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{mol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 15 $PCPN$ – atmospheric precipitation (mm d^{-1} , mm yr^{-1})
- 16 r_d – daytime ecosystem respiration rate ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
- 17 R_d – daytime ecosystem respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 18 R_e – total ecosystem respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 19 RE – annual total ecosystem respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$)
- 20 RH – air relative humidity (%)
- 21 R_n – nighttime ecosystem respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
- 22 R_{net} – net radiation (W m^{-2} ; $\text{MJ m}^{-2} \text{ d}^{-1}$)
- 23 r_0 – ecosystem respiration rate at temperature $T_s = 0$ $^{\circ}\text{C}$ ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

1 r_n – night-time ecosystem respiration rate ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

2 R_n – nighttime ecosystem respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)

3 R_{net} – net radiation (W m^{-2} ; $\text{MJ m}^{-2} \text{ d}^{-1}$)

4 T_a – air temperature ($^{\circ}\text{C}$)

5 t_r – time of sunrise (h)

6 t_s – time of sunset (h)

7 T_s – soil temperature (typically, at 5 cm depth) ($^{\circ}\text{C}$)

8 $V_{c,max}$ – maximum rate of carboxylation ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

9 W_s – volumetric soil moisture ($\text{m}^3 \text{ m}^{-3}$)

10

11 **Greek symbols**

12 α – apparent quantum yield of gross photosynthetic assimilation ($\text{mmol CO}_2 \text{ mol quanta}^{-1}$)

14 ε , ε_{ecol} – gross ecological light-use efficiency ($\text{mmol CO}_2 \text{ (mol incident quanta)}^{-1}$)

15 ε_{phys} – gross physiological light-use efficiency ($\text{mmol CO}_2 \text{ (mol absorbed quanta)}^{-1}$)

16 λ – latent heat of evaporation (MJ kg^{-1})

17 θ – convexity (curvature) coefficient of the light-response equation (dimensionless)

18 ρ_d – diffusion resistance to carbon transport (s m^{-1})

19 ρ_x – carboxylation resistance to carbon transport (s m^{-1})

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ABSTRACT

1
2
3 Grasslands and agroecosystems occupy nearly a third of the land surface area, but their
4 quantitative contribution to the global carbon cycle remains uncertain. We used a set of
5 316 site-years of year-round net CO₂ exchange (F_c) measurements to quantitatively
6 analyze gross primary productivity, ecosystem respiration, and light-response parameters
7 of extensively and intensively managed grasslands, shrublands/savanna, wetlands, and
8 cropland ecosystems worldwide. Analyzed data set included data from 72 flux-tower sites
9 worldwide partitioned into gross photosynthesis (P_g) and ecosystem respiration (R_e)
10 components using the light-response functions method (Gilmanov et al. 2003, Bas. Appl.
11 Ecol. 4:167-183) from the RANGEFLUX and WorldGrassAgriflux data sets
12 supplemented by data from 46 sites partitioned using the temperature-response method
13 (Reichstein et al. 2005, Gl. Change. Biol. 11:1424-1439) from the FLUXNET La Thuile
14 data set. Maximum values of the apparent quantum yield ($\alpha = 75 \text{ mmol mol}^{-1}$),
15 photosynthetic capacity ($A_{max} = 3.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), maximum daily gross
16 photosynthesis ($P_{g,max} = 116 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), and gross ecological light-use efficiency
17 ($\epsilon_{ecol} = 59 \text{ mmol mol}^{-1}$) of intensively managed grasslands and high-productive croplands
18 exceed those for forest ecosystems, indicating high potential of non-forest ecosystems for
19 uptake and sequestration of atmospheric CO₂. Maximum values of annual gross primary
20 production ($8600 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$), total ecosystem respiration ($7900 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$), and
21 net CO₂ exchange ($2400 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) for non-forest ecosystems are observed in
22 intensively managed grasslands and high-yield crops, and are comparable or higher than
23 in forest ecosystems (excluding tropical forests). On the average, 80% of the non-forest

1 sites were sinks for atmospheric CO₂, with mean annual net CO₂ uptake 848 g CO₂ m⁻²
2 yr⁻¹ for intensively managed grasslands and 933 g CO₂ m⁻² yr⁻¹ for croplands. The new
3 flux-tower data indicate the need to revise substantially previous views of grassland and
4 agricultural ecosystems as being predominantly a source of carbon, or having a neutral
5 role, in the regional and continental carbon budgets.

6

7 **Key Words:** gross primary production, ecosystem respiration, net CO₂ flux partitioning,
8 light-response functions method, grasslands, croplands

9

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11

INTRODUCTION

Quantifying the contribution of various ecosystem types in terms of carbon budget and total continental and global exchange of carbon has been recognized as a fundamental task since the very beginning of the carbon cycle science (Rodin and Bazilevich 1968; Whittaker and Likens 1973; Lieth 1975; Rodin et al. 1975; Olson et al. 1983). While generalizations on the role of forest, wetland, and tundra ecosystems in the global carbon budget have been provided recently, resulting in a general consensus on the contribution to the carbon budget of these ecosystem types (Griffiths and Jarvis 2005; Davidson and Janssens 2006; Birdsey et al. 2007; Bridgham et al. 2007; Tarnocai et al, 2007), there is considerably less agreement with respect to grassland and cropland ecosystems.

Available estimates of carbon budgets at the country or continental levels typically characterize grasslands as weak sinks, or as approaching a carbon-neutral state, while croplands are considered moderate to strong sources of atmospheric carbon (Smith and Falloon 2005; Conant et al. 2007). It should be emphasized, however, that those assessments are not based on direct measurements of carbon exchange, but rather on indirect measures such as biomass and soil organic matter inventories. As a rule, indirect measures involve lumping agricultural fields, where organic matter is produced, with locations (feedlots, harvest processing plants, ethanol facilities etc.) where harvested biomass is transported and utilized.

Although fully justified as initial “zero approximations”, indirect measures are fundamentally inadequate as tools for understanding the precise contributions of different land areas to regional CO₂ exchange. In contrast, our objective is to get reliable,

1 measurement-based estimates of carbon fluxes into and out of the system at the
2 ecosystem scale provided by tower records. According to some authors, corn fields
3 producing good harvests of grain with no soil organic matter loss due to advanced
4 agronomic management, but considered together with ethanol producing plants where
5 this corn is processed, will be viewed as only a small net sinks for atmospheric carbon
6 (Powlson et al., 2005; Farrell et al. 2006) or even as net carbon sources (Patzek et al.,
7 2005). This completely overshadows the fact that the field itself is often a very strong
8 sink for atmospheric CO₂ (e.g., Buyanovsky and Wagner, 1998; Hollinger et al. 2005).

9 The last decade has been characterized by an explosive growth in number and
10 duration of observations from nonforest flux tower stations all over the world. Through
11 the La Thuile synthesis process of the FLUXNET network (Baldocchi 2008; Agarwal et
12 al. 2008) and other cooperation initiatives, these observations are now available for
13 comparative analysis and generalization. In this publication we present the first synthesis
14 of results from tower CO₂ flux measurements at 118 tower sites representing grassland,
15 cropland, shrubland, savanna and wetland ecosystems of the world-- with the final goal
16 of obtaining measurement-based estimates of their role as net sinks or sources of
17 atmospheric CO₂. Such estimates provide a scientific basis for establishing carbon credit
18 market and poverty alleviation projects.

19

20

METHODS

21 Data for this study were provided by the WorldGrassAgriFlux data set (Gilmanov et al.
22 2007b) currently including data from 72 nonforest sites (Table 1, method L) for which
23 original 30-min (or 20-min in some sites) net CO₂ flux, F_c , was partitioned into gross

1 primary productivity, P_g , and ecosystem respiration, R_e , components using light-response
2 function methods (Gilmanov et al. 2003a,b, 2004, 2005, 2006, 2007a). These data were
3 combined with an additional 46 nonforest sites (Table 1, method T) from the FLUXNET
4 La Thuile dataset (Agarwal et al. 2008) that were partitioned into P_g and R_e components
5 using temperature-response methods (Reichstein et al. 2005). In most cases, we used
6 daily P_g and R_e estimates directly from the La Thuile dataset, though sometimes it was
7 necessary to correct negative values of daily gross primary production that were
8 occasionally generated by the night-time temperature response method (cf. Stoy et al.
9 2006).

10 In total, tower sites included in our analysis represent 316 site-years of
11 measurements during the 1997-2006 period (Table 1). They are grouped into the
12 following categories: extensively managed grasslands (ungrazed or lightly grazed, uncut
13 or cut occasionally), intensively managed grasslands (regularly cut, grazed, fertilized,
14 irrigated, etc.), croplands, shrublands/savannas, and wetlands. The geographic
15 distribution of sites is illustrated in Fig. 1.

16

17 **Net Tower Flux (F_c) Partitioning into Photosynthesis (P_g) and Respiration (R_e)**

18 Analysis of flux tower measurements requires processing algorithms (Lee et al. 2004;
19 Burba and Anderson 2007; Baldocchi 2008a) that describe the net result of interacting
20 ecosystem components that absorb CO₂ (mostly, photosynthetic assimilation by
21 autotrophic organisms), and those that release CO₂ (metabolic CO₂ production, R_e , is the
22 major component of CO₂ efflux during the growing season). Because photosynthesis and
23 respiration respond rather differently to major environmental drivers (e.g., Thornley and

1 Johnson 2000), partitioning of tower-based $\{F_c\}$ data into photosynthetic assimilation
2 and ecosystem respiration components is recognized as an necessary step in post-
3 processing of net flux data for use in predictive modeling of ecosystem carbon cycling
4 (Gilmanov et al. 2003b, 2004, 2005, 2006, 2007a; Reichstein et al. 2005; Stoy et al.
5 2006).

6 Using the ecophysiological sign convention (positive flux from atmosphere to
7 ecosystem), and excluding plants with CAM-type metabolism, the instantaneous gross
8 photosynthesis rate, P_g , used in this study was obtained as a sum of daytime net CO₂
9 exchange, F_c , and daytime ecosystem respiration, R_d , minus the rate of change of CO₂
10 storage in the atmospheric layer between the soil surface and the CO₂ sensor at the tower
11 (Gilmanov et a. 2007). When estimates of the storage term were not available (e.g. for
12 communities with low canopy height and sufficient turbulent transport) the gross
13 productivity was approximated as:

14

$$15 \quad P_g(t) = \begin{cases} F_c(t) + R_d(t), & Q(t) > 0, \\ 0, & Q(t) = 0. \end{cases} \quad [1]$$

16

17 where $Q(t)$ is the intensity of photosynthetically active radiation (Gilmanov et al. 2004).

18

19 Because direct measurements of the daytime ecosystem respiration R_d are quite
20 difficult to make, two main approaches of its indirect estimation (leading to the two
21 major methods of net flux partitioning into photosynthesis and respiration components)
22 were used:

1 (i) establishing relationship of the night-time respiration:

2

$$3 \quad R_n(t) = \begin{cases} F_c(t), & Q(t) = 0 \\ 0, & Q(t) > 0, \end{cases} \quad [2]$$

4

5 to environmental drivers affecting it (e.g., soil temperature, T_s) and using these
6 relationships to estimate daytime respiration, R_d . This approach has been widely used for
7 forest-type ecosystems (Goulden et al. 1996) and was used in this study for the first round
8 of network-level aggregation of the raw 30-min data into daily gross primary productivity
9 and ecosystem respiration values (<http://www.fluxdata.org/DataInfo/>).

10 (ii) obtaining estimates of daytime ecosystem respiration R_d through identification
11 of the respiration term in the ecosystem-scale light-response functions describing
12 relationships of the daytime flux F_c to photon flux density, Q , leaf area index, L , soil
13 temperature, T_s , water content of the soil, W_s , air relative humidity, HR , and other
14 factors. In general, light-response functions include rather complicated analytical or
15 algorithmic expressions (e.g., those suggested by Thornley and Johnson [2000, p. 248-
16 249]), taking into account most of the major ecophysiological parameters of
17 photosynthesis (quantum yield α , maximum photosynthesis A_{max} , convexity of the light
18 response, θ , leaf area index, L). When fully expanded, these expressions can require
19 several lines of printed text. At the other end of the complexity spectrum lie simple $F_c(Q)$
20 relationships like the ramp function by Blackman (1905), Mitscherlich's saturated
21 exponent (1909), and the rectangular hyperbola by Tamiya (1951); the latter being a
22 nearly standard approach to light-response fitting at the early stages of flux tower data

1 analysis (Ruimy et al. 1995). These simple models are convenient and, in some cases, fit
2 observed data well; however, they share the major drawback of lacking the ability to
3 describe light-response patterns of varying convexity (curvature).

4 Under the widely accepted eco-physiological framework, the convexity of the
5 light-response is represented by the fraction of diffusion resistance to the total (diffusion
6 + carboxylation) resistance to carbon transport: $\theta = \rho_d / (\rho_d + \rho_x)$ (Thornley and Johnson
7 2000). Taking into account the differences in leaf morphology and biochemistry in
8 different plant groups (e.g., C₃ vs. C₄ photosynthesis types), the ability to describe light-
9 response curves of different convexity seems to be a necessary requirement for an
10 adequate light-response function model. Our experience with quantification of the tower-
11 based light-response data from a wide range of nonforest ecosystems led us to use the
12 nonrectangular hyperbolic model (Rabinowich 1951; Thornley and Johnson 2000):

$$14 \quad F_c(Q; \alpha, A_{\max}, \theta, r_d) = \frac{1}{2\theta} \left(\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max} \theta Q} \right) - r_d, \quad [3]$$

15
16 where Q denotes photon flux density, α is the quantum yield, A_{\max} maximum gross
17 photosynthesis, θ is the convexity parameter of the light-response curve, and r_d is
18 daytime ecosystem respiration rate, for days when solar radiation is the major driver of
19 daytime CO₂ exchange. This model provides a powerful and flexible tool to describe
20 light-response at the various nonforest tower sites (Gilmanov et al. 2003a,b, 2004, 2005,
21 2006, 2007a).

22 Under semi-arid and arid conditions, when significant warming of the soil in the
23 afternoon period is observed, the pattern of data points on the light-response plane $\{Q,$

1 $F_c\}$ is often characterized by a hysteresis-like loop with the morning branch of the light-
 2 response curve lying above the afternoon branch. In such cases, these light-response
 3 patterns were effectively described by the modified nonrectangular hyperbolic model
 4 (Gilmanov et al. 2003a):

5

$$6 \quad F_c(Q, T_s; \alpha, A_{\max}, \theta, r_d) = \frac{1}{2\theta} \left(\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max} \theta Q} \right) - r_0 e^{k_T T_s},$$

7 [4]

8 where the daytime respiration term r_d of eq. [3] is modified to $r_0 e^{k_T T_s}$ to represent an
 9 exponential increase of respiration with soil temperature, T_s , and k_T and r_0 are empirical
 10 parameters estimated in the process of fitting eq. [4] to the daytime data

11 $\{Q(t_i), T_s(t_i), F_c(t_i)\}$, and t_i is time between the sunrise and sunset, $t_r \leq t_i \leq t_s$. For days
 12 described by eq. [4], average daytime respiration rate, r_d , was calculated as:

13

$$14 \quad r_d = \frac{r_0}{(t_s - t_r)} \int_{t_r}^{t_s} e^{k_T T_s(t)} dt .$$

15 [5]

16

16 Numerical fitting of parameters α , A_{\max} , θ , r_d or r_0 and k_T of equations [3] or [4] was
 17 achieved using procedures from the “Global Optimization Package” by Loehle
 18 Enterprises (2009) available under the “Mathematica” software system (Wolfram
 19 Research 2009). It should be emphasized that to avoid serious errors of light-response
 20 parameter estimation resulting from fitting equations to data lumped over several days (as
 21 sometimes can be seen in publications on the subject, e.g., Ruimy et al. 1995; Zhang et al.
 22 2006; Zhao et al. 2006), only single day datasets $\{Q(t_i), T_s(t_i), F_c(t_i)\}$ were used in this

1 study to identify the light-curves and the light-temperature response surfaces of CO₂
2 exchange.

3 It should also be noted that parameters obtained by fitting equations [3] or [4] to
4 flux-tower data sets are ecosystem-scale parameters referring to a ground unit (e.g., per 1
5 m² ground surface) and should be distinguished from leaf-level light-response parameters
6 used in physiological studies, which correspond to units of leaf area (e.g., $A_{L,max}$, α_L , etc.).
7 Only under special conditions (monoculture with convexity $\theta = 0$), is photosynthetic
8 capacity per unit ground area (A_{max}) equal to the product of photosynthetic capacity per
9 unit leaf area ($A_{L,max}$) and the leaf area index (L): $A_{max} = A_{L,max} * L$ (cf. Thornley and
10 Johnson 2000).

11 For measurement days that allow identification of parameters of models [3] or [4],
12 total daytime respiration, R_d , was calculated as the product of average daytime rate, r_d ,
13 and the length of the daylight period:

14

$$15 \quad R_d = r_d(t_s - t_r). \quad [6]$$

16

17 For days with daytime data inappropriate for light-response analysis, parameters k_T and r_0
18 were estimated by fitting an exponential equation $F_C = r_0 e^{k_T T_s}$ to the nighttime data
19 $\{T_s(t_i), F_C(t_i)\}_{Q(t_i)=0}$.

20 Eventually, total daily gross primary production, P_g , was obtained as the sum of daytime

21 respiration total R_d and the daytime net flux integral, $P_d = \int_{t_r}^{t_s} F_C(t) dt$:

22

1 $P_g = P_d + R_d.$ [7]

2

3 Gap-filling of P_g and R_e values for days with missing measurements was achieved
4 using various methods characterized in the recent review by Moffat et al. (2007), with
5 particular emphasis on (i) extrapolation of parameters of light- and temperature-response
6 functions to days with missing flux measurements, calculations of fluxes at the 30-min
7 time scale, and estimation of daily P_g and R_e values as integrals of corresponding 30-min
8 estimates; and (ii) nonlinear regressions of daily P_g and R_e values from daily aggregated
9 values of predictors such as photosynthetically active radiation, air and soil temperature,
10 soil water content, etc.

11

12 **Seasonal Patterns of Parameter Dynamics**

13 Numerical estimation of the major light-response parameters on a daily basis, i.e.
14 obtaining the values α , A_{max} , θ , r_d for as many days t as allowed by the quality and
15 quantity of the data, permits evaluation of time-functions $\alpha(t)$, $A_{max}(t)$, $\theta(t)$, $r_d(t)$
16 characterizing seasonal patterns of the dynamics of these parameters. These patterns are
17 revealed most clearly through smoothing of the empirical time series of the parameter
18 estimates. In this study we used one of the simplest and easily interpretable methods –
19 calculation of the mean parameter value and its standard error, e.g.,

20 $\{\bar{\alpha}_j, s_{\bar{\alpha}_j}\}$, $\{\bar{A}_{max,j}, s_{\bar{A}_{max,j}}\}$, etc. for every calendar week, j , of the year of

21 observations ($j = 1, \dots, 52$). Using weekly average values instead of individual daily

22 estimates proved to be most appropriate for comparison between ecosystems and years,

1 particularly for such parameters as quantum yield, α , exhibiting large day-to-day
2 variability.

3

4 **Seasonal Dynamics and Annual Budgets of GPP, RE, and NEE**

5 Estimated values of $P_g(t)$ and $R_e(t)$ for the year-round or observation period were
6 integrated over the 365 days (or over the measurement season – when no year-round data
7 were available) to obtain annual (seasonal) totals of gross primary production, GPP , and
8 total ecosystem respiration, RE . Cumulative NEE total to day t , $CumNEE(t)$, was
9 calculated by integrating daily values of $F_c(t) = P_g(t) - R_e(t)$. The net ecosystem CO_2
10 exchange for years or growing seasons, NEE , was calculated as the difference ($GPP - RE$).

11

12 **Ecosystem-Scale Light-Use Efficiency**

13 Comparative physiological studies at the leaf, individual, or population level commonly
14 calculate the light-use efficiency of gross photosynthesis P_g with respect to absorbed
15 photosynthetically active radiation, Q_a , resulting in a *gross physiological* light-use
16 efficiency coefficient (Larcher 1995):

17

$$18 \quad \varepsilon_{phys} = \frac{P_g}{Q_a}, \quad [8]$$

19

20 where both the photosynthesis P_g and absorbed radiation Q_a are expressed in molar units
21 (e.g., it is convenient to measure ε in mmol CO_2 per mol quanta). However, in
22 comparative ecological studies it is preferable to use the coefficient of *gross ecological*

1 light-use efficiency (cf. Odum 1959 (p. 54); Cooper 1970; Austin et al. 1978; Colinvaux
2 1993):

$$3 \quad \varepsilon_{ecol} = \frac{P_g}{Q}, \quad [9]$$

5
6 calculated per unit of *total incoming* photosynthetically active radiation, Q . It should be
7 emphasized that while the physiological light-use efficiency coefficient, ε_{phys} ,
8 characterizes physiological and biochemical parameters (and is often used in studies
9 performed at the unit leaf area or unit of photosynthetically active biomass basis), ε_{ecol} , as
10 a rule, is calculated per unit ground surface (m^{-2} , ha^{-1} , etc.), and thus also takes into
11 account such ecosystem-level properties as population density, aboveground biomass,
12 and leaf area. Thus, gross ecological light-use efficiency characterizes ecosystems as a
13 whole with respect to ability for utilization of available radiation resources. For example,
14 consider two ecosystems with physiologically similar species and therefore similar light-
15 use efficiencies per unit leaf area, but with LAI in the first ecosystem twice as small as
16 the second (e.g. due to management). For moderate LAI values (e.g., $< 3 \text{ m}^2 \text{m}^{-2}$ in the
17 second ecosystem), the photosynthetic uptake per unit of ground surface, P_g , and the
18 absorbed radiation, Q_a , in the second ecosystem will be approximately twice as large as
19 in the first, so that there will be little difference between the two ecosystems in terms of
20 their physiological light-use efficiency ε_{phys} . On the other hand, the incoming radiation,
21 Q , will be the same in the two ecosystems, resulting in ecological light-use efficiency,
22 ε_{ecol} , in the second ecosystem being two times higher than in the first.

23

RESULTS AND DISCUSSION

Light-Response Functions and Parameters

Within the broad range of climatic conditions and ecosystem types represented in the data set, we observed a variety of patterns of light-response. For comparative purposes, it is convenient to distinguish four major categories differentiated in terms of convexity and presence of the hysteresis-like loop on the light-response scatter diagram $\{Q, F_c\}$ (Fig. 2).

In the latter case, plotting the 3-D scatter diagram of the diurnal dynamics of the measurement data and of the response surface $F_c(Q, T_s)$ (eq. [4]) fitted to them provides a partial explanation the loop on the 2-D $\{Q, F_c\}$ plot caused by the increase of ecosystem respiration with the increase of temperature in the afternoon hours (Fig. 3). For the cases shown in Figures 2 and 3, numerical estimates and statistical characteristics of parameters in equations [3] and [4] are presented in Tables 2 and 3.

Nonrectangular hyperbolic equation [3] and its modification [4] taking into account temperature-dependence of daytime respiration, were found to be good numerical tools to fitting light-responses of nonforest ecosystems for days when photosynthetically active radiation was the dominant factor governing the ecosystem CO_2 exchange. It is important to emphasize that the nonrectangular hyperbola provided a close fit to light-response data and provided consistent estimates of the light-response parameters for days when the $\{Q, F_c\}$ plots showed no saturation with respect to Q and were characterized by convexity parameter θ close to 1 (cf. Fig. 2A). The rectangular hyperbola, Mitscherlich's equation, and other approximations lacking convexity parameter fitted to data with such a pattern, yield highly biased estimates of the initial slope, plateau, and the intercept parameters.

1 Estimates of the apparent quantum efficiency, α , in nonforest ecosystems cover a
2 wide range of values (Fig. 4A), from 5 mmol mol⁻¹ in the desert shrublands of Central
3 Asia (Karrykul) to 75 mmol mol⁻¹ in intensively managed grasslands of the North
4 Atlantic (Cabauw, the Netherlands), with mean value $\alpha_{\text{nonfor}} = 33.3$ mmol mol⁻¹ and
5 standard deviation $s_{\text{nonfor}} = 14.2$ mmol mol⁻¹. The lower 10% quantile of the α values in
6 the sample (5-17 mmol mol⁻¹) included extensively managed arid and semiarid grasslands
7 and shrublands (Karrykul, Cottonwood, Karnap, Audubon, Lethbridge, Kherlenbayan,
8 Tojal, and Fort Peck), while the upper 10% quantile (50-75 mmol mol⁻¹) encompassed
9 intensively managed grasslands (Cabauw, Carlow, Neustift, Easter Bush, Oensingen,
10 Lille Valby, Grillenburg, Haller, Rigi-Seebodenalp), extensively managed grasslands
11 under favorable weather conditions (Laqueuille-extensive, Jornada), and intensive
12 agricultural crops (Lonzee). Interestingly, most productive crop sites, characterized by
13 the highest A_{max} and $P_{g,\text{max}}$ values, did not make it to the upper 10% quantum yield
14 quantile, though they belong to the upper 20% quantum yield quantile.

15 In addition to scatter plots for the pooled data set, understanding relationships
16 between parameters within a particular ecosystem is of interest. Presently, only a subset
17 of extensively managed grasslands shows scatter diagrams with pronounced patterns of
18 co-variation (Fig. 5).

19 In evaluating obtained estimates of the quantum yield, we should first note that
20 our maximum estimate of 75 mmol mol⁻¹ is only two thirds of the theoretical maximum
21 of quantum efficiency of gross photosynthesis estimated by Good and Bell (1980) as 110
22 mmol mol⁻¹. Comparing our nonforest estimates with those reviewed by Ruimy et al.
23 (1995), from which we estimated mean $\bar{\alpha}_{\text{forest}} = 37$ mmol mol⁻¹ with standard

1 deviation $s_{\text{forest}} = 17 \text{ mmol mol}^{-1}$ (we have excluded data in Ruimy et al. 1995 with α
2 values greater than theoretical maximum of quantum efficiency), one can see that
3 quantum efficiency of nonforest ecosystems is not statistically different from forests. In
4 fact, $\alpha_{\text{max, nonforest}}$ estimated for intensively managed Cabauw grassland in The
5 Netherlands (75 mmol mol^{-1}) was numerically higher, but statistically not significantly
6 different from the maximum quantum efficiency determined for the chestnut coppice near
7 Paris, France ($\alpha_{\text{max, forest}} = 73 \text{ mmol mol}^{-1}$) (Mordacq et al 1991).

8 The values of maximum average weekly gross photosynthesis, A_{max} , for nonforest
9 sites of the world (Fig. 4A) span from $0.2 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fort Peck mixed prairie during
10 a drought year) to $3.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Mead, irrigated continuous corn), with the lower
11 10% quantile ($0.2\text{-}0.36 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) including Fort Peck, Dubois, Miles City,
12 Kherlenbayan, Xilinhot, Karrykul, Kubuqi, Burns, and Karnap, and the upper 10%
13 quantile ($2\text{-}3.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) including intensive crops (Mead, Bondville, Lonzee,
14 Ames), intensively managed grasslands (Cabauw, Carlow, Lille Valby), and tallgrass
15 prairies (Shidler, Fort Reno). The mean photosynthetic capacity of nonforest ecosystems,
16 $1.2 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (SD = $0.68 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), lies at the upper end of the mean A_{max}
17 range for different forest types from eddy covariance estimates, $0.66 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to
18 $1.3 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (mean = $0.97 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Falge et al. 2002; Funk and Lerdau
19 2004). At the same time, the highest A_{max} value for nonforest ecosystems found in
20 intensive corn cultures of the Midwest of the USA ($3.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were
21 substantially higher than $A_{\text{max}} = 2.64 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ estimated from data by Jarvis (1994)
22 for a Sitka spruce culture in Scotland.

1 The values of daytime ecosystem respiration rate, r_d , in all ecosystems remained
2 substantially lower than corresponding A_{max} values (cf. Fig. 6, left), but also displayed
3 substantial variability among ecosystem types (Fig. 4B), with maximum weekly average
4 r_d ranging from 0.04 mg CO₂ m⁻² s⁻¹ (Burns, drought year) to 0.50 mg CO₂ m⁻² s⁻¹
5 (Haller, warm and wet year). The lower 10% quantile of maximum weekly r_d values
6 included arid and semiarid grasslands and shrublands (Burns, Karnap, Kherlenbayan,
7 Karrykul, Cottonwood, Burns, Dubois, Kubuqi) and tundra (Barrow), while the upper
8 10% quantile of r_d distribution was represented by intensively managed grasslands
9 (Haller, Neustift, Cabauw, Carlow, Oensingen, Lille Valby, Easter Bush), intensive crops
10 (Ames, Mead), tallgrass prairies (Shidler, Rannels Ranch), and a semidesert grassland in
11 a year with exceptionally high precipitation (Jornada).

12 The weekly maxima of the coefficient of gross ecological light-use efficiency, ϵ ,
13 resulting from this study were in the range from 3 to 59 mmol mol⁻¹ (mean 22, standard
14 deviation 12.4 mmol mol⁻¹), and, understandably, were lower than the weekly maxima of
15 the apparent quantum yield, α (Fig. 6, right). It is interesting, however, that for some
16 ecosystems, particularly for agricultural C₄-crops and tropical grasslands dominated by
17 C₄-species, ϵ values were not considerably lower than α (e.g., see Fig. 6E, 6F and 6H,
18 right). This is a direct result of relatively high values of the convexity coefficient of the
19 light-response curves of C₄ species; at the ultimate case of $\theta = 1$, the values of α and ϵ
20 will become equal, provided input radiation levels remains within the range of linear
21 light-response.

22 On the contrary, in C₃-communities characterized by lower convexity values ($\theta =$
23 0 in the extreme case of rectangular hyperbolic light-response), ecological light-use

1 efficiency remains substantially lower than quantum yield (Fig. 6A, right). The lower
2 10% quantile of light-use efficiency values ϵ (2.6 – 6.4 mmol mol⁻¹) includes deserts,
3 desert and dry steppe grasslands, shortgrass and sagebrush steppes, mixed prairies,
4 California grasslands and chaparral, and tundra (Karrykul, Karnap, Audubon Ranch,
5 Kendall, Xilinhot, CPER, Fort Peck, Cottonwood, Burns, Kubuqi, Kherlenbayan, Sky
6 Oaks, Barrow, Atqasuk, Ivotuk). The upper 10% quantile of the ϵ values (40-59 mmol
7 mol⁻¹) mostly includes high-yield crops (Risbyholm, Langerak, Molenweg, Mead,
8 Bondville, Oensingen, Gebesee, Lonzee, Batavia), as well as highly productive
9 intensively and extensively managed grasslands (Carlow, Lille Valby, Oensingen,
10 Neustift).

11 For comparison with ϵ_{max} estimates for nonforest ecosystems, we calculated
12 average weekly values of light-use efficiency for the twelve most productive forest
13 ecosystems in the FLUXNET La Thuile database. These twelve ϵ_{max} values ranged
14 between 29.1 and 47.7 mmol mol⁻¹, with the highest value corresponding to the 2001 data
15 set for the Duke loblolly pine forest (North Carolina), which is less than $\epsilon_{max} = 59$ mmol
16 mol⁻¹ for a high-yield crop (also, see Table 5 for $P_{g,max}$ comparison of forests and
17 nonforest ecosystems). Thus, the light-use efficiency data are in agreement with
18 observations earlier in this section that the values of the maximum apparent quantum
19 yield in nonforest ecosystems (particularly, intensively managed grasslands) are
20 comparable and even higher than those for forest ecosystems.

21

22 **Parameter Interrelations**

1 As expected, numerical values of light-response parameters among different ecosystems
2 did not vary independently of each other, but demonstrated patterns of correlation shown
3 in Figs. 4 and 5. Our results for this extensive data set are in agreement with earlier
4 studies based on smaller subsets of flux-tower data, suggesting that the plateau parameter
5 of gross photosynthesis, A_{max} , is a good predictor for other light-response parameters,
6 including quantum yield, α , ecosystem respiration rate, r_d , and light-use efficiency, ϵ
7 (Gilmanov et al. 2007a; Owen et al. 2007). Baldocchi and Xu (2005) found that A_{max} is a
8 good predictor for another photosynthetic parameter, the maximum rate of carboxylation,
9 $V_{c,max}$. Nevertheless, while in previous studies mostly linear relationships between A_{max}
10 and other parameters were identified, the wider range of parameter variations in our data
11 set has revealed a number of distinct nonlinearities. For example, an allometric
12 relationship $\alpha = 30.36(A_{max})^{0.55}$ with R^2 value of 0.55 was obtained for the
13 relationship between apparent quantum yield and maximum photosynthesis (Fig. 4A).
14 The better fit of the allometric (nonlinear) description of the $\alpha(A_{max})$ relationship
15 compared with the simple linear model is demonstrated by the fact that the nonlinear
16 model conveys a decrease in α with decreasing A_{max} as the latter is approaching zero,
17 while the linear model predicts an unrealistic α_0 value of $\sim 15 \text{ mmol mol}^{-1}$ even when A_{max}
18 $\rightarrow 0$.

19 Daytime ecosystem respiration, r_d , also demonstrated an allometric relationship to
20 A_{max} described as $r_d = 0.22(A_{max})^{0.71}$ characterized by $R^2 = 0.69$ (Fig. 5B). In this
21 case, the linear model also provided a reasonable fit to the data ($R^2 = 0.67$), though its
22 applicability to areas with low A_{max} values is limited by an unrealistically high intercept
23 of $r_{d0} = 0.09 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ as $A_{max} \rightarrow 0$. From the patterns of data points on Figs. 5C

1 and 5D one may see that the relationships between ecological light-use efficiency,
2 maximum daily gross photosynthesis, and L_{max} may be approximated by both the linear,
3 and the allometric equations, though the latter provides better description in the lower
4 range of A_{max} and L_{max} .

5 For various reasons, not all flux sites collected data on maximum leaf area (L_{max})
6 and/or maximum aboveground green biomass (G_{max}). Nevertheless, with the limited data
7 available (Figs. 5F and 5H) we were able to establish nonlinear allometric (with
8 allometry coefficient < 1) dependence of maximum photosynthesis parameters (A_{max} ,
9 $P_{g,max}$) and the standard morphometric characteristics such as maximum aboveground
10 biomass, G_{max} and maximum leaf area index, L_{max} (Figures. 5F and 5H).

11

12 *Seasonal Patterns of Parameter Dynamics*

13 Because light-response parameters evaluated from flux-tower measurement data sets
14 represent not only physiological characteristics (which also change in time with
15 phenology and environmental conditions) but also the ecosystem-scale attributes like
16 aboveground biomass, leaf area index and others, such parameters exhibit pronounced
17 variation in magnitude during the year. Seasonal changes of these parameters, though
18 specific for particular sites and years, have general patterns that are revealed by time-
19 plots of parameter values aggregated at the weekly time step (Fig. 6). Pronounced
20 seasonal dynamics of light-response parameters shown on Fig. 6 in cold and temperate
21 environments is apparently driven by radiation and temperature inputs (Fig. 6, A, D),
22 while under arid conditions it mainly reflects fluctuation of precipitation (Fig. 6 E, F).
23 This climatically driven unimodal pattern of seasonal parameter change was particularly

1 pronounced in species-poor ecosystems or monocultures with relatively narrow
2 production period, be that a floodplain meadow in the tundra zone (Fig. 6A) or
3 agricultural crops (Figs. 6G and 6H). In ecosystems with higher species diversity and
4 broader production period (up to year-round production in tropical conditions), the
5 general seasonal pattern of parameter dynamics was compounded by additional
6 fluctuations reflecting different reactions of various species groups (e.g., cool and warm-
7 season grasses) to weather variability and management pressure (grazing, mowing)
8 during various parts of the year (Figs. 6 B, C, D). These data may help to explain
9 difficulties experienced by those attempting to simulate year-round dynamics of gross
10 primary productivity and light-response parameters by modification of the hypothetical
11 maximum parameter value by factors-multipliers describing effects of various drivers like
12 radiation, temperature, moisture, etc. (cf. Monteith 1972; Ciais et al. 2001).

13

14 **Seasonal Dynamics and Annual Budgets of GPP, RE, and NEE**

15 Depending on a number of external (e.g. radiation, temperature, precipitation) and
16 internal ecological factors (e.g. leaf area, phenological state, water and nutrient supply),
17 the functions of gross primary productivity, $P_g(t)$, and total ecosystem respiration, $R_e(t)$,
18 demonstrated pronounced temporal dynamics during the year, as exemplified by the
19 measurement-based estimates of $P_g(t)$ and $R_e(t)$ presented on Fig. 7. On the other hand,
20 the curve of cumulative net ecosystem exchange, $CumNEE(t)$ showed much smoother
21 behavior, and its value at the end of the year, NEE, provides a summary of ecosystem
22 carbon budget.

1 Data from the WorldGrassAgriFlux data set demonstrated a great variety of
2 seasonal patterns of productivity and respiration dynamics, some of the typical curves are
3 illustrated in Fig. 7. There are three major seasonal patterns of the cumulative NEE curve:
4 (i) equilibrium (S-shaped), (ii) permanent accumulation, and (iii) permanent release of
5 carbon. The equilibrium pattern (i) characterizing non-harvested ecosystems with marked
6 seasonality of primary productivity was exemplified by data from a floodplain tundra
7 meadow at Cherskii in the Far North-East of Russia (Fig. 7A). With the period of
8 decomposition activity (May-September) completely encompassing the production period
9 (June-August) and with maximum decomposition lagging behind maximum production,
10 the curve of cumulative *NEE* assumed a characteristic S-shaped form with the net annual
11 ecosystem CO₂ exchange nearly zero. The accumulative pattern (ii) is described by the
12 more or less monotonous accumulation of net ecosystem production in ecosystems with a
13 period of marked domination of production over decomposition processes observed in
14 both grassland (Fig. 7F) and cropland ecosystems (Fig. 7G). The third pattern (iii) –
15 nearly permanent domination of respiratory efflux over assimilatory uptake resulting in
16 significant net loss of carbon from the ecosystem at the end of the year, as exemplified by
17 measurements at the Audubon (AZ) desert grassland on a high carbonate soil (Emmerich
18 2003) (Fig. 7D). These three major patterns were accompanied by a variety of
19 intermediate variants with local maxima and minima of the *CumNEE(t)* curve reflecting
20 weather fluctuations and harvesting, finally leading to either net uptake (Fig. 7C) or net
21 loss of carbon from the ecosystem (Fig. 7B, 7E and 7H).

22 Year-round integration of the $P_g(t)$, $R_e(t)$, and $F_c(t)$ curves provided estimates of
23 annual *GPP*, *RE*, and *NEE* totals for all the site-years in this study. These data stratified

1 by major ecosystem groups (extensively and intensively managed grasslands, shrublands
2 and savanna, wetlands, and croplands) are summarized in Table 4. The highest mean
3 gross primary production ($5767 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) and ecosystem respiration (4990 g CO_2
4 $\text{m}^{-2} \text{ yr}^{-1}$) were achieved in intensively managed grasslands. Not surprisingly, the highest
5 mean annual net ecosystem CO_2 exchange ($933 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) was found in croplands.
6 To supplement these basic statistical characteristics, Fig. 8 shows the distributions of the
7 *GPP*, *RE*, and *NEE* values in the pooled data set of estimates from all site-years in the
8 database. They show that while the *GPP* and *RE* values in our sample had a wide range
9 of variation ($95 - 8600 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ for gross production and $112 - 7880 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$
10 for respiration), with *GPP* and *RE* values fairly well distributed over their ranges (Fig. 8A
11 and 8B), the net CO_2 exchange values concentrated between $-1342 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ and
12 $2394 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ had a distinctly unimodal distribution (Fig. 8 C). The average *NEE*
13 value for our sample of 316 nonforest ecosystems is $485 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ ($\text{SD} = 696 \text{ g CO}_2$
14 $\text{m}^{-2} \text{ yr}^{-1}$). Comparing these statistics with the mean ($671 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) and standard
15 deviation ($988 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) of published *NEE* values for 506 site-years from flux
16 towers worldwide (Baldocchi 2008b), we did not detect a difference between the two
17 *NEE* averages at the 1% level of significance. The higher mean *NEE* value for
18 Baldocchi's sample is easily explained, taking into account that it contains a number of
19 growing forest sites with high *NEE*, while the WorldGrassAgriFlux data set includes
20 mostly nonforest sites (with occasional near-climax shrubland and savanna ecosystems).
21 A particularly interesting question, in the context of comparing basic parameters of the
22 carbon cycle, regards identifying maximum rates of photosynthetic CO_2 assimilation in
23 various ecosystems. For this purpose, in Table 5 we have compiled the data of the two

1 dozen (or maximum available) site-years with maximum values of daily photosynthesis,
2 $P_{g,max}$, and annual GPP for our five types of nonforest ecosystems and for the forest sites
3 represented in the most recent FLUXNET database. With respect to the annual GPP ,
4 forest ecosystems achieved the highest estimates of photosynthetic CO_2 uptake, with
5 maximum $GPP = 14339 \text{ g } CO_2 \text{ m}^{-2} \text{ yr}^{-1}$ for a tropical forest in French Guyana (Table 5F)
6 compared to maximum $GPP = 8600 \text{ g } CO_2 \text{ m}^{-2} \text{ yr}^{-1}$ for a tropical grassland in Rondonia,
7 Brazil (Table 5 A). In contrast, maximum daily rates of photosynthetic uptake were
8 recorded not in forests, but in the intensive crops of the Midwestern United States, with
9 $P_{g,max} = 116 \text{ g } CO_2 \text{ m}^{-2} \text{ d}^{-1}$ estimated for irrigated corn in a corn-soybean rotation (Mead,
10 NE) in 2001 (Table 5E). These data clearly demonstrate that even in other types of
11 nonforest ecosystems (e.g. shrublands and savanna), in addition to intensive agricultural
12 crops, maximum rates of gross photosynthetic assimilation ($50 - 76 \text{ g } CO_2 \text{ m}^{-2} \text{ d}^{-1}$) are
13 quite comparable to those in most productive forests ($55 - 99 \text{ g } CO_2 \text{ m}^{-2} \text{ d}^{-1}$). Apparently,
14 the major reason why annual GPP in forests is typically higher than nonforested
15 ecosystems is the length of production period. In tropical forests, production may
16 encompass the whole year, while in most nonforest ecosystems it is temporally limited by
17 temperature and water availability.

18 **Source/Sink Activity of Nonforest Ecosystems**

19 The data on annual budgets of production, respiration, and net exchange of nonforest
20 ecosystems obtained in our study allow quantitative consideration of important question
21 about the magnitude and significance of the source or sink activity of various ecosystem
22 types. Since H.T. Odum (1956) (see also Baldocchi 2008b), a convenient way to
23 visualize the net carbon budget of ecosystems for comparative purposes is to construct an

1 *RE versus GPP* scatter diagram and compare the distribution of data points with respect
2 to the 1:1 diagonal. Points below the diagonal correspond to sinks ($GPP > RE$, $NEE > 0$),
3 while points above the diagonal describe sources of carbon ($GPP < RE$, $NEE < 0$).
4 H.T. Odum's plot for the whole nonforest data set (Fig. 9) demonstrates that for four out
5 of every five site-years, gross production was higher than ecosystem respiration,
6 indicating net ecosystem sink activity. Stratification of the data with respect to ecosystem
7 type (Fig. 10) shows that for all types of nonforest ecosystem in our database there were
8 considerably more years with net CO₂ uptake than release. However, years with net
9 source activity occasionally occurred in all ecosystems except wetlands.
10 The distributions of *NEE* for different ecosystems presented in Fig. 11 provide a more
11 detailed description of the matter. Source-type activity more frequently occurred in
12 extensively managed grasslands, shrublands/savanna, and croplands, than in intensively
13 managed grasslands and wetlands. As a rule, source-type activity was associated with
14 years of drought, excessive grazing and hay mowing, high organic matter content of soils
15 (e.g. grasslands on peat) or high CaCO₃ reserves in the soil profile, and transitional
16 successional status of the ecosystem (e.g., grasslands of previously forested soils). For
17 agroecosystems, source activity is often observed in crops with intensive soil preparation
18 and relatively short leaf duration periods (e.g. soybeans). However, it should be
19 emphasized that for all ecosystems examined in our study, carbon sink activity was
20 frequently observed, with the highest net carbon uptakes in intensively managed
21 grasslands and cropland ecosystems (Fig. 11, Table 4).

22 These observations are in obvious contradiction with conclusion of the first State
23 Of the Carbon Cycle Report (SOCCR) (King et al. 2007) and some earlier authors (e.g.,

1 Reicosky 1997; Smith and Falloon 2005) who emphasized net source or neutral activity
2 of agricultural ecosystems. In this context, it is appropriate to consider the argument by
3 C. Körner (2003) regarding the critical significance of the representativeness of flux
4 tower data sets. Recognizing the relevance of Körner's arguments to the situation in the
5 early 2000s, it should be emphasized that, at least with regard to nonforested ecosystems,
6 the present set of flux tower sites includes a wide range of climatic conditions and
7 management regimes and, therefore, is much less biased towards highly productive
8 ecosystems.

9 **Ecosystem-Scale Production and Respiration in Relation to Major Ecological** 10 **Factors**

11 Relationships of production and decomposition to major ecological factors attracted
12 attention of ecologists and geographers of the 20th century (Weaver 1924; Walter 1939;
13 Budyko and Efimova 1968; Rosenzweig 1968; Lieth 1975) and were later approached
14 under the framework of dynamic global vegetation models (DGVM) and related models
15 (e.g., Woodward et al. 2001; Cramer et al. 2001). Presently, these problems are back in
16 the focus of ecosystem, regional and global ecology, not only because of the recognition
17 of their relevance to global climatic change, but also because today, for the first time,
18 measurement-based quantitative estimates of gross productivity and total ecosystem
19 respiration are readily available through post-processing of net CO₂ exchange
20 measurements at flux towers.

21 Besides radiation and temperature, which are already taken into account by the
22 light-temperature-response function method, the next most important factor influencing
23 ecosystem productivity and respiration is water (e.g., Slatyer 1967; Boyer 1982). Though

1 water content or water potential of top-soil horizons are the most desirable predictors for
2 production and decomposition modeling, such data are not yet readily available for many
3 flux tower stations, making it necessary for us to limit consideration to available
4 precipitation data.

5 Both theory and empirical data indicate nonlinear relationships between
6 photosynthesis, productivity, and decomposition rates on water content and/or water
7 potential (Denmead and Shaw 1962; Wildung et al. 1975; Singh et al. 1980; Eastin and
8 Sullivan 1984; Mielnick and Dugas 2000). In contrast, observations of the linear response
9 of productivity in certain ecosystem types occasionally appear in the literature (Walter
10 1939; Le Houèrou and Hoste. 1977; Sala et al. 1988). Our data allow a fresh look at this
11 old problem using new ecosystem-scale estimates of *GPP* and *RE* values in relation to
12 precipitation *PCPN* (Fig. 12-14). Within the whole WorldGrassAgriFlux data set, we
13 found that the subsets of extensively managed grasslands, intensively managed
14 grasslands, and shrublands-savanna exhibit patterns of relationship of *GPP* and *RE* to
15 precipitation and dryness index, while the data for wetlands and croplands did not
16 produce recognizable patterns.

17 Gross production and ecosystem respiration of extensively managed grasslands
18 demonstrate nonlinear patterns in response to annual precipitation that may be expressed
19 by Mitscherlich's equation (Fig. 12A and 12B) describing a saturated relationship (cf.
20 Lieth 1975). Deviation of the data points from the trend, which increases in amplitude
21 with increasing precipitation, indicates a diminishing response to precipitation. As shown
22 in Figs. 12C and 12D, the decrease of precipitation use efficiency is linked to the dryness
23 index (ratio of annual net radiation, R_{net} , to the amount of energy required for evaporation

1 of precipitation, $\lambda * PCPN$, where λ is the latent heat coefficient) (Budyko and Efimova,
2 1968; Long et al. 1991).

3 Intensively managed grasslands, which are typically located in climates with more
4 favorable precipitation and less drought stress, still exhibit responses to precipitation and
5 dryness; this response is especially pronounced for gross primary production (Fig. 13).

6 Shrublands and savanna ecosystems, with their broad range of precipitation and dryness
7 index, demonstrate strong nonlinearity of response to precipitation and dryness for both
8 the assimilation and respiration components of the carbon cycle (Fig. 14).

9

10

CONCLUSIONS AND IMPLICATIONS

The light-response parameters of nonforest terrestrial ecosystems have a wide range of variability, from relatively low values of photosynthetic capacity ($A_{max} = 0.2 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in drought-stressed grasslands), quantum yield ($\alpha = 5 \text{ mmol mol}^{-1}$ in deserts), daytime ecosystem respiration ($r_d = 0.04 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in drought-stressed sagebrush steppe), and gross ecological light-use efficiency ($\epsilon = 2.6 \text{ mmol mol}^{-1}$ in sedge and tussock tundras of Alaska), to the highest values ever recorded for terrestrial ecosystems (intensively managed grasslands and agricultural crops: $A_{max} = 3.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $\alpha = 75 \text{ mmol mol}^{-1}$, $r_d = 0.50 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $\epsilon = 59 \text{ mmol mol}^{-1}$). Under optimal conditions, gross primary productivity in nonforest terrestrial ecosystems can surpass productivity of forests, with maximum rates of daily gross photosynthetic assimilation, $P_{g,max}$, achieving values greater $100 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ in intensive agricultural crops ($P_{g,max} = 116 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), while for forest ecosystems $P_{g,max}$ values remain below $100 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ (FLUXNET data base: www.fluxdata.org). Nevertheless, due to limitation by radiation, temperature, water, and nutrient resources, as well as management practices, maximum values of annual gross photosynthesis (GPP) of nonforest ecosystems estimated from flux-tower measurements remain below $10000 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, while in many types of forests they considerably exceeded this value (with maximum $GPP > 14000$ calculated for a tropical forest in French Guyana). The annual values of both GPP and RE for extensively and intensively managed grasslands, and shrubland/savanna ecosystems are nonlinearly related to annual precipitation, $PCPN$, and dryness index, $R_{net}/(\lambda*PCPN)$, indicating the potential sensitivity of these ecosystems to anthropogenic climate change.

1 The average annual net CO₂ exchange of our sample of 316 *NEE* values for
2 nonforest ecosystems indicates that on average, nonforest ecosystems act as net sinks for
3 atmospheric CO₂, with the highest rates of annual CO₂ uptake in agricultural crops (mean
4 $NEE_{crop} = 933 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) and intensively managed grasslands (mean $NEE_{grassint} =$
5 $848 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$). These data, based on continuous long-term flux-tower
6 measurements, confirm that grasslands and agricultural crops play a significant role in the
7 carbon budget and have high carbon sequestration potential (Lal et al. 1998; Follett et al.
8 2001; Follett and Schuman 2005). These findings directly contradict conclusions of
9 earlier authors (e.g., Smith and Faloon 2005; Conant et al. 2007 in SOCCR) about the
10 negative or nearly neutral role agroecosystems play in continental carbon budgets. These
11 earlier studies were based on C-inventory methods and did not utilize flux-tower
12 measurements. Clearly, further analyses are needed to determine the extent to which
13 flux-tower networks and the GIS and remote-sensing methods used to up-scale flux
14 measurements to the regional level are representative, and to support our conclusion
15 about the significant sink role of managed grasslands and intensive agricultural crops in
16 the carbon budget.

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FIGURES AND TABLES

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3 Figure 1. Geographical distribution of the 118 nonforest flux tower sites considered in
4 this study.

5

6 Figure 2. Major types of ecosystem light-response functions: A - linear, convexity $\theta = 1$
7 (corn crop, Bondville, IL, USA, 1999, day 188); B - nonrectangular hyperbolic,
8 convexity $0 < \theta < 1$ (soybeans, Rosemount, MN, USA, 2004, day 207); C - rectangular
9 hyperbolic, $\theta = 0$ (meadow bromegrass/alfalfa, Lacombe, Alberta, Canada, 2003, day
10 151); D - hysteresis (floodplain meadow, Cherskii, East Siberia, Russia, 2005, day 1900,
11 $k_T = 0.056 \text{ } ^\circ\text{C}^{-1}$).

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13 Figure 3. Light-temperature response surfaces fitted by modified nonrectangular equation
14 [4] for representative days for: A - Douulun steppe, China, 2006, day 218; B – Brookings
15 sown pasture, SD, USA, 2005, day 190; C – Howard wet-dry savanna, Australia, 2002,
16 day 34; and D – Rondonia tropical grassland, Brazil, 1999, day 270.

17

18 Figure 4. Scatter diagrams of maximum weekly values of light-response (α , A_{max} , $P_{g,max}$,
19 L_{max}), metabolic (r_d , $R_{e,max}$), and efficiency (ϵ , G_{max}) parameters for the pooled data set
20 including grasslands (extensively and intensively managed), shrublands and savannas,
21 wetlands, and croplands: A - α vs A_{max} ; B - r_d vs A_{max} ; C - ϵ vs A_{max} ; D - A_{max} vs L_{max} ; E -
22 $P_{g,max}$ vs A_{max} ; F - A_{max} vs G_{max} ; G - $R_{e,max}$ vs $P_{g,max}$; and H - $P_{g,max}$ vs L_{max} . Dashed lines

1 describe linear or allometric equations characterizing patterns of co-variation between
2 parameters.

3

4 Figure 5. Scatter diagrams of maximum weekly values of light-response (α , A_{max} , $P_{g,max}$,
5 L_{max}), metabolic (r_d , $R_{e,max}$), and efficiency (ϵ , G_{max}) parameters for the extensively
6 managed grasslands data subset: A - α vs A_{max} ; B - r_d vs A_{max} ; C - ϵ vs A_{max} ; D - A_{max} vs
7 L_{max} ; E - $P_{g,max}$ vs A_{max} ; F - A_{max} vs G_{max} ; G - $R_{e,max}$ vs $P_{g,max}$; and H - $P_{g,max}$ vs L_{max} .

8 Dashed lines describe linear or allometric equations characterizing patterns of co-
9 variation between parameters.

10

11 Figure 6. Seasonal dynamics of light-response parameters: maximum photosynthesis,
12 A_{max} , daytime ecosystem respiration, r_d , quantum yield, α , and gross ecological light-use
13 efficiency, ϵ , in selected nonforest ecosystems: A – floodplain meadow, Cherskii, 2003;
14 B – mixed prairie, Cottonwood, 2006; mixed prairie, Gudmundsen Ranch, 2006; D-
15 tallgrass prairie, Fort Reno, 2005; E – wet-dry savanna, Howard, 2002; F – tropical
16 grassland, Rondonia, 1999; G – sugar beet, Lonzee, 2004; H – corn crop, Bondville,
17 1999.

18

19 Figure 7. Seasonal dynamics and annual budgets of gross primary productivity, $P_g(t)$,
20 total ecosystem respiration, $R_e(t)$, and cumulative net ecosystem CO₂ exchange,
21 $CumNEE(t)$ for selected nonforest sites and years: A – floodplain meadow, Cherskii,
22 2003; B – sown northern temperate grassland, Jokioinen, 2001-2002; C – temperate
23 grassland, Grillenburg, 2005; D – desert grassland, Audubon Ranch, 2004; E - dry

1 savanna, Skukuza, 2002; F – tropical grassland, Rondonia, 1999; G – corn crop,
2 Bondville, 2003; H – soybean crop, Mead, 2002.

3

4 Figure 8. Frequency distributions of gross primary production (A), ecosystem respiration
5 (B), and net ecosystem CO₂ exchange (C) estimates in the pooled set site-years from
6 nonforest flux tower sites.

7

8 Figure 9. Scatter plot of *RE* versus *GPP* values for the pooled set of site-years from
9 nonforest flux tower stations of the world. The 1:1 diagonal is shown as a dashed line.

10

11 Figure 10. Scatter plots of the *RE* versus *GPP* values for various types of nonforest
12 ecosystems: A - extensively managed grasslands; B – intensively managed grasslands; C
13 – shrublands and savanna; D – wetlands; E – croplands.

14

15 Figure 11. Histograms of statistical distributions of the annual net ecosystem CO₂
16 exchange values (*NEE*) in various types of nonforest ecosystems: A - extensively
17 managed grasslands; B – intensively managed grasslands; C – shrublands and savanna; D
18 – wetlands; E – croplands.

19

20 Figure 12. Response of gross primary production, *GPP*, (A, C) and ecosystem
21 respiration, *RE*, (B, D) of extensively managed grasslands on the annual precipitation
22 *PCPN* (A, B) and the dryness index $DI = R_{net}/(\lambda*PCPN)$. The dashed lines indicate
23 nonlinear regressions describing predominant trends.

1

2 Figure 13. Response of gross primary production, *GPP*, (A, C) and ecosystem
3 respiration, *RE*, (B, D) of intensively managed grasslands on the annual precipitation
4 *PCPN* (A, B) and the dryness index $DI = R_{net}/(\lambda*PCPN)$. The dashed lines indicate
5 nonlinear regressions describing predominant trends.

6

7 Figure 14. Response of gross primary production, *GPP*, (A, C) and ecosystem
8 respiration, *RE*, (B, D) of shrublands and savanna on the annual precipitation *PCPN* (A,
9 B) and the dryness index $DI = R_{net}/(\lambda*PCPN)$. The dashed lines indicate nonlinear
10 regressions describing predominant trends.

11

12

13 Table 1. Nonforest flux tower sites analyzed in this study.

14

| Site | Latitude | Longitude | Elevation | PCPN | Tyear | Years | Investigator(s) | Method* |
|----------------------------------|----------|-----------|-----------|------|-------|-----------|--|---------|
| Croplands | | | | | | | | |
| Ames, IA, USA, corn | 41.720 | -93.410 | 300 | 814 | 8.9 | 2003 | J. Prueger | L |
| Auradé, France | 43.549 | 1.108 | 243 | 690 | 13.3 | 2005 | E. Ceschia, P. Beziat | T |
| Batavia-agro, IL, USA | 41.859 | -88.223 | 227 | 921 | 10.5 | 2005-2006 | R. Matamala; D. Cook | T |
| Bondville, IL, USA, corn | 40.006 | -88.292 | 300 | 990 | 11.3 | 1997-2005 | S. Hollinger; C. Bernacchi, T. Meyers | L |
| Bondville, IL, USA, soybeans | 40.006 | -88.292 | 300 | 990 | 11.3 | 1998-2006 | S. Hollinger; C. Bernacchi, T. Meyers | L |
| Bondville- companion, IL, USA | 40.006 | -88.292 | 219 | 990 | 11.3 | 2005-2006 | S. Hollinger; C. Bernacchi | T |
| Borgo Cioffi-crop, Italy | 40.524 | 14.957 | 20 | 490 | 19.0 | 2004-2006 | V. Magliulo | T |
| Cartow, Ireland | 52.859 | -6.918 | 59 | 824 | 9.4 | 2004-2006 | M. Jones; G. Lanigan | L |
| Doulun, China | 42.046 | 116.280 | 1350 | 399 | 3.3 | 2005-2006 | Shiping Chen | L |
| Foulum-crop, Denmark | 56.484 | 9.587 | 51 | 712 | 8.0 | 2005 | J. Olesen; K. Schelde C. Rebmann, W. | T |
| Gebesee, Germany | 51.100 | 10.914 | 162 | 492 | 9.6 | 2004-2006 | Kutsch | T |
| Grignon, France | 48.844 | 1.952 | 125 | 600 | 11.1 | 2005-2006 | P. Cellier | T |
| Haller, PA, USA | 48.860 | -77.840 | 352 | 974 | 9.7 | 2003 | R.H. Skinner | L |

| | | | | | | | | |
|--------------------------------------|--------|---------|-----|------|------|-----------|---------------------------------|---|
| Klingenberg, Germany | 50.893 | 13.222 | 480 | 850 | 7.0 | 2004-2006 | C. Bernhofer; T. Gruenwald | T |
| Lamasquère, France, irrigated | 43.493 | 1.237 | 180 | 690 | 13.3 | 2005 | E. Ceschia | T |
| Langerak, France | 52.004 | 4.806 | -1 | 786 | 9.8 | 2005-2006 | E. Moors, J. Elbers, W. Jans | T |
| Lonze, Belgium | 50.552 | 4.745 | 165 | 800 | 10.0 | 2004-2006 | C. Moureaux, M. Aubinet | L |
| Mase, Japan, paddy field | 36.054 | 140.027 | 13 | 1200 | 13.7 | 2002-2003 | A. Miyata | T |
| Mead, NE, USA, corn rainfed | 41.180 | -96.440 | 363 | 887 | 9.7 | 2001-2003 | S. Verma, A. Suyker | L |
| Meadm NE, USA, soybeans rainfed | 41.180 | -96.440 | 363 | 887 | 9.7 | 2002-2004 | S. Verma, A. Suyker | L |
| Mead, maize rotation irrigated | 41.165 | -96.470 | 362 | 887 | 9.7 | 2001-2003 | S. Verma, A. Suyker | T |
| Mead, NE, USA, corn irrigated | 41.165 | -96.477 | 361 | 728 | 10.1 | 2001-2004 | S. Verma, A. Suyker | T |
| Mead, NE, USA, soybeans irrigated | 41.165 | -96.470 | 362 | 728 | 10.1 | 2002-2004 | S. Verma, A. Suyker | T |
| Molenweg, Netherlands | 51.650 | 4.639 | 1 | 800 | 9.8 | 2005 | E. Moors, J. Elbers | T |
| Oensingen, Switzerland | 47.286 | 7.734 | 452 | 1100 | 9.0 | 2005 | N. Buchmann; W. Eugster | T |
| Ponca City, OK, USA, winter wheat | 36.767 | -97.133 | 310 | 866 | 14.8 | 1997 | S. Verma | L |
| Risbyholm, Denmark | 51.530 | 12.097 | 10 | 575 | 9.0 | 2004-2005 | H. Soegaard | T |
| Rosemount, MN, USA | 44.714 | -93.090 | 260 | 799 | 6.8 | 2004-2005 | T. Griffis, J. Baker | L |

Extensively managed grasslands

| | | | | | | | | |
|------------------------------|--------|----------|------|------|-------|-----------|-------------------------------------|---|
| Alinya, Spain | 42.202 | 1.449 | 1770 | 669 | 13.0 | 2003-2005 | M.J. Sanz | L |
| Amplero, Italy | 41.867 | 13.633 | 884 | 1365 | 10.0 | 2003-2005 | M. Balzarolo | L |
| Atquasuk, AK, USA | 70.470 | -157.409 | N/A | 127 | NA? | 1999-2006 | W. Oechel | T |
| Audubon Ranch, AZ, USA | 31.591 | -110.510 | 985 | 382 | 16.0 | 2002-2006 | T. Meyers | L |
| Barrow, AK, USA | 71.323 | -156.626 | 1 | 124 | -12.5 | 1998-2002 | W. Oechel | T |
| Batavia Prairie, IL, USA | 41.841 | -88.241 | 226 | 921 | 10.5 | 2005-2006 | R. Matamala | L |
| Bily Kriz, Czech Republic | 49.495 | 18.545 | 855 | 1200 | 5.5 | 2004-2006 | M. Marek, R. Czerny | T |
| Brookings, SD, USA | 44.311 | -96.798 | 495 | 550 | 5.8 | 2004-2006 | T. Meyers, T. Gilmanov, M. Heuer | L |
| Bugacpuszta, Hungary | 46.800 | 18.900 | 100 | 500 | 10.8 | 2003-2006 | Z. Tuba, | L |
| Canaan Valley, WV, USA | 39.063 | -79.421 | 988 | 900 | 8.2 | 2004 | T. Meyers | L |
| Cheyenne, WY, USA | 41.183 | -104.900 | 1910 | 397 | 7.2 | 1997-1998 | J. Morgan | L |
| Cottonwood, SD, USA | 43.950 | -101.847 | 735 | 447 | 7.7 | 2004-2006 | T. Meyers, A. Detwyler, K. Brehe | L |
| CPER, CO, USA | 40.683 | -104.750 | 1660 | 332 | 9.2 | 2001-2004 | J. Morgan | L |
| Doulun, China | 42.047 | 116.284 | 1350 | 399 | 3.3 | 2006 | Shiping Chen | L |
| Duke grassland, NC, USA | 35.971 | -79.090 | 163 | 1145 | 15.5 | 2001-2005 | G. Katul | L |
| Fort Peck, MT, USA | 48.308 | -105.101 | 634 | 310 | 7.7 | 2000-2006 | T. Meyers | L |
| Fort Reno, OK, USA | 35.557 | -98.017 | 421 | 870 | 14.9 | 2005 | M. Torn, D. Billesbach | L |
| Freeman Ranch, TX, USA | 29.930 | -98.010 | 244 | 959 | 19.4 | 2004 | J. Heilman | L |

| | | | | | | | | |
|-----------------------------------|---------|----------|------|------|------|-----------|---|---|
| Goodwin Creek, MS, USA | 34.250 | -89.970 | 70 | 1455 | 15.7 | 2002-2006 | T. Meyers | L |
| Grillenburg, Germany | 50.951 | 13.514 | 400 | 853 | 7.2 | 2004-2006 | C. Bernhofer, T. Gruenwald | L |
| Gudmundsen Ranch, NE, USA | 42.069 | -101.407 | 1081 | 560 | 7.9 | 2006 | D. Billesbach | L |
| Haibei, China | 37.617 | 101.317 | 3250 | 561 | -1.7 | 2002-2003 | T. Kato | T |
| Ivotuk, Alaska | 68.486 | -155.750 | 550 | 250 | -9.0 | 2004-2006 | W. Oechel W. Dugas, P. Mielnick | T |
| Jornada, NM, USA | 32.600 | -106.750 | 1320 | 272 | N/A | 2000-2001 | M. Nasyrov, N. Saliendra | L |
| Karnap, Uzbekistan | 40.000 | 65.500 | 310 | 237 | 14.6 | 2001 | Saliendra | L |
| Kendall, AZ, USA | 31.737 | -109.942 | 1531 | 356 | 17.0 | 1999-2006 | W. Emmerich | L |
| Khakasia, Russia | 54.773 | 90.002 | 430 | 304 | 0.5 | 2002-2004 | L. Belelli | L |
| Khakasia-3, Russia | 54.705 | 89.078 | N/A | N/A | N/A | 2004 | L. Belelli | T |
| Kherlenbayan, Mongolia | 47.214 | 108.737 | 1235 | 196 | 1.2 | 2003 | S. Li J.-F. Soussana, V. Allard | L |
| Laqueuille, France | 45.643 | 2.736 | 1040 | 1013 | 8.6 | 2002-2006 | Allard | L |
| Lethbridge, Canada | 49.709 | -112.940 | 960 | 378 | 6.4 | 1998-2002 | L. Flanagan | L |
| Little Washita, OK, USA | 34.967 | -97.983 | 335 | 750 | 16.3 | 1997-1998 | T. Meyers | L |
| Malga Arpaco, Italy | 46.117 | 11.703 | 1699 | 1200 | 6.3 | 2003-2004 | A. Raschi | L |
| Mandan, ND, USA | 46.767 | -100.917 | 518 | 404 | 5.0 | 1999-2001 | A. Frank | L |
| Matra, Hungary | 47.842 | 19.726 | 350 | 605 | 10.6 | 2004-2005 | J. Balogh | T |
| Miles City, MT, USA | 46.300 | -105.967 | 719 | 343 | 7.9 | 2000-2001 | M. Haferkamp | L |
| Monte Bondone, Italy | 46.016 | 11.047 | 1550 | 1189 | 5.5 | 2003-2006 | D. Gianelle | T |
| Neal Smith, IA, USA | 41.558 | -93.296 | 280 | 826 | 9.1 | 2005 | J. Prueger | L |
| Neustift, Austria | 47.117 | 11.317 | 970 | 850 | 6.3 | 2001-2006 | G. Wohlfahrt | L |
| Oensingen, Switzerland | 47.283 | 7.733 | 450 | 1100 | 9.0 | 2002-2003 | C. Ammann, J. Fuhrer | L |
| Rannels Ranch, KS, USA | 39.139 | -96.523 | 324 | 840 | 12.9 | 1998-1999 | C. Owensby | L |
| Rigi-Seebodenalp, Switzerland | 47.058 | 8.457 | 1025 | 1327 | 7.3 | 2003 | W. Eugster, N. Rogiers M. Waterloo, A. Manzi | L |
| Rondonia, Brazil | -10.762 | -62.357 | 306 | 1664 | 23.9 | 1999 | Manzi | L |
| Santarem, Brazil | -3.012 | -54.537 | N/A | N/A | N/A | 2001-2002 | D. Fitzjarrald | L |
| Shidler, OK, USA | 36.933 | -96.683 | 356 | 942 | 14.8 | 1997-1999 | S. Verma, A. Suyker K. Akshalov, N. Saliendra, D. A. Johnson | L |
| Shortandy, Kazakhstan | 51.667 | 71.000 | 367 | 323 | 1.6 | 1998-2001 | W. Dugas, P. Mielnick | L |
| Temple, TX, USA | 31.100 | -97.333 | 219 | 878 | 19.6 | 1998-1999 | Mielnick | L |
| Tojal, Portugal | 38.477 | -8.025 | 190 | 750 | 15.5 | 2004-2006 | C. Pio, L. Aires | L |
| Viara Ranch, CA, USA | 38.407 | -120.951 | 129 | 500 | 15.9 | 2001-2006 | D. Baldocchi | L |
| Walnut River, KS, USA | 37.521 | -96.855 | 408 | 1030 | 13.1 | 2002-2004 | R. Coulter, D. Cook | L |
| Woodward, OK, USA | 36.600 | -99.583 | 630 | 586 | 14.3 | 1997-2002 | P. Sims, J. Bradford | L |
| Xilinhot grazed, China | 43.554 | 116.671 | 1250 | 360 | 2.0 | 2006 | Shiping Chen | L |
| Xilinhot-fenced, China | 43.546 | 116.678 | 1250 | 360 | 2.0 | 2006 | Shiping Chen | T |
| Xilinhot-typical fenced, China | 44.134 | 116.329 | 1030 | 290 | 2.0 | 2004-2006 | Guangsheng Zhou | T |

| Intensively managed grasslands | | | | | | | | |
|---------------------------------------|---------|----------|------|------|-------|-----------|---|---|
| Cabauw- extension. The Netherlands | 51.954 | 4.903 | -1 | 786 | 9.8 | 2005 | E. Moors, J. Elbers | T |
| Cabauw, The Netherlands | 51.967 | 4.917 | -1 | 800 | 10.0 | 2003 | A. Hensen | T |
| Cabauw, The Netherlands | 51.971 | 4.927 | -1 | 786 | 9.8 | 2004-2006 | E. Moors, J. Elbers | T |
| Carlow-grassland, Ireland | 52.850 | -6.900 | 50 | 804 | 10.1 | 2003 | M. Jones, G. Lanigan | L |
| Dripsey-grass, Ireland | 51.919 | -8.751 | 187 | 1450 | 9.5 | 2002-2005 | G. Kiely, P. Leahy | T |
| Easter Bush, UK | 55.867 | -3.200 | 190 | 890 | 8.0 | 2003-2004 | M. Sutton | L |
| Haarweg, The Netherlands | 51.970 | 5.630 | 7 | 760 | 9.5 | 2002 | A. Jacobs | T |
| Haastrect, Netherlands | 52.004 | 4.806 | -2 | 786 | 9.8 | 2003 | E. Moors | T |
| Haller, PA, USA | 40.862 | -77.840 | 352 | 974 | 9.7 | 2003-2005 | R.H. Skinner | L |
| Hegihátsál, Hungary | 46.950 | 16.650 | 248 | 759 | 8.9 | 1999 | Z. Barcza, L. Haszpra | T |
| Horstermeer, Netherlands | 52.029 | 5.068 | -2 | 797 | 9.8 | 2004-2006 | H. Dolman | T |
| Jokioinen, Finland | 60.899 | 23.514 | 104 | 581 | 3.9 | 2002 | A. Lohila, T. Laurila | L |
| Lacombe, Canada | 52.436 | -113.808 | 871 | 446 | 2.1 | 2003 | V.S. Baron J.-F. Soussana, V. Allard | L |
| Laqueuille, France | 45.643 | 2.736 | 1040 | 1013 | 8.6 | 2002-2006 | | L |
| Lelystad, The Netherlands | 52.500 | 5.500 | 0 | 780 | 10.0 | 2004 | A. Hensen | L |
| Lille Valby, Denmark | 55.700 | 12.117 | 15 | 1119 | 8.5 | 2004-2006 | E. Dellwik C. Ammann; J. Fuhrer | L |
| Oensingen, Switzerland | 47.283 | 7.733 | 450 | 1100 | 9.0 | 2002-2006 | | L |
| Shrublands and savanna | | | | | | | | |
| Burns, OR, USA | 43.483 | -119.717 | 1380 | 283 | 7.6 | 1995-2001 | T. Svejcar N. Saliendra, D.A. Johnson | L |
| Dubois, ID, USA | 44.267 | -112.133 | 1700 | 302 | 6.2 | 1996-2001 | | L |
| Howard Springs, Australia | -12.329 | 131.000 | 38 | 1824 | 25.9 | 2002-2005 | J. Berringer M. Dourikov, N. Saliendra, D.A. Johnson | L |
| Karrykul, Turkmenistan | 38.600 | 58.400 | 90 | 148 | 15.6 | 1998-2000 | | L |
| Kubuqi, China | 40.381 | 108.549 | 1160 | 180 | 7.5 | 2006 | Shiping Chen | L |
| Santa Rita, AZ, USA | 31.821 | -110.866 | 1120 | 330 | 17.6 | 2004-2006 | R. Scott | T |
| Sao Paulo, Brazil | -21.619 | -47.650 | N/A | 953 | N/A | 2001-2002 | H. da Rocha | T |
| Skukuza, South Africa | -24.983 | 31.600 | 263 | 561 | 21.6 | 2001-2003 | N. Hanan | L |
| Sky Oaks, CA, USA, old stand | 33.374 | -116.623 | 1394 | 491 | 12.2 | 1997-2006 | W. Oechel | L |
| Sky Oaks, CA, USA, young stand | 33.377 | -116.623 | 1429 | 491 | 12.2 | 1997-2001 | W. Oechel | T |
| Tonzi Ranch, CA, USA | 38.432 | -120.966 | 177 | 559 | 15.4 | 2002-2006 | D. Baldocchi | T |
| Wetlands | | | | | | | | |
| Cherskii, Russia | 68.615 | 161.339 | 4 | 200 | -12.5 | 2003-2004 | C. Corradi | T |
| CzechWet, Czech Republic | 49.025 | 14.772 | 420 | 740 | 7.2 | 2006 | M. Marek; D. Janous Bin Zhao; Guo | T |
| Dongtan marsh-1, China | 31.517 | 121.961 | 31 | 2192 | 15.7 | 2005 | Haiquang | T |
| Dongtan marsh-2, | 31.585 | 121.903 | 31 | 2074 | 15.7 | 2005 | Bin Zhao; Guo | T |

| | | | | | | | | |
|---------------------------|--------|---------|-----|------|------|-----------|------------------------|---|
| China | | | | | | | Haiquang | |
| Dongtan marsh-3, China | 31.517 | 121.972 | 31 | 1957 | 15.5 | 2005 | Bin Zhao; Guo Haiquang | T |
| Kaamanen wetland, Finland | 69.141 | 27.295 | 155 | 395 | -1.3 | 2000-2006 | T. Laurila; M. Aurela | T |
| PolWet, Poland | 52.762 | 16.309 | 54 | 550 | 8.1 | 2004 | J. Olejnik | T |
| Siikaneva, Finland | 61.833 | 24.193 | N/A | 713 | 3.0 | 2004-2006 | M. Aurela | T |
| Tadham Moore, UK | 51.207 | -2.829 | 3 | 750 | 11.1 | 2001 | R. Harding | T |

1
2 * Method on net flux partitioning into photosynthesis and respiration: L – light-response
3 function analysis; T – nighttime temperature dependence.

4

5

6 Table 2. Parameters α , A_{max} , r_d , and θ from the nonrectangular hyperbolic light-response

7 function $F_C(Q) = \frac{1}{2\theta} \left(\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max} \theta Q} \right) - r_d$, for representative

8 days at the Bondville, Rosemount, Lacombe, and Brookings flux tower stations.

9

| Statistical characteristics | Parameters | | | |
|---|--|--|--|--------------------------------------|
| | Slope, α mg CO ₂ μmol^{-1} | Plateau, A_{max} mg CO ₂ m ⁻² s ⁻¹ | Respiration, r_d mg CO ₂ m ⁻² s ⁻¹ | Convexity, θ dimensionless |
| A. Corn crop, Bondville, IL, USA, 1999, day 188 $R^2 = 0.98$; SE = 0.158 mg CO ₂ m ⁻² s ⁻¹ | | | | |
| Estimate | 0.0014 | 3.2 | 0.1936 | 1.0 |
| Standard Error | 0.0001 | - | 0.0423 | 0.0012 |
| Student's t | 19.92 | - | 4.58 | 84.20 |
| p -level | 0.0000 | - | 0.0000 | 0.0000 |
| Soybeans, Rosemount, MN, USA, 2004, day 207 $R^2 = 0.98$; SE = 0.045 mg CO ₂ m ⁻² s ⁻¹ | | | | |
| Estimate | 0.0009 | 0.9930 | 0.2002 | 0.6947 |
| Standard Error | 0.0002 | 0.1899 | 0.0221 | 0.3329 |
| Student's t | 4.77 | 5.23 | 9.07 | 2.09 |
| p -level | 0.0000 | 0.0000 | 0.0000 | 0.0243 |
| Sown pasture, Lacombe, Alberta, Canada, 2003, day 151 $R^2 = 0.94$; SE = 0.061 mg CO ₂ m ⁻² s ⁻¹ | | | | |

| | | | | |
|--------------------|--------|--------|--------|-----|
| Estimate | 0.0026 | 0.8321 | 0.3413 | 0.0 |
| Standard Error | 0.0009 | 0.0969 | 0.0273 | - |
| Student's <i>t</i> | 2.98 | 8.58 | 12.50 | - |
| <i>p</i> -level | 0.0023 | 0.0000 | 0.0000 | - |

Floodplain meadow, Cherskii, East Siberia, Russia, 2003, day 214

$R^2 = 0.93$; SE = 0.033 mg CO₂ m⁻² s⁻¹

| | | | | |
|--------------------|--------|--------|--------|--------|
| Estimate | 0.0006 | 0.2987 | 0.1038 | 0.9333 |
| Standard Error | 0.0001 | 0.0252 | 0.090 | 0.090 |
| Student's <i>t</i> | 5.31 | 11.85 | 11.58 | 10.38 |
| <i>p</i> -level | 0.0000 | 0.0000 | 0.0000 | 0.0000 |

1

2

3 Table 3. Parameters α , A_{max} , r_0 , k_T and θ from the modified nonrectangular hyperbolic

4 light-temperature response function

$$5 \quad F_c(Q, T_s) = \frac{1}{2\theta} \left(\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max}\theta Q} \right) - r_0 e^{k_T T_s}, \text{ for}$$

6 representative days at Douulun, Brookings, Howard, and Rondonia sites.

7

| Statistical characteristics | Parameters | | | | |
|--|--|--|--|--|--------------------------------------|
| | Slope, α mg CO ₂ μmol^{-1} | Plateau, A_{max} mg CO ₂ m ⁻² s ⁻¹ | Respiration, r_0 mg CO ₂ m ⁻² s ⁻¹ | Temperature coefficient, k_T , (°C) ⁻¹ | Convexity, θ dimensionless |
| A. Steppe, Douulun, China, 2006, day 218 | | | | | |
| $R^2 = 0.98$; SE = 0.037 mg CO ₂ m ⁻² s ⁻¹ | | | | | |
| Estimate | 0.0009 | 0.5542 | 0.0377 | 0.0671 | 0.9644 |
| Standard Error | 0.00001 | 0.0241 | 0.0102 | 0.0116 | 0.0408 |
| Student's <i>t</i> | 9.08 | 22.98 | 3.68 | 5.78 | 23.64 |
| <i>p</i> -level | 0.0000 | 0.0000 | 0.0003 | 0.0000 | 0.0000 |
| B. Sown pasture, Brookings, SD, USA, 2005, day 190 | | | | | |
| $R^2 = 0.99$; SE = 0.032 mg CO ₂ m ⁻² s ⁻¹ | | | | | |
| Estimate | 0.0014 | 1.0867 | 0.0631 | 0.0614 | 0.0000 |
| Standard Error | 0.0001 | 0.0498 | 0.0141 | 0.0094 | 0.0000 |
| Student's <i>t</i> | 13.87 | 21.81 | 4.48 | 6.53 | - |
| <i>p</i> -level | 0.0000 | 0.0000 | 0.0000 | 0.0000 | - |
| C. Wet-dry savanna, Howard, Australia, 2002, day 34 | | | | | |
| $R^2 = 0.97$; SE = 0.074 mg CO ₂ m ⁻² s ⁻¹ | | | | | |
| Estimate | 0.0017 | 1.147 | 0.0278 | 0.0690 | 0.8376 |
| Standard Error | 0.0003 | 0.1019 | 0.0167 | 0.0186 | 0.1529 |
| Student's <i>t</i> | 5.83 | 11.25 | 1.67 | 3.71 | 5.48 |

| | | | | | |
|--|--------|--------|--------|--------|--------|
| <i>p</i> -level | 0.0000 | 0.0000 | 0.0522 | 0.0004 | 0.0000 |
| D. Tropical grassland, Rondonia, Brazil, 1999, day 270 | | | | | |
| $R^2 = 0.97$; SE = 0.052 mg CO ₂ m ⁻² s ⁻¹ | | | | | |
| Estimate | 0.0008 | 0.8048 | 0.0339 | 0.0760 | 0.9902 |
| Standard Error | 0.0001 | 0.0721 | 0.0183 | 0.0217 | 0.0230 |
| Student's <i>t</i> | 9.38 | 11.16 | 1.85 | 3.50 | 43.04 |
| <i>p</i> -level | 0.0000 | 0.0000 | 0.0408 | 0.0014 | 0.0000 |

1 * Not significantly different from zero

2

3 Table 4. Statistical characteristics of annual gross primary production (*GPP*), total
 4 ecosystem respiration (*RE*), and net ecosystem exchange (*NEE*) for major groups within
 5 nonforest terrestrial ecosystems.

6

| Statistical characteristics | Ecosystem group | | | | |
|--|--------------------------------|--------------------------------|------------------------|----------|-----------|
| | Grasslands extensively managed | Grasslands intensively managed | Shrublands and savanna | Wetlands | Croplands |
| Gross primary production, <i>GPP</i> (g CO ₂ m ⁻² yr ⁻¹) | | | | | |
| Number of site-years | 179 | 34 | 28 | 48 | 66 |
| Mean | 2708 | 5767 | 2949 | 2328 | 4521 |
| Standard deviation | 1842 | 1144 | 1950 | 1836 | 1365 |
| Minimum | 95 | 3141 | 645 | 749 | 1376 |
| Maximum | 8600 | 7720 | 6836 | 5643 | 6774 |
| Total ecosystem respiration, <i>RE</i> (g CO ₂ m ⁻² yr ⁻¹) | | | | | |
| Number of site-years | 169 | 34 | 27 | 18 | 66 |
| Mean | 2535 | 4990 | 2537 | 1824 | 3588 |
| Standard deviation | 1689 | 1024 | 1396 | 1373 | 909 |
| Minimum | 112 | 3186 | 756 | 665 | 1052 |
| Maximum | 7880 | 7003 | 5094 | 4751 | 5905 |
| Net Ecosystem Exchange, <i>NEE</i> (g CO ₂ m ⁻² yr ⁻¹) | | | | | |
| Number of site-years | 169 | 36 | 27 | 18 | 66 |
| Mean | 239 | 848 | 493 | 504 | 933 |
| Standard deviation | 521 | 658 | 740 | 719 | 814 |
| Minimum | -1342 | -961 | -585 | -40 | -770 |
| Maximum | 1762 | 2934 | 2254 | 2226 | 2382 |

7

8

9 Table 5. Maximum values of daytime gross primary productivity, $P_{g,max}$, and annual net
 10 primary production, *GPP*, estimated for nonforest and forest flux-tower sites

| Site | Year | $P_{g,max}$ | Site | Year | <i>GPP</i> |
|------|------|-------------|------|------|------------|
|------|------|-------------|------|------|------------|

| | | $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ | | | $\text{g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ |
|------------------------------------|------|---|------------------------------------|------|--|
| A. Grasslands extensively managed | | | | | |
| Neustift, Austria | 2004 | 76.2 | Rondonia, Brazil | 1999 | 8600 |
| Jornada, NM, USA | 2000 | 63.1 | Neustift, Austria | 2006 | 7415 |
| Rannels Ranch, KS, USA | 1998 | 60.8 | Goodwin Creek, MS, USA | 2004 | 6391 |
| Batavia Prairie Site, IL, USA | 2006 | 59.9 | Grillenburg, Germany | 2005 | 6299 |
| Grillenburg, Germany | 2005 | 57.34 | Duke grassland, NC, USA | 2003 | 6039 |
| Monte Bondone, Italy | 2006 | 56.9 | Laqueuille, France, extensive | 2006 | 5943 |
| Shidler, OK, USA | 1999 | 56.9 | Neal Smith, IA, USA | 2005 | 5756 |
| Temple, TX, USA | 1999 | 56.2 | Batavia Prairie Site, IL, USA | 2006 | 5435 |
| Oensingen, Switzerland | 2003 | 53.6 | Oensingen, Switzerland | 2003 | 5326 |
| Neal Smith, IA, USA | 2005 | 52.7 | Laqueuille, France, extensive | 2004 | 5322 |
| Laqueuille, France, extensive | 2004 | 51.7 | Rigi-Seebodenalp, Switzerland | 2003 | 5320 |
| Goodwin Creek, MS, USA | 2003 | 51.4 | Shidler, OK, USA | 1997 | 5208 |
| B. Grasslands intensively managed | | | | | |
| Cabauw- extension. The Netherlands | 2005 | 76.3 | Oensingen, Switzerland | 2004 | 7720 |
| Easter Bush, UK | 2003 | 63.6 | Dripsey-grass, Ireland | 2004 | 7388 |
| Oensingen, Switzerland | 2004 | 63.5 | Haastrect, Netherlands | 2003 | 7267 |
| Lille Valby, Denmark | 2006 | 63.4 | Lille Valby, Denmark | 2004 | 6873 |
| Haastrect, Netherlands | 2003 | 63.1 | Laqueuille, France, intensive | 2004 | 6838 |
| Laqueuille, France, intensive | 2006 | 59.0 | Carlow-grassland, Ireland | 2003 | 6807 |
| Carlow-grassland, Ireland | 2003 | 57.9 | Easter Bush, UK | 2003 | 6793 |
| Haarweg, The Netherlands | 2002 | 57.5 | Cabauw- extension. The Netherlands | 2005 | 6785 |
| Dripsey-grass, Ireland | 2003 | 54.7 | Haarweg, The Netherlands | 2002 | 5915 |
| Lacombe, Alberta, Canada | 2003 | 53 | Hegihátsál, Hungary | 1999 | 5867 |
| Haller, State College, PA, USA | 2004 | 52.2 | Cabauw, The Netherlands | 2004 | 5837 |
| Cabauw, The Netherlands | 2004 | 47.9 | Horstermeer, Netherlands | 2006 | 5337 |
| C. Shrubs and savannas | | | | | |
| Howard Springs, Australia | 2005 | 54.2 | Sao Paulo cerrado, Brazil | 2002 | 6836 |
| Sao Paulo cerrado, Brazil | 2002 | 42.7 | Howard Springs, Australia | 2002 | 5874 |
| Tonzi Ranch, California | 2005 | 38.6 | Skukuza, South Africa | 2001 | 3947 |
| Skukuza, South Africa | 2001 | 34.6 | Tonzi Ranch, CA, USA | 2005 | 3837 |

| | | | | | |
|-------------------------------|------|------|-------------------------------|------|------|
| Tonzi Ranch, California | 2003 | 34.1 | Sky Oaks Old stand, CA, USA | 1997 | 2682 |
| Sky Oaks Young stand, CA, USA | 1998 | 22.7 | Sky Oaks Young stand, CA, USA | 1998 | 2021 |
| Sky Oaks Old stand, CA, USA | 1997 | 21.0 | Skukuza, South Africa | 2003 | 1873 |
| Santa Rita mesquite, AZ, USA | 2005 | 19.8 | Santa Rita mesquite, AZ, USA | 2005 | 1125 |
| Kubuqi, shrubland, China | 2006 | 12.8 | Kubuqi, shrubland, China | 2006 | 1021 |
| Karrykul, Turkmenistan | 2000 | 7.79 | Karrykul, Turkmenistan | 2000 | 769 |

D. Wetlands

| | | | | | |
|---------------------------|------|------|---------------------------|------|------|
| Dongtan marsh-2, China | 2005 | 70.1 | Dongtan marsh-2, China | 2005 | 5643 |
| CzechWet, Czech Republic | 2006 | 56.9 | CzechWet, Czech Republic | 2006 | 5368 |
| Dongtan marsh-1, China | 2005 | 51.9 | Dongtan marsh-1, China | 2005 | 5150 |
| Dongtan marsh-3, China | 2005 | 43.3 | Tadham Moore, UK | 2001 | 4767 |
| Tadham Moore, UK | 2001 | 41.1 | Dongtan marsh-3, China | 2005 | 3662 |
| PolWet, Poland | 2005 | 41.1 | PolWet, Poland | 2005 | 3393 |
| Cherskii, Russia | 2003 | 20.1 | Siikaneva, Finland | 2005 | 1359 |
| Kaamanen wetland, Finland | 2005 | 19.8 | Kaamanen wetland, Finland | 2005 | 1210 |
| Siikaneva, Finland | 2004 | 19.8 | Cherskii, Russia | 2003 | 834 |

E. Croplands

| | | | | | |
|--------------------------------------|------|--------------|-------------------------------------|------|------|
| Mead, corn rot. irrigated, NE, USA | 2001 | 116.1 | Langerak-crop, France | 2005 | 6774 |
| Mead, maize cont. irrigated, NE, USA | 2001 | 107.8 | Mead, rot. corn irrigated, NE, USA | 2003 | 6720 |
| Bondville, corn, IL, USA | 1999 | 99.9 | Borgo Cioffi-crop, Italy | 2005 | 6513 |
| Batavia-agro, IL, USA | 2006 | 99.0 | Mead, cont. corn irrigated, NE, USA | 2001 | 6437 |
| Bondville, corn, IL, USA | 1999 | 94.1 | Borgo Cioffi-crop, Italy | 2006 | 6393 |
| Borgo Cioffi-crop, Italy | 2006 | 93.1 | Mead, maize rotation irrigated | 2001 | 6316 |
| Mead, corn rainfed, NE, USA | 2003 | 87.6 | Lonzee, Belgium, sugar beet | 2005 | 6313 |
| Langerak-crop, France | 2006 | 87.5 | Oensingen-crop, Switzerland | 2005 | 6295 |
| Bondville-companion, IL, USA | 2006 | 83.03 | Mead corn rainfed, NE, USA | 2001 | 5834 |
| Grignon-crop, France | 2005 | 81.3 | Bondville, corn, IL, USA | 1999 | 5602 |
| Lonzee, winter wheat, Belgium | 2005 | 80.5 | Bondville, soybeans, IL, USA | 2005 | 5582 |
| Bondville, soybeans, IL, USA | 2005 | 80.1 | Risbyholm, Denmark, crop | 2004 | 5525 |

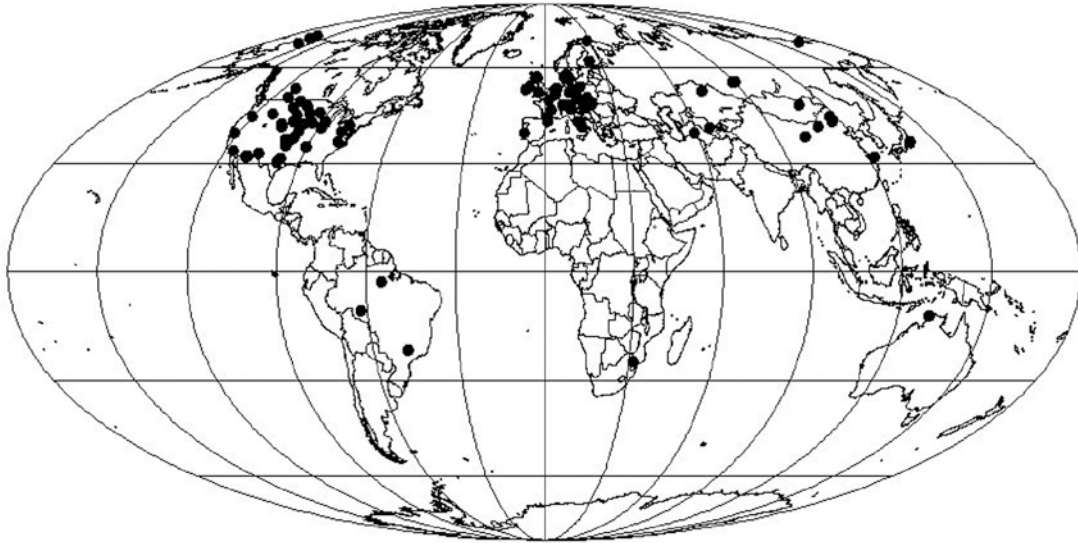
F. Forests and plantations

| | | | | | |
|--|------|-------------|-------------------------|------|--------------|
| Duke Forest Loblolly Pine, NC, USA | 2001 | 99.0 | French Guyana | 2004 | 14339 |
| Campbell River, British Columbia, Canada | 1998 | 86.6 | Vanuatu - CocoFlux | 2002 | 13057 |
| Hampshire Forest, UK | 2004 | 73.9 | Rondonia forest, Brazil | 2002 | 12727 |
| Duke Forest Loblolly Pine | 2005 | 69.0 | Palangkaraya, Indonesia | 2003 | 12236 |

| | | | | | |
|--|------|-------|--|------|-------|
| Vanuatu - CocoFlux | 2003 | 68.2 | Santarem km67 primary forest, Brazil | 2003 | 11703 |
| Duke Forest Hardwood, NC, USA | 2003 | 67.6 | Caxiuana Forest-Almeirim, Brasil | 2002 | 11436 |
| French Guyana | 2005 | 64.21 | Santarem km67 primary forest, Brazil | 2002 | 11271 |
| Rondonia forest, Brazil | 2002 | 60.8 | Loblolly Pine plantation, NC, USA | 2006 | 10173 |
| Campbell River, British Columbia, Canada | 2000 | 60.1 | Donaldson Slash Pine Plantation, FL, USA | 1999 | 9249 |
| Loblolly Pine plantation, NC, USA | 2006 | 59.7 | Campbell River, British Columbia, Canada | 2005 | 9162 |
| Duke Forest Hardwood, NC, USA | 2004 | 57.5 | Duke Forest Loblolly Pine, NC, USA | 2002 | 9067 |
| Donaldson Slash Pine Plantation, FL, USA | 1999 | 54.6 | Duke Forest Hardwood, NC, USA | 2003 | 8892 |

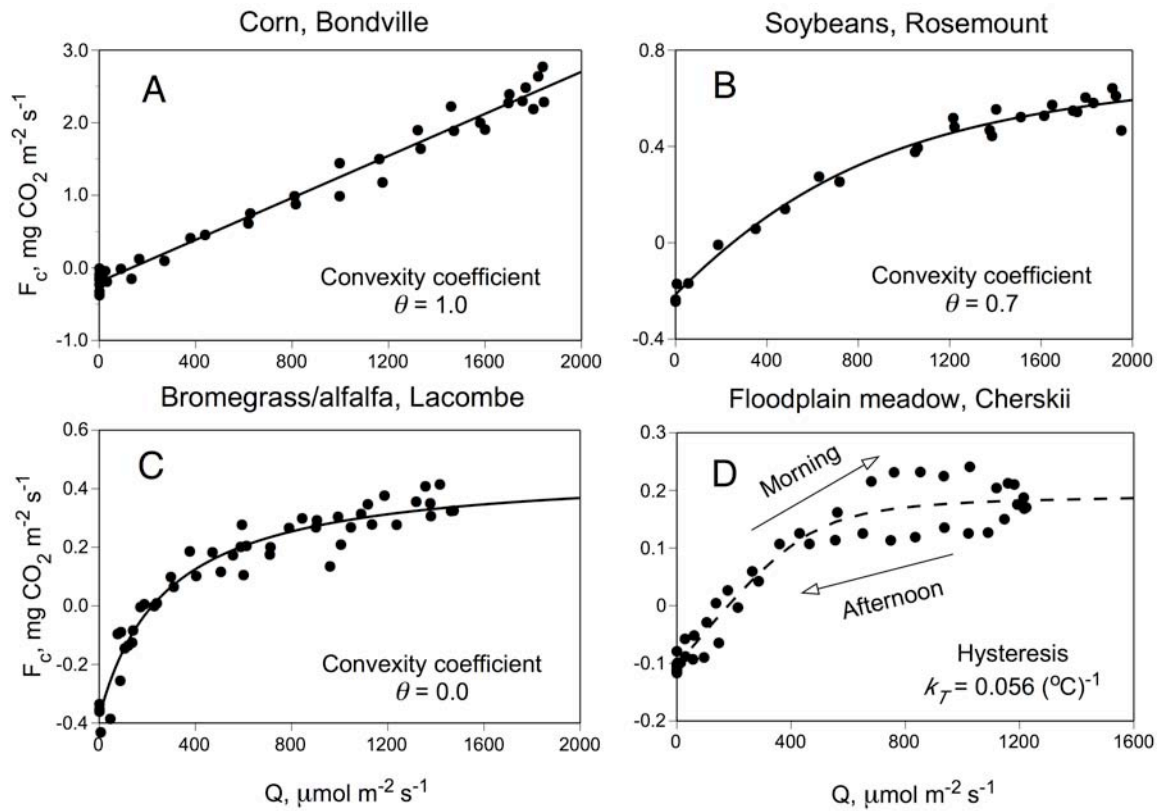
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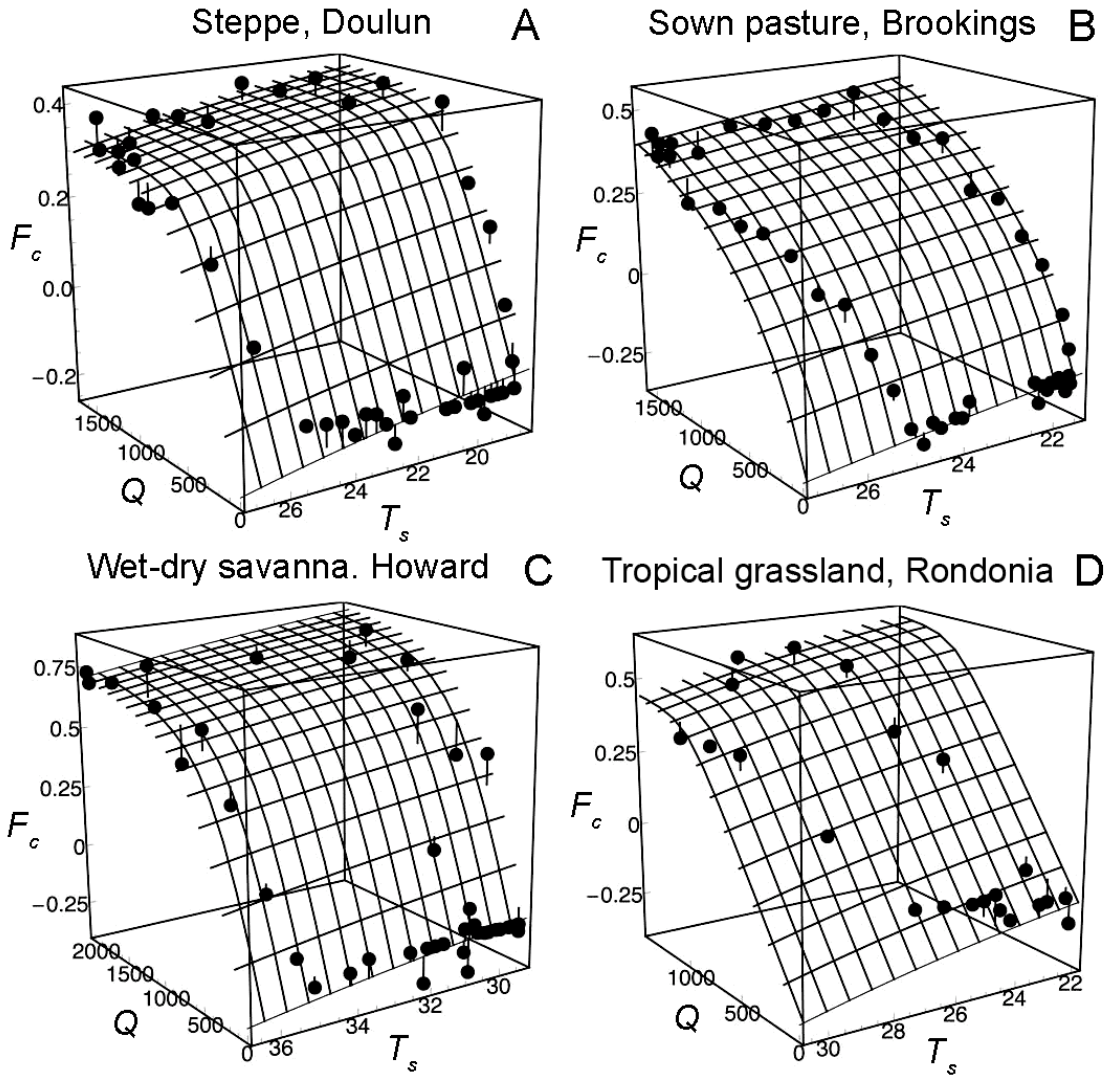
2 **Figure 1.**



3

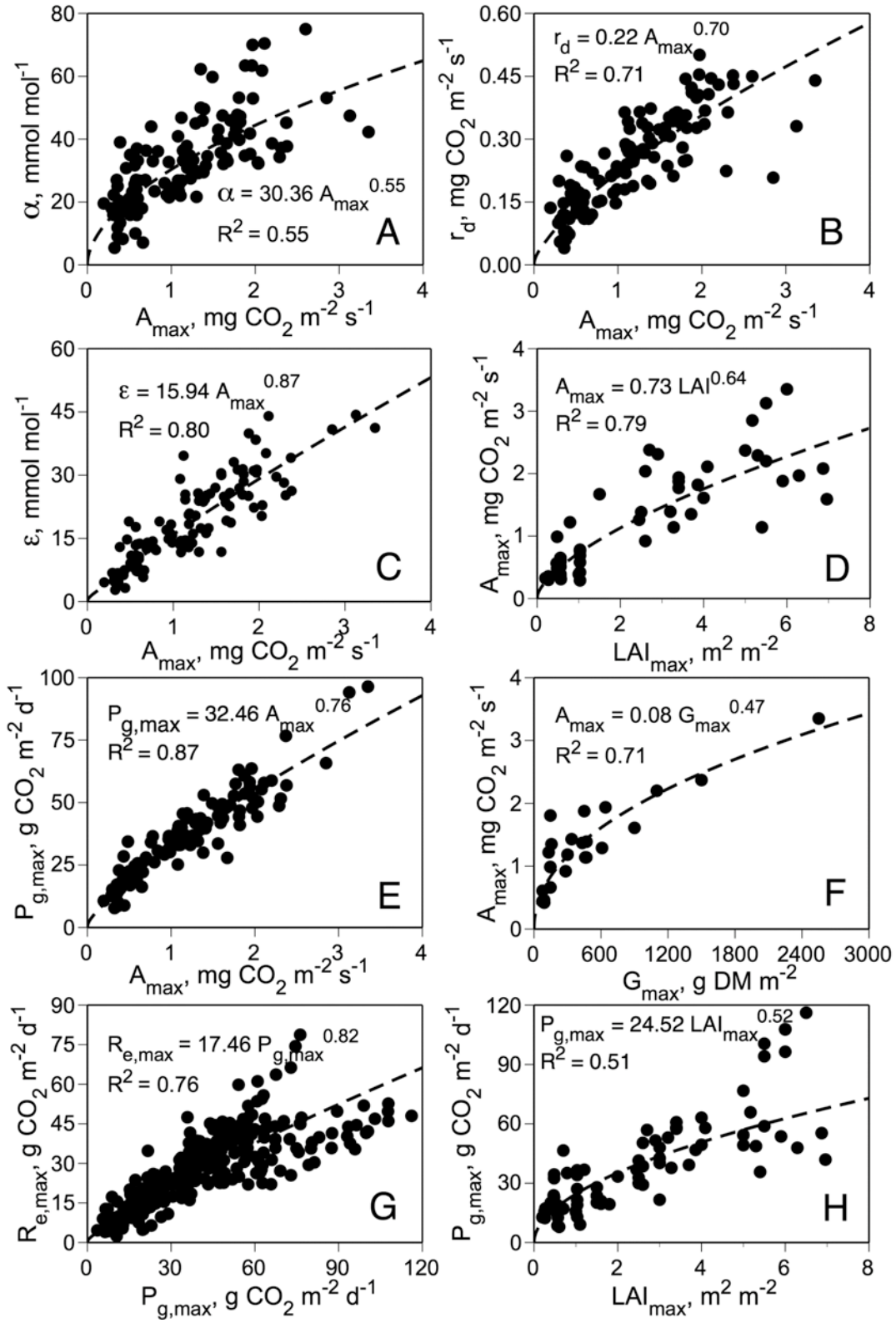
4 **Figure 2.**

5



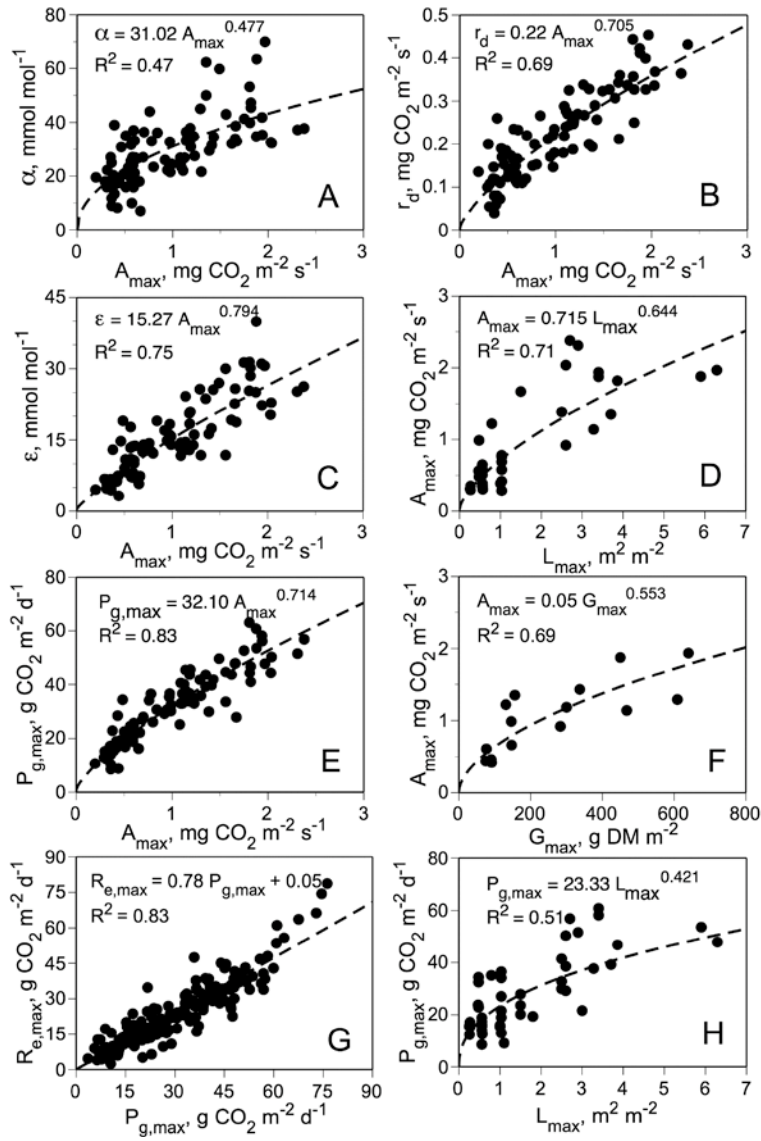
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2 **Figure 3.**



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2 **Figure 4.**

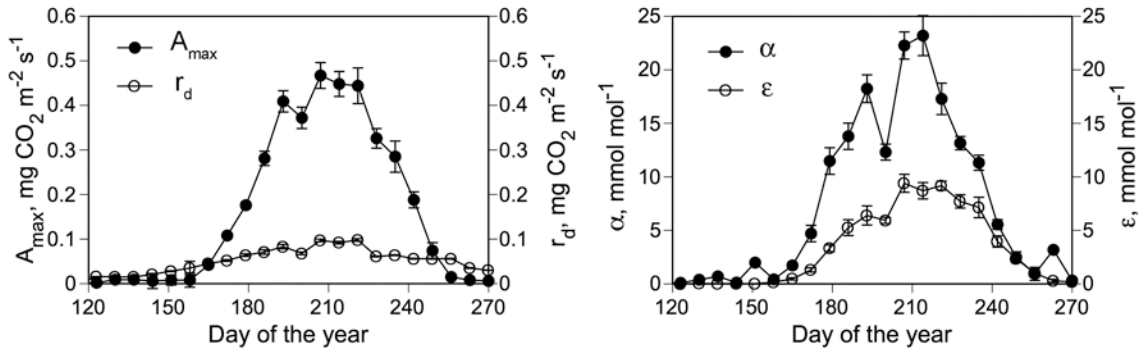


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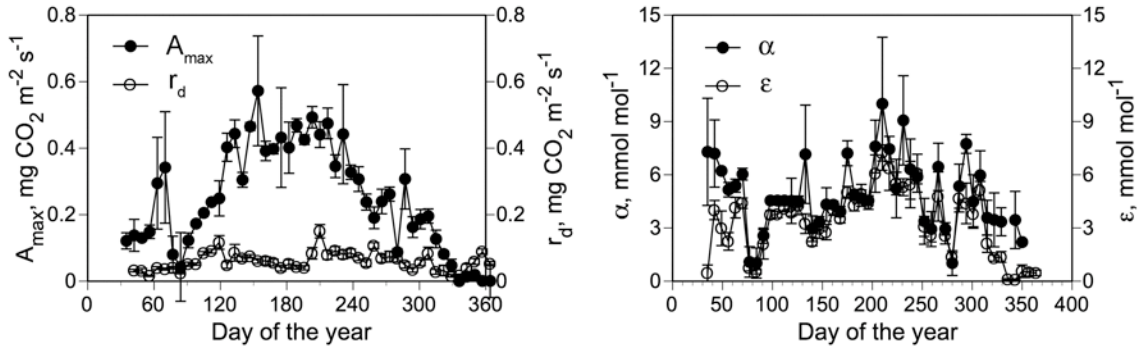
2 **Figure 5.**

3

A. Cherskii, floodplain meadow, 2003

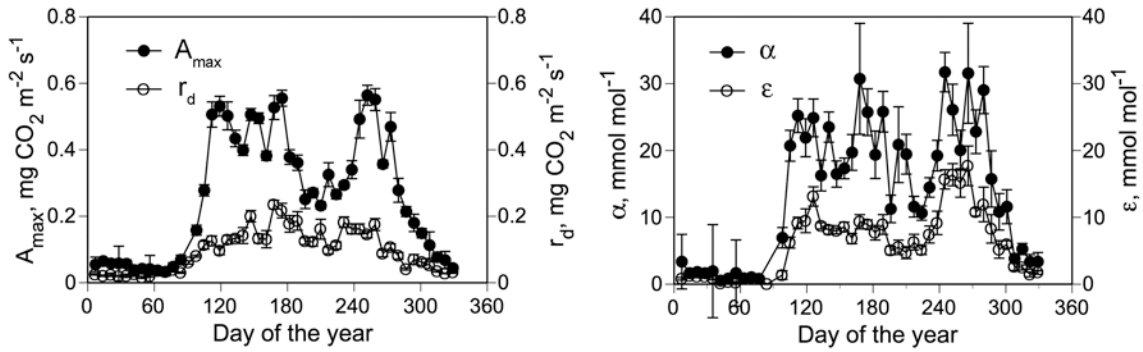


B. Cottonwood, mixed prairie, 2006

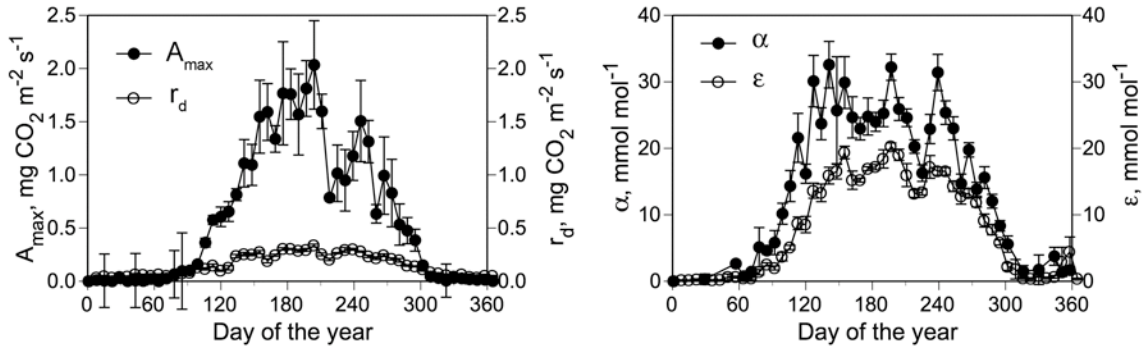


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C. Gudmundsen, mixed prairie, 2006



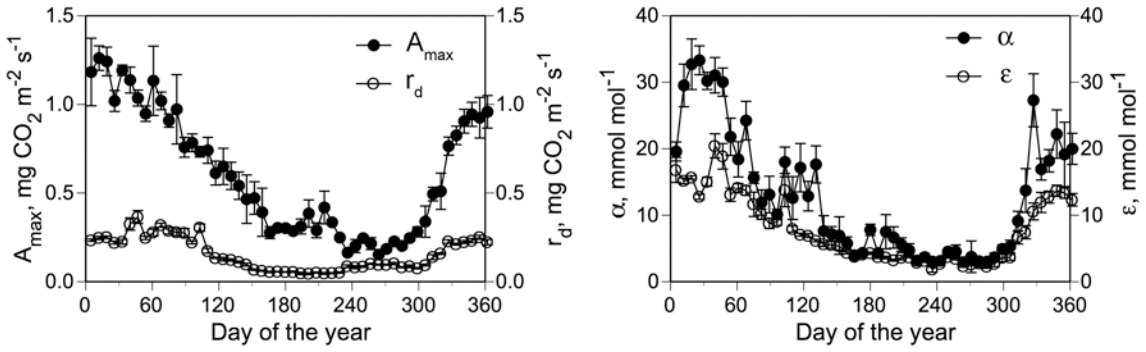
D. Fort Reno, tallgrass prairie, 2005



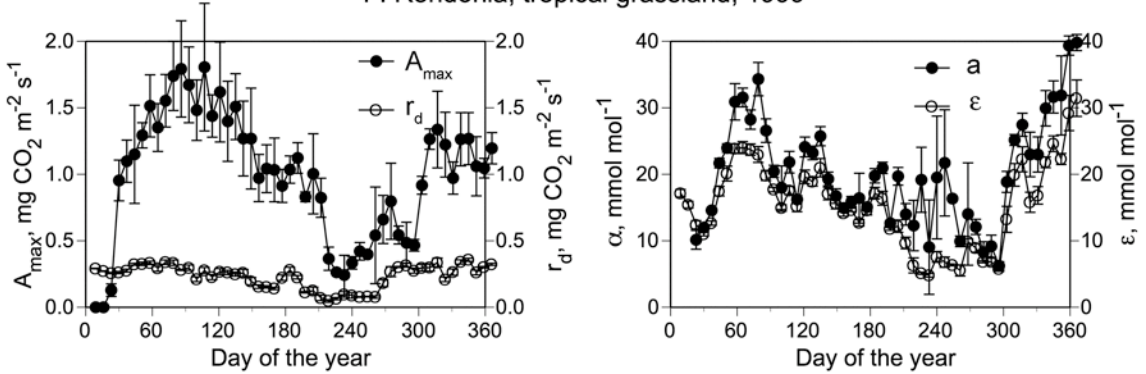
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E. Howard, wet-dry savanna, 2002

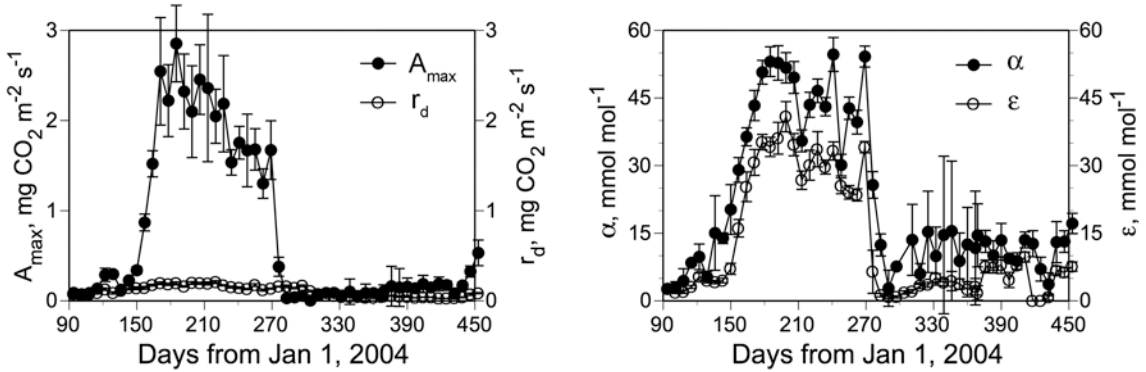


F. Rondonia, tropical grassland, 1999

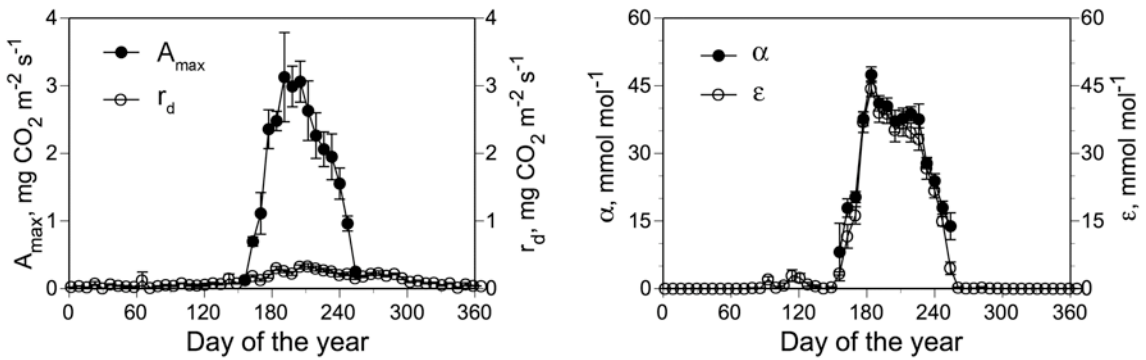


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G. Lonze, sugar beet, 2004

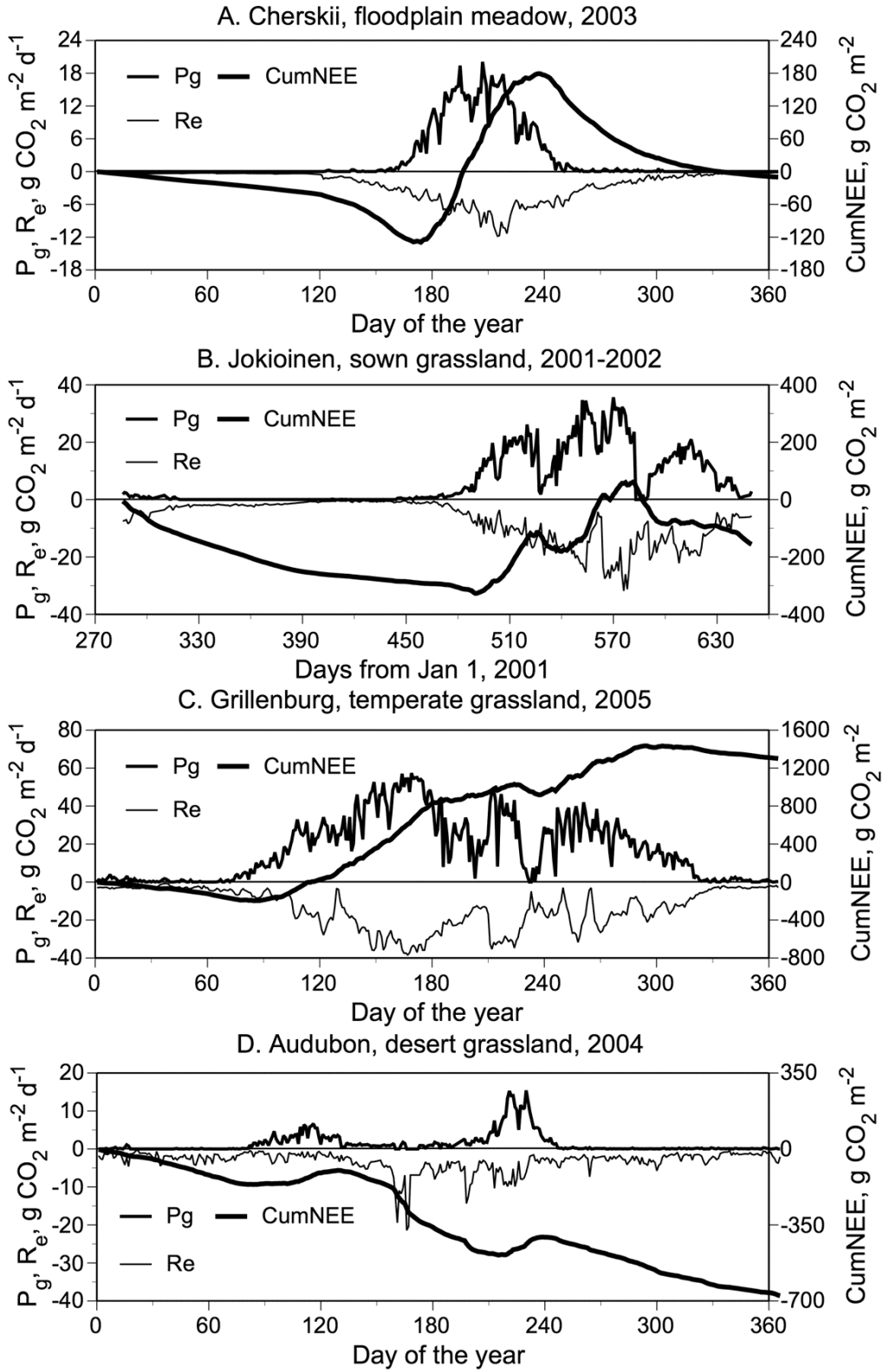


H. Bondville, corn, 1999

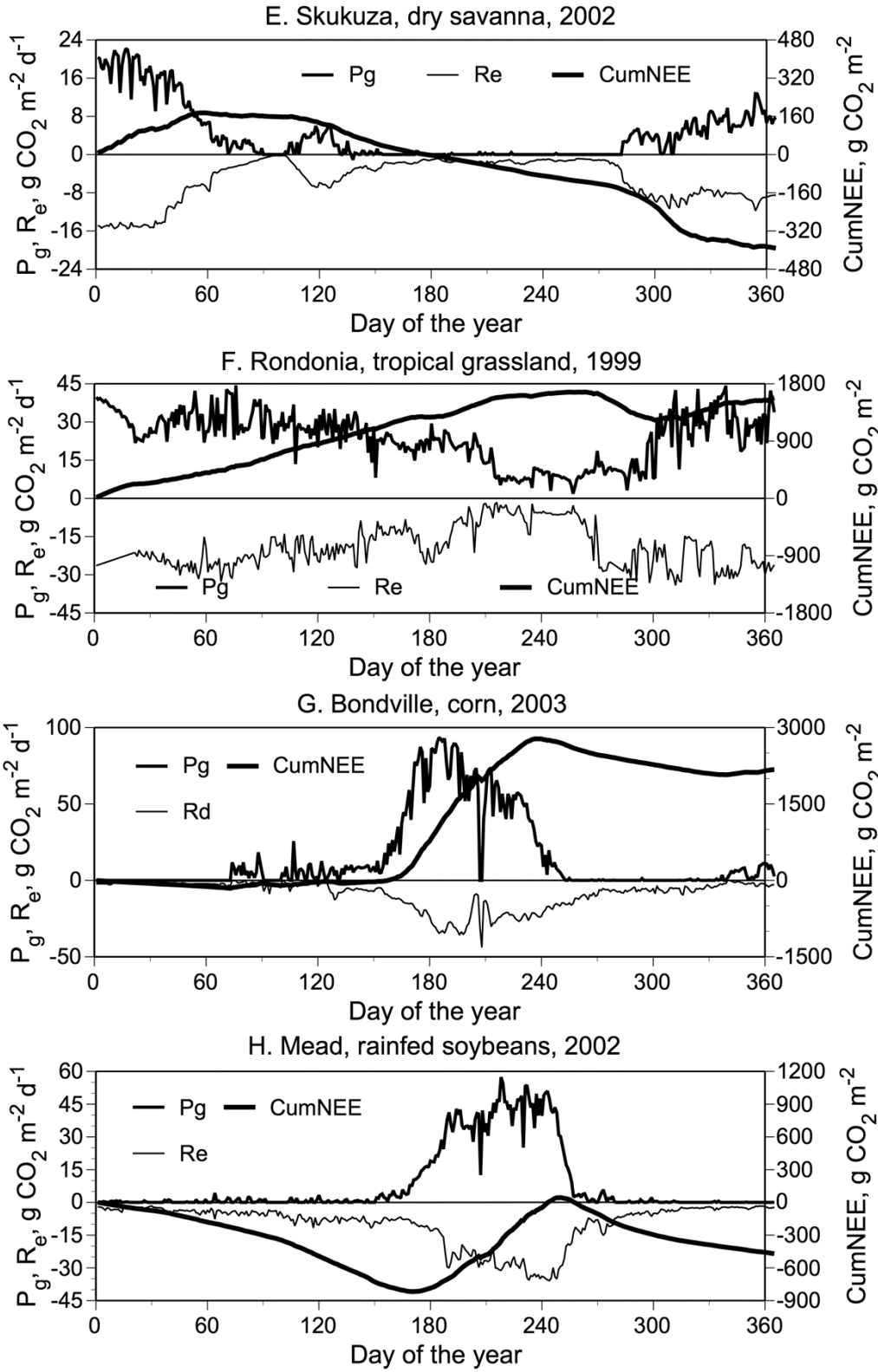


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3 **Figure 6.**

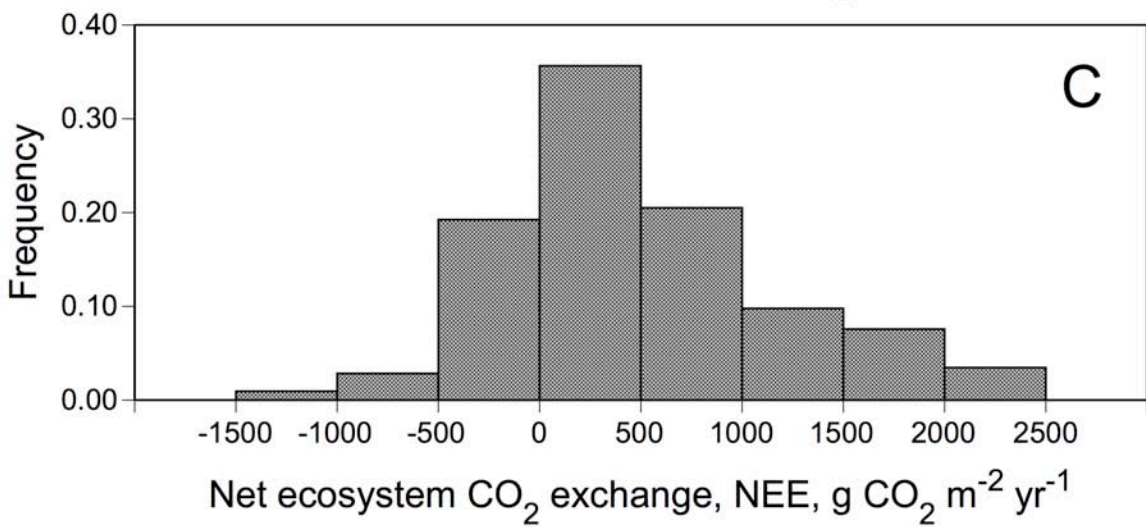
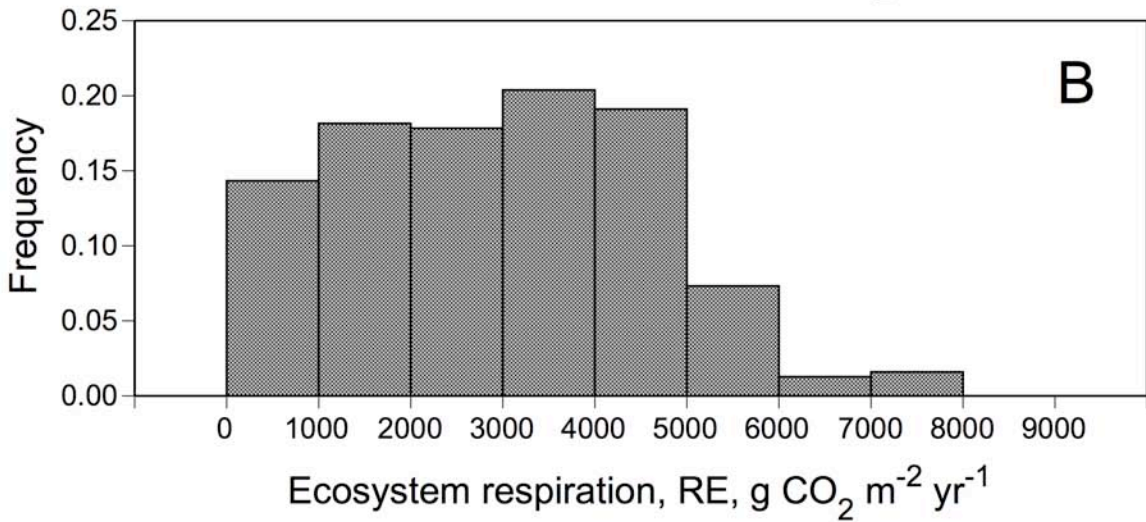
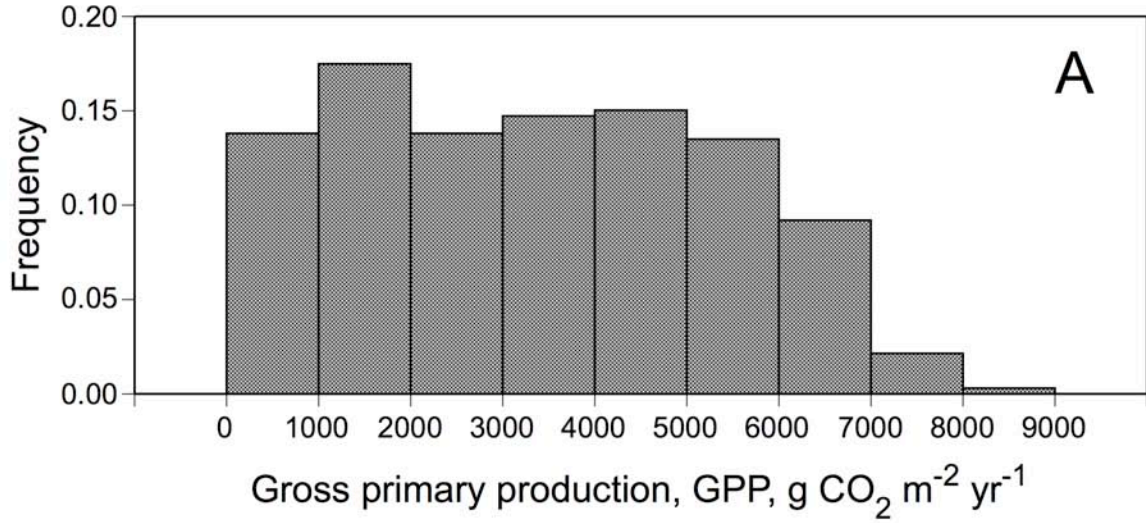


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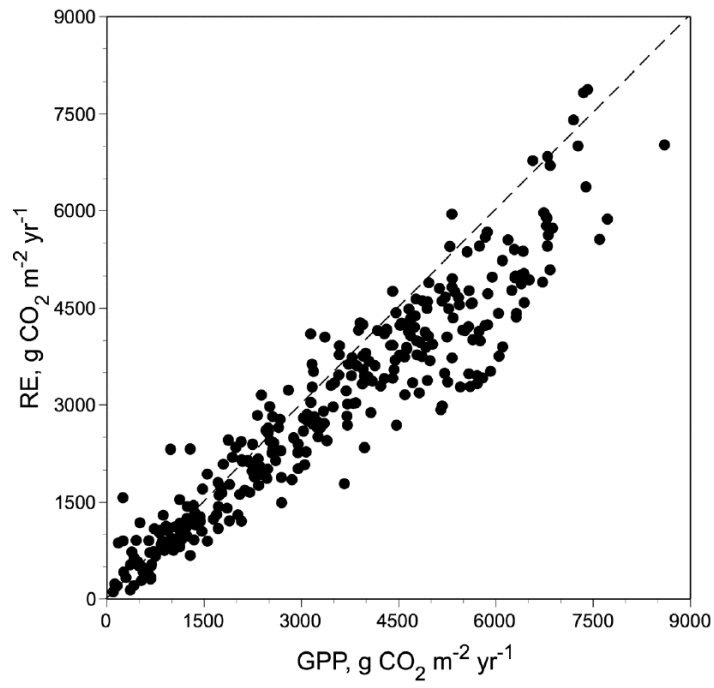
2 **Figure 7.**



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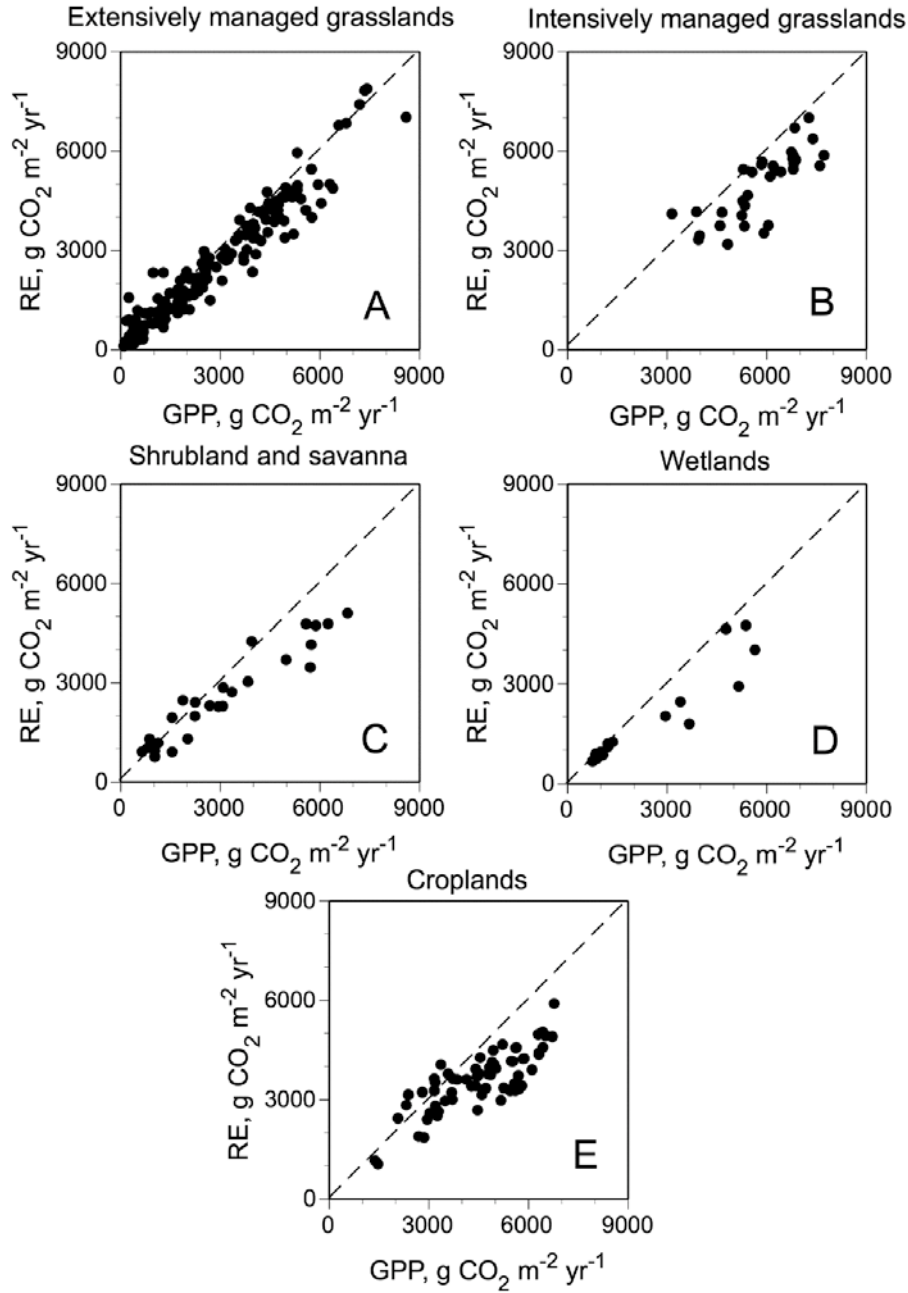
2 **Figure 8.**

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2 **Figure 9.**



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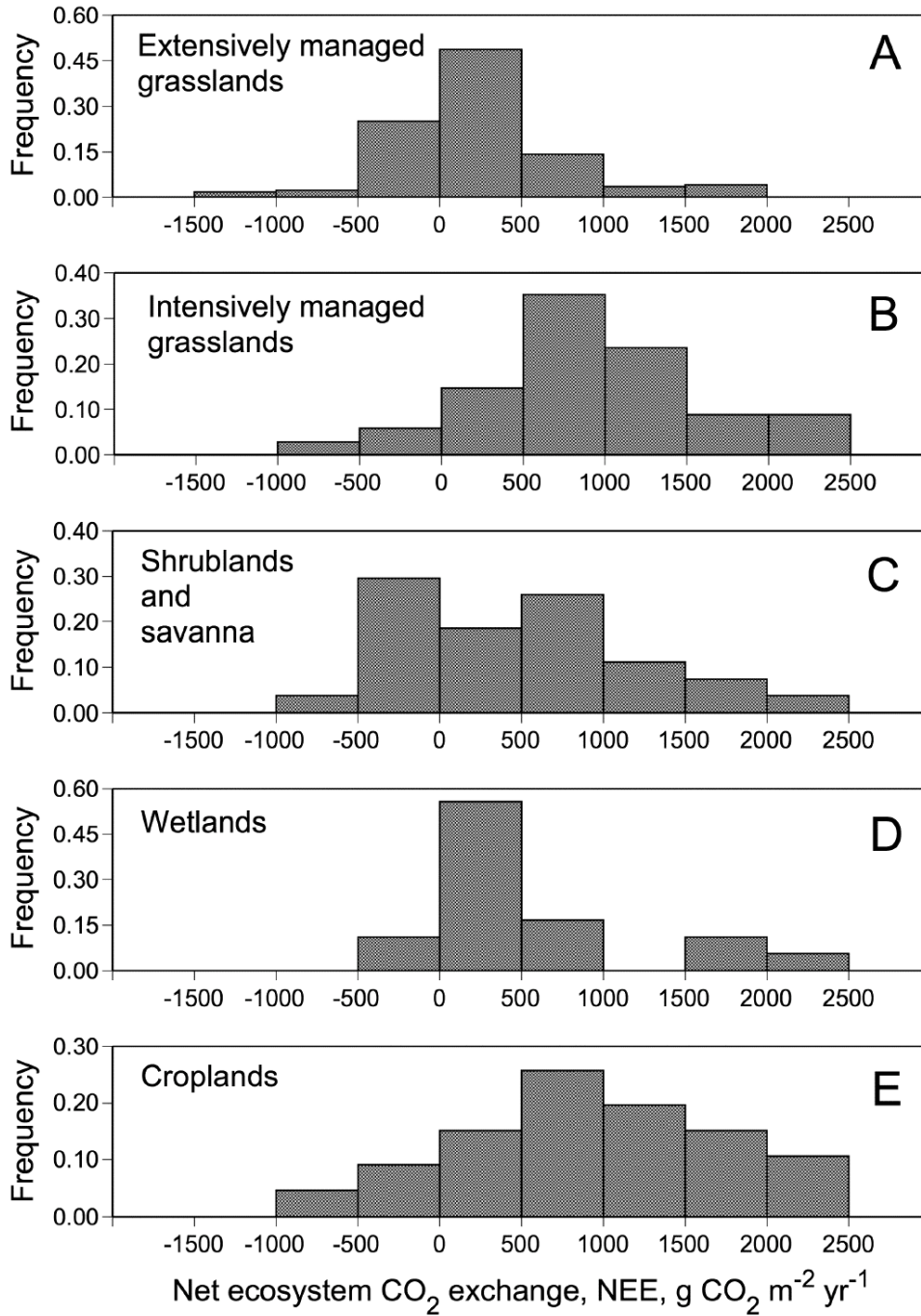
2 **Figure 10.**

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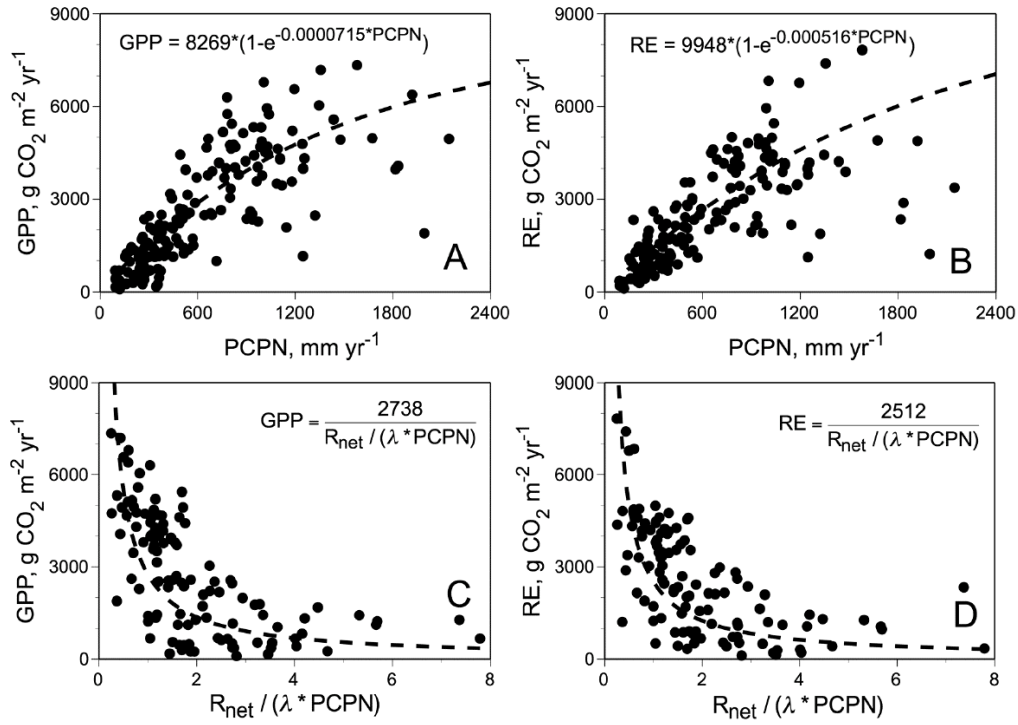
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2 **Figure 11**

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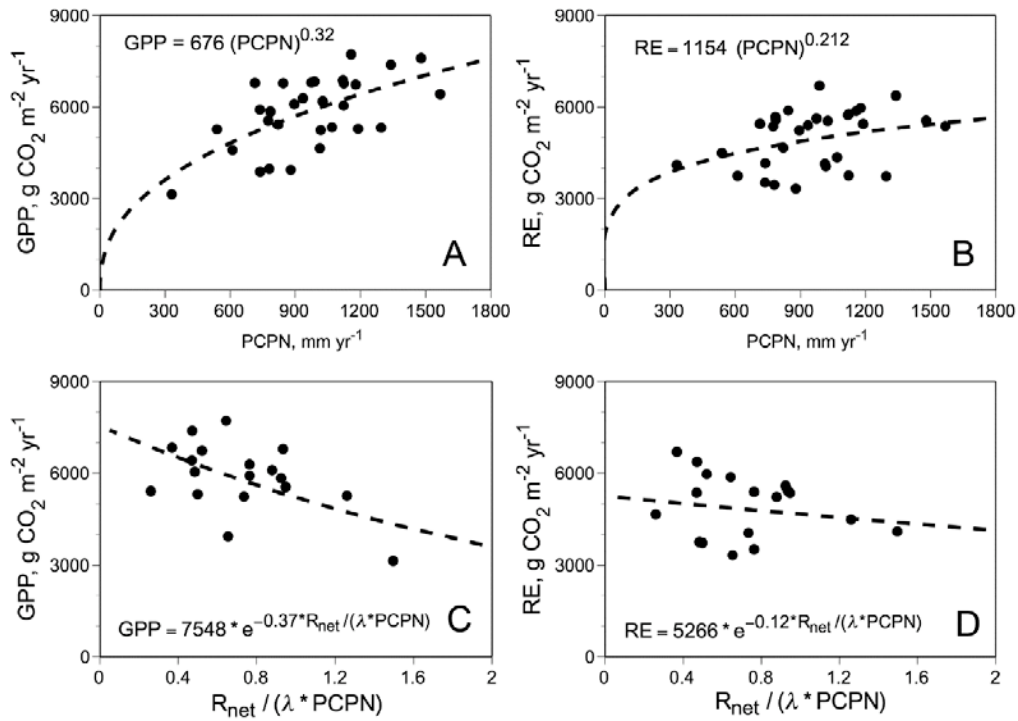
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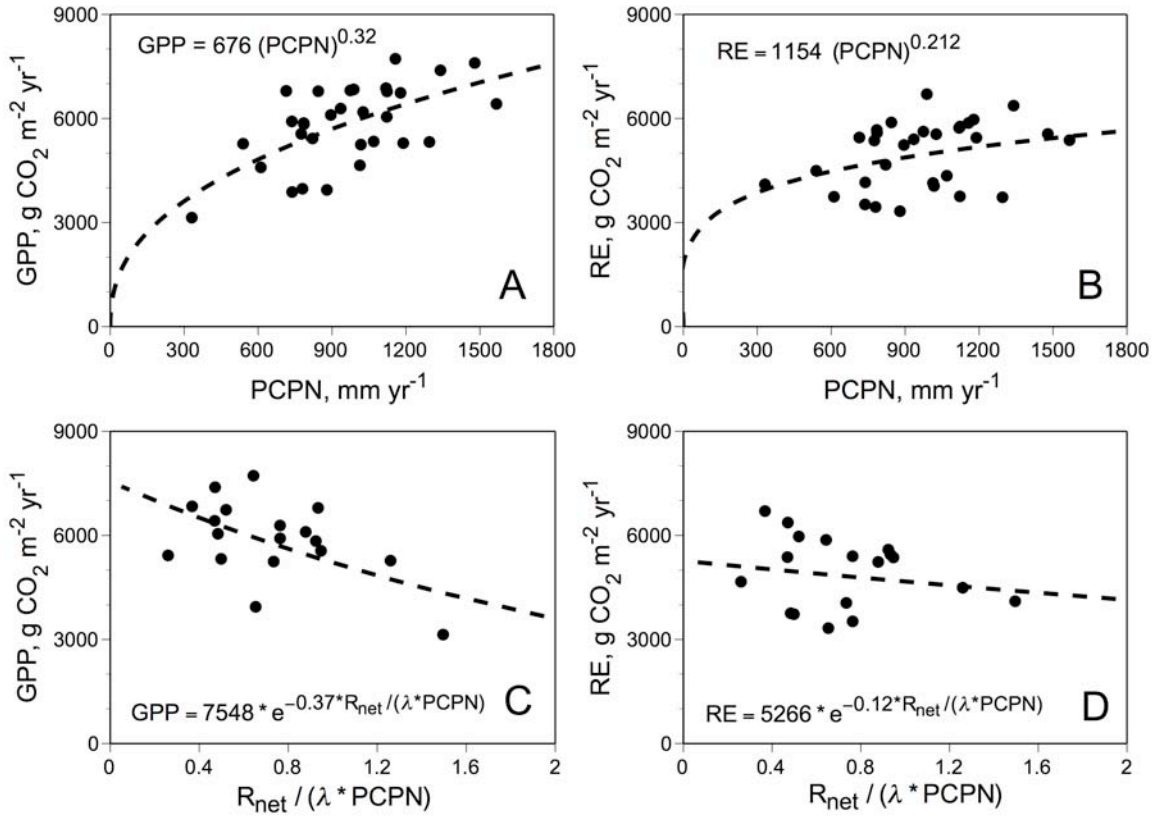
2 **Figure 12**

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5 **Figure 13**



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2 **Figure 14.**

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