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Productivity and Carbon Dioxide Exchange of Leguminous Crops: Estimates from Flux Tower Measurements

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Productivity and Carbon Dioxide Exchange of Leguminous Crops: Estimates from Flux Tower Measurements

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ABSTRACT

Net CO₂ exchange data of legume crops at 17 flux tower sites in North America and three sites in Europe representing 29 site-years of measurements were partitioned into gross photosynthesis and ecosystem respiration by using the nonrectangular hyperbolic light-response function method. The analyses produced net CO₂ exchange data and new ecosystem-scale ecophysiological parameter estimates for legume crops determined at diurnal and weekly time steps. Dynamics and annual totals of gross photosynthesis, ecosystem respiration, and net ecosystem production were calculated by gap filling with multivariate nonlinear regression. Comparison with the data from grain crops obtained with the same method demonstrated that CO₂ exchange rates and ecophysiological parameters of legumes were lower than those of maize (*Zea mays* L.) but higher than for wheat (*Triticum aestivum* L.) crops. Year-round annual legume crops demonstrated a broad range of net ecosystem production, from sinks of 760 g CO₂ m⁻² yr⁻¹ to sources of -2100 g CO₂ m⁻² yr⁻¹, with an average of -330 g CO₂ m⁻² yr⁻¹, indicating overall moderate CO₂-source activity related to a shorter period of photosynthetic uptake and metabolic costs of N₂ fixation. Perennial legumes (alfalfa, *Medicago sativa* L.) were strong sinks for atmospheric CO₂, with an average net ecosystem production of 980 (range 550–1200) g CO₂ m⁻² yr⁻¹.

Agricultural crops differ from each other with respect to their contribution to the global CO₂ exchange, as demonstrated by ecosystem-scale measurements at flux towers (Gilmanov et al., 2010, 2013). A number of grass crop species are recognized as strong sinks for atmospheric CO₂ and are widely cultivated as food, forage, and biofuel crops (Long et al., 1992; Hollinger et al., 2005; Suyker et al., 2005; Stella et al., 2009; Endres et al., 2010; Skinner and Adler, 2010; Zeri et al., 2011; Gilmanov et al., 2013). Considerably more uncertainty exists in evaluation of the source/sink activity of leguminous crops. On the one side, there are data indicating high photosynthetic and yield potentials of legume

crops (Platt and Bassham, 1978; Specht et al., 1999). Thomas and Hill (1949) reported maximum daily gross photosynthesis of experimental plots of alfalfa at 56 g dry matter m⁻² d⁻¹. Ludwick (2000) reported maximum yields of 54 Mg ha⁻¹ (24.1 t acre⁻¹) on irrigated alfalfa fields in California. On the other hand, based on year-round CO₂ exchange measurements on legume fields, some researchers have come to the conclusion that legume fields (e.g., soybean [*Glycine max* (L.) Merr.]) are near CO₂ neutral or even act as net sources for atmospheric CO₂ (Baker and Griffis, 2005; Verma et al., 2005; Hernandez-Ramirez et al., 2011; Gebremedhin et al., 2012).

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Abbreviations: GPP, gross primary production; LUE, light use efficiency; NEP, net ecosystem production; RE, ecosystem respiration; VPD, vapor pressure deficit.

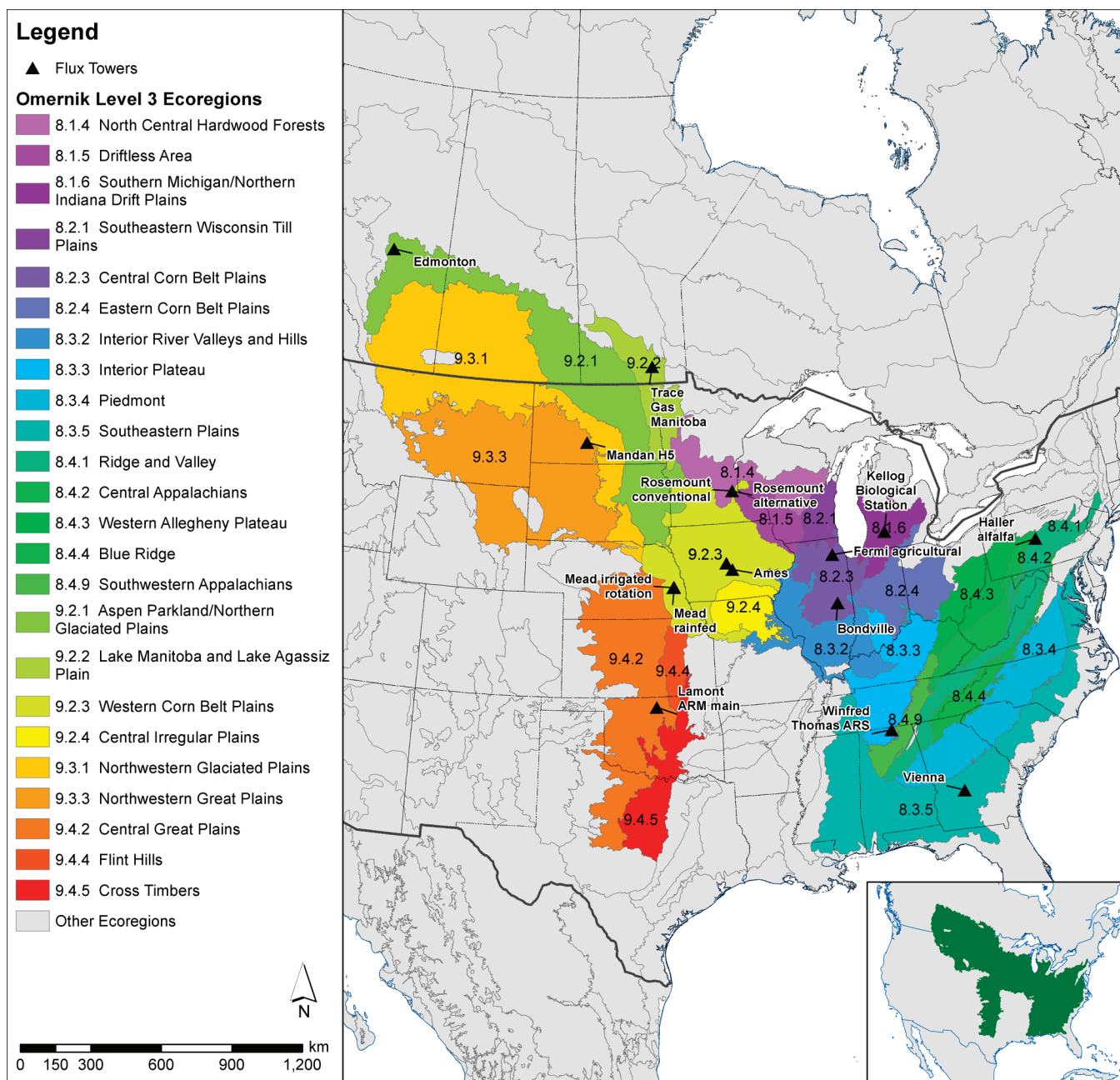


Fig. 1. Flux-tower sites in legume crops and Omernik Level 3 ecoregions of North America.

Legume crops (mostly soybean, alfalfa, and peanut [*Arachis hypogaea* L.]) occupy >20% of the cultivated land of the United States, playing a significant role in shaping the C balance of North America. A number of site-specific studies analyzing CO₂–exchange processes and their C budget implications for legume crops of the region have been published (Baldocchi et al., 1981a, 1981b, 1983; Hollinger et al., 2005; Baker and Griffis, 2005; Verma et al., 2005; Bernacchi et al., 2005, 2006; Fischer et al., 2007; Glenn et al., 2010; Pingintha et al., 2010; Hernandez-Ramirez et al., 2011; Gebremedhin et al., 2012). In these studies, including legume crops with different physiology and agronomy, annuals and perennials, the researchers used various methods based on either direct integration of net CO₂ exchange data or various models for C budget components. Nevertheless, the productivity, respiration, and ecophysiological parameters of legume crops derived from flux-tower measurements have not

yet been subjected to comparative analysis and synthesis. We present a unified approach based on partitioning of the flux-tower data into photosynthesis and respiration components by using a standardized method based on the nonrectangular hyperbolic model (Thornley and Johnson, 2000) to obtain new measurement-based estimates of CO₂ exchange of leguminous crops and facilitate comparability of the results from different sites and crops. The same technique was recently applied to cereals of midcontinent North America as the major agricultural crops (Gilmanov et al., 2013), and the present study expands the analysis to legumes, as the second significant crop type of the region. Quantification of the CO₂ exchange and ecophysiological parameters presented here will provide agriculturalists with valuable information to optimize the economic and sustainability aspects of the production of various leguminous crops.

Table 1. Eddy covariance tower sites used in the study.

No.	Site	Crop	Latitude	Longitude	Elevation	Year	T_{air}^{\dagger} °C	PCPN ‡ mm yr $^{-1}$	Thermal growing season § d	Tsum5 ¶ °C d	Principal investigator	Partitioning method $^{\#}$
1	Edmonton, AB, Canada	alfalfa	53.4964	-113.5524	650	2010	4.18	381	189	1545	J.A. Gamon	Q-T $_s$ -VPD
2	Trace Gas Manitoba, MB, Canada	faba bean	49.6453	-97.1579	235	2007	2.88	463	192	1887	M. Tenuta	Q-T $_s$ -VPD
3	Oensingen-2, Switzerland	pea	47.2865	7.7338	452	2010	8.39	1142	238	1996	W. Eugster	Q-T $_s$ -VPD
4	Mandan H5, North Dakota	alfalfa	46.7753	-100.9516	592	2010	5.34	605	206	2088	R.L. Phillips	Q-T $_s$ -VPD
5	Rosemount alternative, Minnesota	soybean/rye	44.7217	-93.0893	260	2004	7.31	766	219	2288	J.M. Baker	Q-T $_s$ -VPD
6	Rosemount conventional, Minnesota	soybean	44.7143	-93.0898	260	2004	7.31	766	219	2288	J.M. Baker	Q-T $_s$ -VPD
7	Rosemount conventional, Minnesota	soybean	44.7143	-93.0898	260	2006	9.20	669	214	2548	J.M. Baker	Q-T $_s$ -VPD
8	Avignon, France	pea	43.9165	4.8785	31	2005	14.01	491	298	3476	O. Marloie	Q-T $_s$ -VPD
9	Lennox, SD	soybean	43.2408	-96.9020	386	2012	10.47	336	239	2999	T.P. Meyers	Q-T $_s$ -VPD
10	Kellogg Biological Station, Michigan	alfalfa	42.4099	-85.3757	286	2006	10.05	1156	233	2496	J. Chen	Q-T $_s$ -VPD
11	Brooks Field-10, Iowa	soybean	41.9749	-93.6914	313	2008	7.78	1179	212	2538	J.H. Prueger	Q-T $_s$ -VPD
12	Fermi agricultural site, Illinois	soybean	41.8593	-88.2227	225	2007	9.92	1166	231	2940	R. Matamala	Q-T $_s$ -VPD
13	Fermi agricultural site, Illinois	soybean	41.8593	-88.2227	225	2009	8.02	1162	226	2429	R. Matamala	Q-T $_s$ -VPD
14	Ames, IA	soybean	41.72	-93.41	300	2003	9.01	718	225	2688	J.H. Prueger	Q-T $_s$
15	Mead rainfed, Nebraska	soybean	41.1797	-96.4396	363	2002	10.71	544	234	2958	A.E. Suyker	Q-T $_s$ -VPD
16	Mead rainfed, Nebraska	soybean	41.1797	-96.4396	363	2004	10.35	670	248	2919	A.E. Suyker	Q-T $_s$ -VPD
17	Mead irrigated rotation, Nebraska	soybean	41.1649	-96.4701	362	2002	10.55	831	231	2911	A.E. Suyker	Q-T $_s$
18	Haller, PA	alfalfa	40.8632	-77.8406	346	2003	8.87	1193	239	2383	R.H. Skinner	Q-T $_s$
19	Borgo Cioffi, Italy	alfalfa	40.5238	14.9574	20	2002-2003	16.31	787	356	3933	V. Magliulo	Q-T $_a$ -VPD
20	Bondville, IL	soybean	40.0061	-88.2919	300	1998	12.55	930	266	3290	T.P. Meyers	Q-T $_s$
21	Bondville, IL	soybean	40.0061	-88.2919	300	2000	10.71	582	249	3051	T.P. Meyers	Q-T $_s$
22	Bondville, IL	soybean	40.0061	-88.2919	300	2002	11.65	704	244	3063	T.P. Meyers	Q-T $_s$ -VPD
23	Bondville, IL	soybean	40.0061	-88.2919	300	2004	11.31	1010	266	3046	T.P. Meyers	Q-T $_s$ -VPD
24	Bondville, IL	soybean	40.0061	-88.2919	300	2006	11.83	1025	262	2887	T.P. Meyers	Q-T $_s$ -VPD
25	Lamont ARM main, Oklahoma ††	soybean	36.6058	-97.4888	314	2006	16.46	486	313	4385	M. Torn	Q-T $_s$ -VPD
26	Winfred Thomas ARS, Alabama	soybean/winter wheat	34.8943	-86.5672	191	2007	17.60	567	314	4806	M.T. Gebremedhin	Q-T $_s$
27	Winfred Thomas ARS, Alabama	soybean/winter wheat	34.8943	-86.5672	191	2008	16.20	1310	307	4312	M.T. Gebremedhin	Q-T $_s$
28	Winfred Thomas ARS, Alabama	soybean/winter wheat	34.8943	-86.5672	191	2009	16.78	1383	307	4381	M.T. Gebremedhin	Q-T $_s$
29	Vienna, GA	peanut	32.1308	-83.6770	122	2005	16.77	1265	323	4386	M. Leclerc	Q-T $_s$ -VPD

 † Mean annual air temperature. ‡ Annual precipitation. § Number of days with mean daily air temperature $\geq 5^{\circ}\text{C}$. ¶ Tsum5 = $\sum_{t=1}^{365} \max\{0, [\bar{T}_{air}(t) - 5]\}$. $^{\#}$ Q-T $_s$ method takes into account combined effects of light and soil temperature (Eq. [2]); Q-T $_s$ -VPD method takes into account combined effects of light, soil temperature, and vapor pressure deficit (VPD) (Eq. [3-4]); Q-T $_a$ -VPD method takes into account combined effects of light, air temperature, and vapor pressure deficit. †† Example of a low-production crop year: due to an unfavorable water regime, the bean yield was only 5 bushels acre $^{-1}$ = 0.34 Mg ha $^{-1}$.

MATERIALS AND METHODS

We have compiled a data set of year-round net CO₂ exchange measurements at flux-tower stations in legume fields covering a geographic range from Alberta, Canada, to Georgia and from Oklahoma to Pennsylvania to quantitatively compare gross photosynthesis, ecosystem respiration, and ecophysiological parameters of legume crops in North America (Fig. 1). For comparison, we have also included measurements from three existing European flux towers on legume crops. The data set includes flux towers in all major legume crops: 20 site-yr of soybean; 5 site-yr of alfalfa; 2 site-yr of pea (*Pisum sativum* L.); 1 site-yr of faba bean (*Vicia faba* L.); and 1 site-yr of peanut (Table 1).

Flux towers in the data set covered a wide range of climatic conditions, with mean annual temperatures from 2.9 to 17.6°C, annual precipitation totals from 336 to 1380 mm, growing seasons (5°C) from 189 to 356 d, and the sum of daily temperatures >5°C from 1545 to 4806 degree days (Table 1). All sites in the data set had eddy-covariance instrumentation, with measurements following the Ameriflux/CarboEurope/Fluxnet protocol (Meyers and Hollinger, 2004; Aubinet et al., 2012), except for the Trace Gas Manitoba site, where the flux gradient micrometeorological technique was used (Glenn et al., 2010).

Partitioning of Net Carbon Dioxide Flux Data into Photosynthesis and Respiration

Using ecophysiological sign convention, where CO₂ flux from the atmosphere to the ecosystem is positive, gross photosynthesis, P_g , and total ecosystem respiration, R_e , are considered as process rates, combined in the conservation equation with signs corresponding to their contribution to the respective processes. In non-forest terrestrial ecosystems with insignificant canopy CO₂ storage (Loescher et al., 2006), the net CO₂ flux, F (mg CO₂ m⁻² s⁻¹), provided by flux-tower measurements represents the difference between gross photosynthesis and ecosystem respiration:

$$F = P_g - R_e \quad [1]$$

In general, factors controlling photosynthesis and respiration at the crop level are not the same (although they overlap), and the patterns of their response to a given factor are not identical (Thornley and Johnson, 2000). Therefore, decomposition of the F data into photosynthesis and respiration (Eq. [1]) is recognized as an essential part of flux-tower data processing. While in the earlier period of flux data analysis partitioning was usually based on estimation of daytime respiration from nighttime fluxes, more recently derivation of daytime respiration from daytime measurements has become the dominant approach (Gilmanov et al., 2003, 2013; Reichstein et al., 2005; Lasslop et al., 2010). Analysis of tower CO₂ exchange data from a wide range of grassland and crop ecosystems demonstrated that the modified nonrectangular hyperbolic equation provides a robust and flexible tool for partitioning of the eddy-covariance net CO₂ exchange data into gross photosynthesis and ecosystem respiration components (Stoy et al., 2006). In temperate and humid climates, the partitioning equation in the form (Gilmanov et al., 2007)

$$F(Q, T) = \frac{1}{2\theta} [\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max} \theta Q}] - r_0 \exp(k_T T_s) \quad [2]$$

may be used, where Q is photosynthetically active radiation, T is the temperature, α is the initial slope (apparent quantum yield), A_{\max} is the plateau (photosynthetic capacity) of the light response, θ is the convexity parameter (Thornley and Johnson, 2000), and r_0 and k_T are the coefficients of the exponential temperature response [$r_0 = R_e(0)$]. Under conditions of pronounced water stress, partitioning based on Eq. [2] may lead to overestimation of the daytime respiration and gross photosynthesis because reduction of daytime flux under water stress may not only occur due to the increase in temperature but may also reflect the decrease in photosynthesis due to stomatal regulation (Gilmanov et al., 2010; Pingintha et al., 2010). In such cases, a modification of Eq. [2] is used (Gilmanov et al., 2013):

$$F(Q, T_s, \text{VPD}) = \frac{\varphi(\text{VPD})}{2\theta} [\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max} \theta Q}] - r_0 \exp(k_T T_s) \quad [3]$$

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

where T_s is soil temperature, and the normalized vapor pressure deficit (VPD) response function $\varphi(\text{VPD})$ depends on two parameters: the critical VPD value, VPD_{cr} , below which water deficit doesn't affect photosynthesis ($\varphi = 1$ for $\text{VPD} \leq \text{VPD}_{\text{cr}}$) and the curvature parameter, σ_{VPD} ($1 \leq \sigma_{\text{VPD}} \leq 30$), with lower values describing a strong water-stress effect and higher values indicating a weak effect (Gilmanov et al., 2013). Although, generally speaking, the values of the VPD_{cr} parameter may vary among crops and ecosystems, following El-Sharkawy et al. (1984), Lasslop et al. (2010), and Pingintha et al. (2010), we accepted a critical value $\text{VPD}_{\text{cr}} = 1$ kPa and considered a one-parameter VPD response function in the form

$$\varphi(\text{VPD}) = \begin{cases} 1, & \text{VPD} \leq 1 \\ \exp\left[-\left(\frac{\text{VPD} - 1}{\sigma_{\text{VPD}}}\right)^2\right], & \text{VPD} > 1 \end{cases} \quad [5]$$

Estimation of the Parameters

The parameter estimation and gap-filling methods used in this study followed procedures in the parallel study for the grain crops (Gilmanov et al., 2013), where they were described in detail. The parameters α , A_{\max} , θ , r_0 , k_T , and σ_{VPD} (when

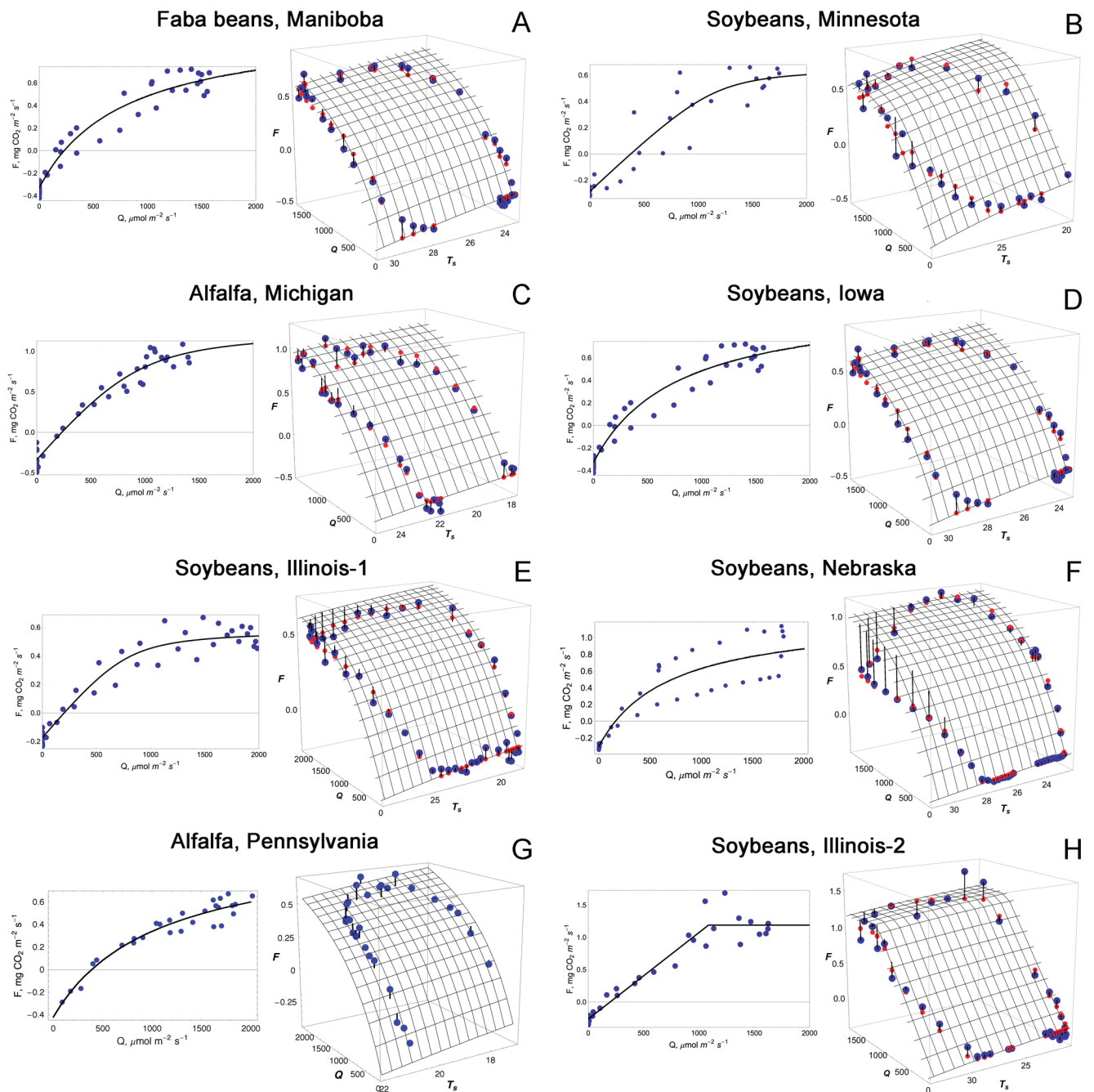


Fig. 2. Light–soil temperature–vapor pressure deficit (VPD) response functions for legume crops at several sites during the period of active photosynthesis: (A) faba bean, Manitoba, Canada; (B) soybean, Minnesota; (C) alfalfa, Michigan; (D) soybean, Iowa; (E) soybean, Illinois-1; (F) soybean, Nebraska; (G) alfalfa, Pennsylvania; and (H) soybean, Illinois-2. On each panel, the left graph shows a simple light-response plot and a fitted light curve, the light–soil temperature–VPD response is shown on the right (light–soil temperature response for G).

necessary) of the functions Eq. [2–5] were numerically estimated for every day of the growing season using available Q , T_s , VPD, and F data. Using the optimization tools of the Mathematica system (Wolfram Research), for every day's $\{Q(i), T_s(i), \text{VPD}(i), F(i), i = 1, 2, \dots, n\}$ data set of $n \leq 48$ records with a 30-min time step, we identified best-fit parameter values $\{\alpha, A_{\max}, \theta, \sigma_{\text{VPD}}, r_0, k_T\}$ of Eq. [2–5]. The series of graphs in Fig. 2 (specifications in Table 2) show examples of the response functions for several sites for the period of active photosynthesis. The data in Tables 3 and 4 illustrate parameter estimates using the models of Eq. [2] and [3–5], respectively.

The rate of ecosystem respiration, r_e ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), was described by an exponential function of soil temperature:

$$r_e(T_s) = r_0 \exp(k_T T_s) \quad [6]$$

where, during the growing season, parameters $r_0 = r_e(0)$ and k_T were estimated by fitting Eq. [2] or [3] to 30-min $\{F, Q, T_s, \text{VPD}\}$ data for individual measurement days, while outside the period of photosynthetic activity, r_0 and k_T were estimated by fitting Eq. [6] to pooled 30-min $\{F, T_s\}$ data for moving (typically, 9-d-wide) windows centered at the day of measurements.

Vapor Pressure Deficit Limitation of Photosynthesis

The significance of the VPD as a factor controlling the net CO₂ flux may be determined by consideration of the whole array of estimated curvature parameter σ_{VPD} values for a given site-year. The σ_{VPD} values typically lie in the interval from 2 to 30 kPa, the lower range characterizing a strong VPD effect (rapid decrease of F with VPD increasing to values $\gg 1$ kPa), while higher values of σ_{VPD} describe functions $\varphi(\text{VPD})$ that decrease only gradually with increasing aerial drought. A detailed characteristic of the VPD limitation of crop photosynthesis may be provided by a graph of the cumulative distribution of the number of days with curvature coefficient $\sigma_{\text{VPD}} \leq \sigma$ (Fig. 3). Nevertheless, in comparing ecosystems, a simpler parameter may be used, e.g., the number of days for which $\sigma_{\text{VPD}} \leq 4$ kPa and the maximum vapor pressure deficit $\text{VPD}_{\text{max}} \geq 1$ kPa (D_{VPD}).

Gap Filling and Calculation of Annual Totals of Production and Respiration

Estimates of half-hourly rates of gross photosynthesis, P_g , and ecosystem respiration, R_e , for days with missing flux data were obtained by use of the assimilation and respiration terms of Eq. [2] or [3], respectively, with parameter estimates for the missing calendar days obtained by smooth interpolation across the data set of available parameters $\{\alpha(t_j), A_{\text{max}}(t_j), \theta(t_j), r_0(t_j), k_T(t_j), \sigma_{\text{VPD}}(t_j)\}$. Daily totals of gross photosynthesis, $P_g(t)$ (g CO₂ m⁻² d⁻¹), daytime ecosystem respiration, $R_{\text{day}}(t)$

(g CO₂ m⁻² [light period]⁻¹), and nighttime ecosystem respiration, $R_{\text{night}}(t)$ (g CO₂ m⁻² [light period]⁻¹), for calendar days $t = 1, 2, \dots, 365$ were obtained by numerical integration of half-hourly rates over corresponding periods of the day. The total 24-h ecosystem respiration $R_e(t)$ (g CO₂ m⁻² d⁻¹) and the net 24-h ecosystem CO₂ exchange, $F(t)$, were calculated as

$$R_e(t) = R_{\text{day}}(t) + R_{\text{night}}(t) \quad [7]$$

$$F(t) = P_g(t) - R_e(t) \quad [8]$$

Finally, the annual totals of gross primary production (GPP) and ecosystem respiration (RE) were calculated as annual sums:

$$\text{GPP} = \sum_{t=1}^{365} P_g(t) \quad [9]$$

and

$$\text{RE} = \sum_{t=1}^{365} R_e(t) \quad [10]$$

while the annual net ecosystem production (NEP) was obtained as

$$\text{NEP} = \text{GPP} - \text{RE} \quad [11]$$

Table 2. Specifications for graphs in Fig. 2.

Symbol	Site	Crop	Year	Day of the year
A	Trace Gas Manitoba, MB, Canada	fabia bean	2007	201
B	Rosemount conventional, Minnesota	soybean	2006	184
C	Kellogg Biological Station, Michigan	alfalfa	2006	182
D	Brooks Field 10, Iowa	soybean	2008	216
E	Fermi agricultural site, Illinois	soybean	2007	182
F	Mead rainfed, Nebraska	soybean	2002	223
G	Haller, PA	alfalfa	2003	179
H	Bondville, IL	soybean	2002	215

Table 3. Numerical values and the goodness-of-fit characteristics of the parameters apparent quantum yield (α), photosynthetic capacity (A_{max}), convexity of the light response (θ ratio), respiration rate at zero temperature (r_0), and the exponential temperature coefficient (k_T) in Eq. [2] for Day of the Year 179 at the Haller alfalfa site, 2003.

Parameter	α	A_{max}	θ ratio	r_0	k_T
	mg CO ₂ μmol^{-1}	mg CO ₂ m ⁻² s ⁻¹		mg CO ₂ m ⁻² s ⁻¹	°C ⁻¹
Value	0.00134	1.541	2.567×10^{-8}	0.0964	0.0688
SE	0.00038	0.142	0.0938	0.0707	0.0301
t value	3.554	10.85	2.736×10^{-7}	1.364	2.286
p value	0.0017	1.6×10^{-10}	1.0	0.186	0.032

Table 4. Numerical values and the goodness-of-fit characteristics of the parameters apparent quantum yield (α), photosynthetic capacity (A_{max}), convexity of the light response (θ ratio), respiration rate at zero temperature (r_0), the exponential temperature coefficient (k_T), and the curvature parameter of the vapor pressure deficit response (σ_{VPD}) of Eq. [3–4] for Day of the Year 223 at the Mead rainfed soybean site, 2002.

Parameter	α	A_{max}	θ ratio	r_0	k_T	σ_{VPD}
	mg CO ₂ μmol^{-1}	mg CO ₂ m ⁻² s ⁻¹		mg CO ₂ m ⁻² s ⁻¹	°C ⁻¹	kPa
Value	0.00192	1.748	0.718	0.108	0.0404	3.246
SE	0.00013	0.097	0.107	0.027	0.0098	0.114
t value	14.90	18.09	6.72	3.98	4.2	28.47
p value	0	0	3.69×10^{-8}	2.68×10^{-4}	1.74×10^{-4}	0

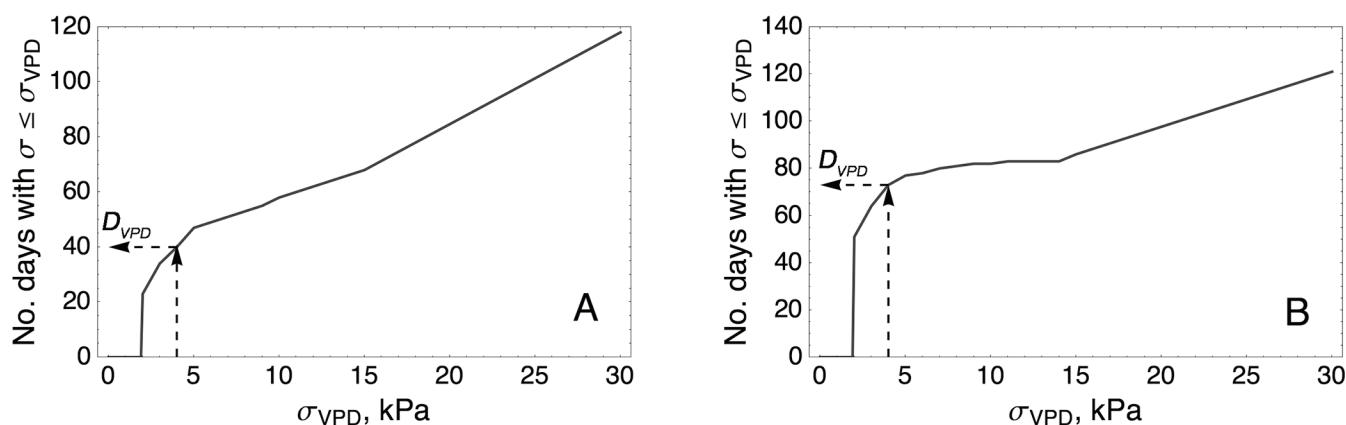


Fig. 3. Cumulative distribution functions of the daily vapor pressure deficit (VPD) response curvature parameter values, σ_{VPD} , for: (A) a faba bean crop at the Trace Gas Manitoba site, 2007; and (B) a soybean crop at the Bondville site, 2002. The dashed arrows illustrate determination of the D_{VPD} parameter as the number of days when the curvature parameter of the VPD-dependent factor (Eq. [5]) was less than or equal to the critical value $\sigma_{VPD} = 4$ kPa.

We found that for comparative purposes, it was useful to introduce additional parameters of average daytime respiration rate, $r_{day}(t)$, and average nighttime respiration rate, $r_{night}(t)$, calculated as

$$r_{day}(t) = \frac{1000R_{day}(t)}{\tau_2(t) - \tau_1(t)} \quad [12]$$

$$r_{night}(t) = \frac{1000R_{night}(t)}{86,400 - [\tau_2(t) - \tau_1(t)]} \quad [13]$$

where $\tau_1(t)$ and $\tau_2(t)$ are the moments of sunrise and sunset for the t th calendar day respectively (measured in seconds to obtain r_{day} and r_{night} in milligrams of CO_2 per square meter per second if R_{day} is in grams of CO_2 per square meter per light period and R_{night} is in grams of CO_2 per square meter per dark period).

Photosynthetic Light-Use Efficiency

Light-use efficiency characteristics are often used as important tools of comparative ecological analysis. From a number of coefficients suggested for this purpose, we used the coefficient of gross photosynthetic light-use efficiency, LUE, defined as a ratio of daily gross photosynthesis P_g to daily incoming of photosynthetically active radiation Q (Cooper, 1970; Gilmanov et al., 2005):

$$LUE = \frac{P_g}{Q} \quad [14]$$

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

RESULTS AND DISCUSSION

The modified nonrectangular hyperbolic model with VPD limitation in the form of Eq. [3–5] proved to be an adequate tool for describing tower-based net CO_2 exchange measurements in legume crops and partitioning them into photosynthesis and respiration components. Figure 2 illustrates application of the

model: Fig. 2A–2F and 2H show models with VPD limitation (Eq. [3–5]), while Fig. 2G illustrates the model driven only by the light and soil temperature factors (Eq. [2]). The left graph on each panel shows a simple light-response scatterplot fitted by nonrectangular hyperbolae $F(Q)$ with daytime respiration constant during the day; the surface on the right panel shows the (Q, T_s) response described by Eq. [3–5] with the average daily VPD value; the blue dots at the right show the original measured F values and the red dots show actual model predicted $F(Q, T_s, VPD)$ accounting for VPD variability.

To illustrate parameter estimation procedures, Table 3 shows estimated values and the goodness-of-fit characteristics for the model of Eq. [2] fitted for Day 179 of the 2003 season at the Haller alfalfa site (Fig. 2G) when no substantial VPD limitation was observed (mean daily VPD = 1.0 kPa, $VPD_{max} = 2.1$ kPa). The model shows a significant temperature-response coefficient $k_T = 0.069$ $^{\circ}C^{-1}$, with the value close to van't Hoff's $Q_{10} = 2.0$. For this case, the close-to-zero estimate of the convexity parameter θ should also be noted, indicating that the light response for this day may apparently be described by a rectangular hyperbola, characterized by $\theta = 0$.

The data in Table 4 illustrate the parameters of Eq. [3–5] fitted for Day 223 of 2002 at the Mead soybean site. As can be seen on the light-response diagram of Fig. 2F, this day at this site was marked by a substantial decrease in net CO_2 uptake (VPD reached 3.4 kPa in the afternoon hours), resulting in a hysteresis-like loop on the (Q, F) diagram. The model reflects this fact by generating highly significant (high t values) estimates of all the parameters, including the parameters of temperature response, r_0 and k_T , and VPD limitation, σ_{VPD} (Table 4).

Ecosystem-scale ecophysiological parameters generated by the partitioning method described above exhibited pronounced seasonal dynamics, which reflects physiological and phenological changes of the biota in the field, as well as changes in biomass and leaf area characteristics. To facilitate comparison of parameters among sites and years, we found it useful to calculate weekly means and the errors of the means for each site-year. The data in Fig. 4 provide an example of seasonal patterns of parameters at the weekly time scale, demonstrated by the soybean field at the Fermi agricultural site in 2007.

Maximum daily and maximum mean weekly values of the ecophysiological parameters of legume crops for the site-years of

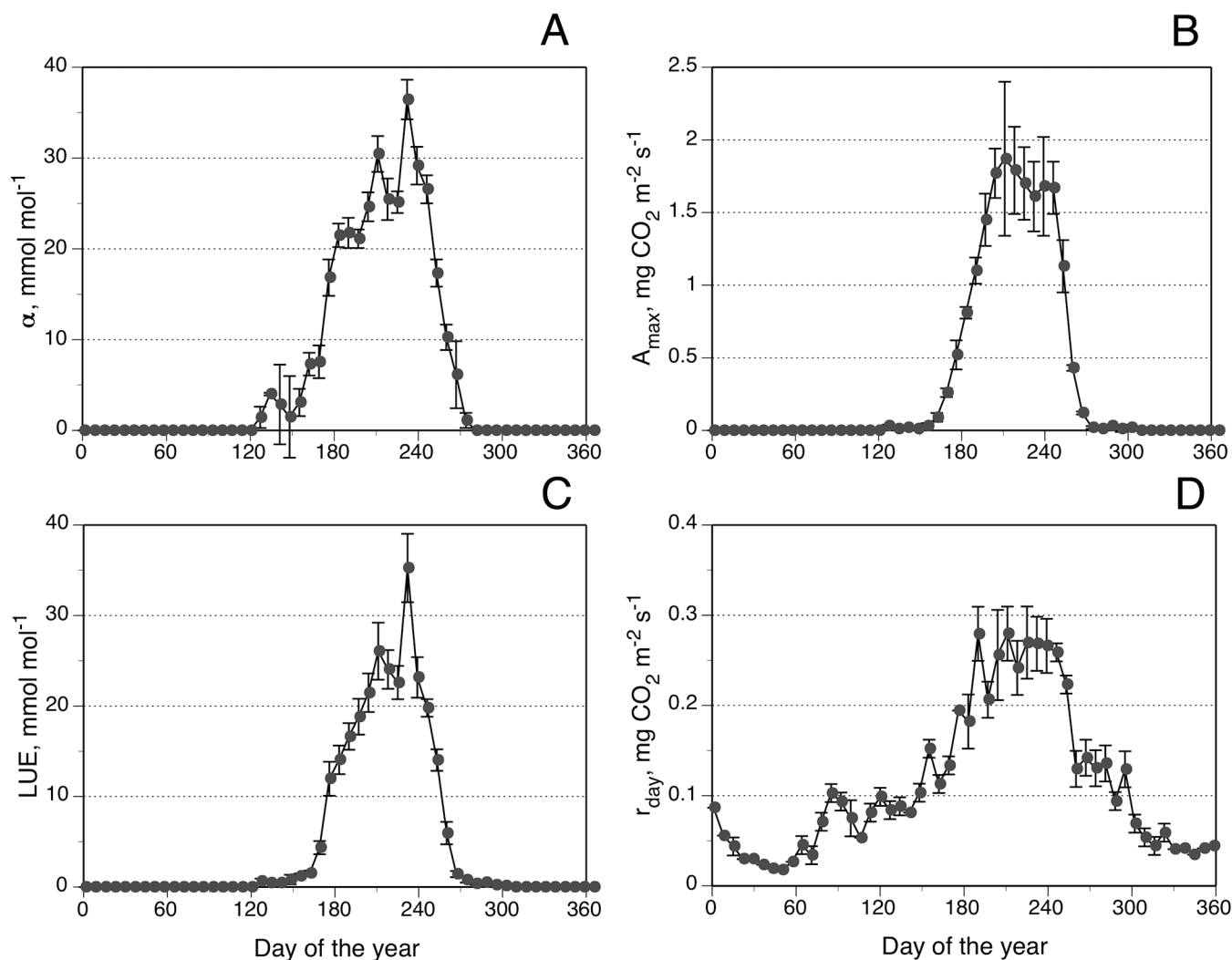


Fig. 4. Seasonal dynamics of major ecophysiological parameters of the soybean crops at the Fermi agricultural site, 2007: (A) apparent quantum yield, α ; (B) photosynthetic capacity, A_{\max} ; (C) gross photosynthetic light-use efficiency, LUE; and (D) daytime ecosystem respiration rate, r_{day} . Dots show weekly means of the parameters and the error bars show standard errors of the mean.

this study are summarized in Table 5. These data illustrate the magnitudes and variability of the parameters among leguminous crops as well as for different years at the same crop site. They may also be compared with corresponding parameters for grain crops. The maximum mean weekly apparent quantum yield for legumes, 47 to 48 mmol mol^{-1} achieved for the alfalfa crop at the Kellogg Biological Station in 2006 and Mandan in 2010, is less than the value of 50.30 mmol mol^{-1} estimated for a maize crop at the Bondville site in 2003 but higher than 37.23 mmol mol^{-1} recorded for the hard red spring wheat field at the Trace Gas Manitoba site in 2008 (Gilmanov et al., 2013). Our estimate of the maximum daily photosynthetic capacity, $A_{\max} = 2.3 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, for alfalfa at the Haller site compares well with the estimate of $A_{\max} = 2.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for alfalfa reported by Asseng and Hsiao (2000) using the BREB/ CO_2 gradient technique. The maximum mean weekly $A_{\max, \text{wk}} = 2.35 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for legumes recorded at the soybean field of the maize–soybean rotation at Bondville in 2004 is smaller than 3.63 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ estimated for the irrigated maize crop of the same rotation at the Mead site in 2003 but higher than 2.02 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ found for the spring wheat crop from the Trace Gas Manitoba site in 2008.

The maximum mean weekly respiration rate of 0.48 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ registered in the pea field of the Oensingen site

in 2010 is lower than 0.63 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ measured in the maize field at the Fermi agricultural site in 2006 but higher than the 0.27 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ estimated for the winter wheat crop of the Ponca City site in 1999 (Gilmanov et al., 2013).

For the peanut crop at the Vienna site with $\text{LAI}_{\max} = 3.8 \text{ m}^2 \text{ m}^{-2}$, we estimated $\alpha_{\max, \text{wk}} = 28.4 \text{ mmol mol}^{-1}$, $A_{\max, \text{wk}} = 1.88 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and $r_{\text{day}, \max, \text{wk}} = 0.23 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. This compares well with the values $\alpha_{\max, \text{wk}} = 43.8 \text{ mmol mol}^{-1}$, $A_{\max, \text{wk}} = 2.75 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and $r_{\text{day}, \max, \text{wk}} = 0.23 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ obtained by Pingintha et al. (2010) for a much more productive peanut crop in Georgia with much higher LAI_{\max} ($7.6 \text{ m}^2 \text{ m}^{-2}$).

The maximum daily values and maximum mean weekly parameter values presented in Table 5 show the ranges of variability of the ecophysiological parameters of legume crops, demonstrating coefficients of variation from 18 to 28%. Comparison of the ecophysiological parameters of legumes with the corresponding parameters estimated for grain crops in North America, summarized by Gilmanov et al. (2013) using the same methods, demonstrate (Table 6) that both the daily and the weekly maximums of the apparent quantum yield (α_{\max}) of legumes are not significantly different from those of maize but are significantly higher than for wheat fields. The photosynthetic

Table 5. Maximum values of the daily (index *max*) and mean weekly (index *max,wk*) estimates of the major ecophysiological parameters apparent quantum yield (α), photosynthetic capacity (A), daytime respiration rate (r_{day}), light use efficiency (LUE), and the number of days with a vapor pressure deficit limitation on photosynthesis (D_{VPD}) of the legume crops.

Site	Crop	Year	α_{max} mmol mol ⁻¹ s ⁻¹	$\alpha_{\text{max,wk}}$ mmol mol ⁻¹ s ⁻¹	A _{max} mg CO ₂ m ⁻² s ⁻¹	A _{max,wk} mg CO ₂ m ⁻² s ⁻¹	$r_{\text{day,max}}$ mg CO ₂ m ⁻² s ⁻¹	$r_{\text{day,max,wk}}$ mg CO ₂ m ⁻² s ⁻¹	LUE _{max} mmol mol ⁻¹	LUE _{max,wk} mmol mol ⁻¹	D_{VPD} d
Edmonton, AB, Canada	alfalfa	2010	54.30	32.58	1.99	1.77	0.388	0.279	36.97	25.50	53
Trace Gas Manitoba, MB, Canada	faba bean	2007	56.81	45.43	2.69	1.88	0.533	0.400	54.73	24.92	40
Oensingen-2, Switzerland	pea	2010	59.09	43.31	2.05	1.39	0.725	0.479	39.89	29.17	33
Mandan H5, North Dakota	alfalfa	2010	56.00	47.80	1.83	1.31	0.510	0.350	48.10	28.86	29
Rosemount alternative, Minnesota	soybean/rye	2004	46.57	33.32	2.13	1.68	0.440	0.250	36.37	25.30	50
Rosemount conventional, Minnesota	soybean	2004	47.55	34.90	1.80	1.59	0.291	0.234	38.21	24.17	—
Rosemount conventional, Minnesota	soybean	2006	68.18	42.36	1.83	1.52	0.464	0.348	42.58	25.5	45
Avignon, France	pea	2005	54.81	36.90	2.05	1.57	0.410	0.296	38.61	22.26	53
Lennox, SD	soybean	2012	35.14	26.88	1.50	0.96	0.211	0.164	23.79	15.97	68
Kellogg Biological Station, Michigan	alfalfa	2006	56.82	47.39	1.99	1.67	0.399	0.317	52.08	34.74	62
Brooks Field-10, Iowa	soybean	2008	56.72	40.89	1.89	1.44	0.448	0.310	36.04	19.957	56
Fermi agricultural site, Illinois	soybean	2007	52.7	36.45	2.27	1.87	0.460	0.291	50.785	30.58	50
Fermi agricultural site, Illinois	soybean	2009	48.65	34.50	2.33	1.75	0.319	0.227	44.40	31.04	41
Ames, IA	soybean	2003	54.03	37.83	2.1	1.57	0.460	0.352	37	22.95	—
Mead rainfed, Nebraska	soybean	2002	51.79	42.18	2.03	1.85	0.438	0.396	42.8	30.11	51
Mead rainfed, Nebraska	soybean	2004	49.27	39.99	2.35	2.20	0.357	0.321	35.30	25.16	61
Mead irrigated rotation, Nebraska	soybean	2002	61.28	38.27	2.50	2.18	0.491	0.396	38.82	28.58	—
Borgo Cioffi, Italy	alfalfa	2003	59.02	42.30	2.15	1.72	0.375	0.292	41.83	28.17	42
Haller, PA	alfalfa	2003	65.91	45.96	2.30	1.705	0.471	0.379	48.47	33.69	—
Bondville, IL	soybean	1998	55.37	26.64	1.57	1.27	0.34	0.254	36.158	23.66	—
Bondville, IL	soybean	2000	50.18	35.97	2.10	1.73	0.366	0.280	39.98	25.32	—
Bondville, IL	soybean	2002	48.97	36.85	2.30	1.89	0.394	0.3146	35.375	31.66	73
Bondville, IL	soybean	2004	61.45	46.17	2.75	2.35	0.429	0.306	53.57	40.30	34
Bondville, IL	soybean	2006	48.95	36.45	2.40	1.88	0.452	0.322	46.21	29.96	50
Bondville, IL	soybean	2006	28.89	14.51	0.55	0.44	0.258	0.111	10.11	7.17	58
Lamont ARM main, Oklahoma	soybean	2007	—	34	—	1.30	—	0.223	—	13.72	—
Winfred Thomas ARS, Alabama	soybean/winter wheat	2008	—	45.6	—	1.13	—	0.229	—	13.31	—
Winfred Thomas ARS, Alabama	soybean/winter wheat	2009	—	45.7	—	1.10	—	0.138	—	18.62	—
Winfred Thomas ARS, Alabama	soybean/winter wheat	2005	31.82	28.40	2.05	1.88	0.301	0.228	26.94	22.15	61
Vienna, GA	peanut		28.89	14.51	0.55	0.44	0.21	0.11	10.11	7.17	29
Min.			68.18	47.8	2.75	2.35	0.73	0.48	54.73	40.30	73
Max.			52.32	37.91	2.06	1.61	0.41	0.29	39.81	25.26	51
Mean			9.29	7.51	0.43	0.40	0.10	0.08	9.62	7.00	11.72
SE			18	20	21	25	25	28	24	2 =	23
CV			26	29	26	29	26	29	26	29	20
n											

Table 6. Mean ecophysiological parameters of the maximum daily (index *max*) and weekly (index *max,wk*) apparent quantum yield (α), photosynthetic capacity (A), daytime respiration rate (r_{day}), and light use efficiency (LUE) for legume, maize, and wheat crops estimated from flux-tower measurements (maize and wheat data according to Gilmanov et al., 2013).

Crop	Parameter	α_{max}	$\alpha_{\text{max,wk}}$	A_{max}	$A_{\text{max,wk}}$	$r_{\text{day,max}}$	$r_{\text{day,max,wk}}$	LUE_{max}	$\text{LUE}_{\text{max,wk}}$
		mmol mol ⁻¹	mmol mol ⁻¹	mg CO ₂ m ⁻² s ⁻¹	mg CO ₂ m ⁻² s ⁻¹	mg CO ₂ m ⁻² s ⁻¹	mg CO ₂ m ⁻² s ⁻¹	mmol mol ⁻¹	mmol mol ⁻¹
Legumes	avg.	52.3	37.9	2.06	1.61	0.41	0.29	39.8	25.3
	<i>n</i>	26	29	26	29	26	29	26	29
Maize	avg.	49.4 ns	39.8 ns	2.93***	2.62***	0.51*	0.37**	44.1 ns	34.3***
	<i>n</i>	17	17	17	17	17	17	17	17
Wheat	avg.	35.9***	29.7**	1.7*	1.34*	0.31**	0.23*	29.7**	20.8 ns
	<i>n</i>	9	9	9	9	9	9	9	9

* For maize, hypothesis that maize mean > legume mean is significant at $p \leq 0.05$; for wheat, hypothesis that wheat mean < legume mean is significant at $p \leq 0.05$; ns, not significant.

** For maize, hypothesis that maize mean > legume mean is significant at $p \leq 0.01$; for wheat, hypothesis that wheat mean < legume mean is significant at $p \leq 0.01$.

*** For maize, hypothesis that maize mean > legume mean is significant at $p \leq 0.001$; for wheat, hypothesis that wheat mean < legume mean is significant at $p \leq 0.001$.

capacity (A_{max}) of the legume crops at both daily and weekly scales is significantly lower than that of maize and significantly higher than for wheat crops. The metabolic parameter of daytime respiration rate (r_{day}) of legumes is significantly different from both maize and wheat, being lower than for maize but higher than for wheat. Maximum daily values of LUE of legumes are not significantly different from those of maize (which is in agreement with the apparent quantum yield, α_{max} , data in Table 6), but mean weekly LUE data for legumes are significantly lower than in maize. Compared with wheat, the maximum daily LUE values for legumes are significantly higher, but this is not true for the weekly values. Thus, high physiological potentials of the legumes are not always realized in long-term (weekly) performance, resulting in $\text{LUE}_{\text{max,wk}}$ values for legumes significantly lower than for maize and not significantly higher than for wheat (Table 6).

For comparison of the extent of VPD limitation between sites and years for those sites for which the model of Eq. [3–5] with VPD dependence of the CO₂ exchange was applied, we used the D_{VPD} parameter calculated from the cumulative distribution of the curvature parameter, σ_{VPD} , of Eq. [5] as the total number of days for which $\text{VPD}_{\text{max}} \geq 1$ kPa and $\sigma_{\text{VPD}} \leq 4$ kPa (Fig. 3). We found that the number of days when an atmospheric water deficit was affecting the productivity of the legume crops varied from 29 to 73 d (Table 5), with a trend of increasing from north to south, most closely correlating with the sum of temperatures $>5^\circ\text{C}$ [correlation coefficient $r(\text{Tsum5}, D_{\text{VPD}}) = 0.37$].

Source–Sink Activity of the Legume Crop Fields

Time series of daily values of photosynthesis $P_g(t)$, respiration $R_e(t)$, net daily CO₂ flux $F(t)$, and its cumulative sum, the cumulative net ecosystem production, $\text{iNEP}(t)$, provide a comprehensive description of the dynamics of the CO₂ exchange in the legume crop fields. Examples in Fig. 5 show that the legume crops exhibited a variety of patterns of the integrated net ecosystem production curves $\text{iNEP}(t)$, from predominantly accumulative, demonstrated by alfalfa crops (Fig. 5C and 5G) through nearly equilibrium, recorded in the faba bean crop cultivated for forage and in highly productive soybean crops (Fig. 5A, 5E, and 5H), to the negative net CO₂ balance observed on other soybean fields (Fig. 5B, 5D, and 5F).

The annual integrals of gross primary production, total ecosystem respiration, and the net ecosystem production calculated according to Eq. [3–5], with $P_g(t_j)$ and $R_e(t_j)$ for missing days t_j gap-filled using interpolated parameters, are

presented in Table 7 along with the maximum annual values of daily $P_{g,\text{max}}$, $R_{e,\text{max}}$, and F_{max} . The maximum daily rate of photosynthetic assimilation of the legume crops, $P_{g,\text{max}}$, in Table 7 was 71.1 g CO₂ m⁻² d⁻¹ recorded for the soybean crop at the Bondville site in 2004, which is lower but comparable to the maximum of 82 g CO₂ m⁻² d⁻¹ obtained from the Thomas and Hill (1949) estimate of $P_{g,\text{max}} = 56$ g dry matter m⁻² d⁻¹ for an experimental alfalfa crop (assuming 40% C content of the dry matter). This $P_{g,\text{max}} = 71.1$ g CO₂ m⁻² d⁻¹ for legumes is lower than 110 and 79 g CO₂ m⁻² d⁻¹ established at the maize and wheat flux tower sites, respectively, of midcontinent North America (Gilmanov et al., 2013). At the same time, the maximum daily respiration $R_{e,\text{max}} = 62.6$ g CO₂ m⁻² d⁻¹ for legumes was higher than 32 g CO₂ m⁻² d⁻¹ established for wheat fields and comparable to 64 g CO₂ m⁻² d⁻¹ for maize fields (Gilmanov et al., 2013).

Our estimates of the $P_{g,\text{max}}$, $R_{e,\text{max}}$, and F_{max} in legume fields are consistent with data of other researchers who used different methods. Suyker et al. (2005) estimated $P_{g,\text{max}} = 66$ and $R_{e,\text{max}} = 44$ g CO₂ m⁻² d⁻¹ for the soybean rotation of the irrigated Mead site in 2002, which compares with our estimates of 59 and 41 g CO₂ m⁻² d⁻¹ for the same site-year. Peng and Gitelson (2012) estimated the error of the daily soybean P_g values for the same site as $\text{SE} = \pm 8.3$ g CO₂ m⁻² d⁻¹. Applying this error value to statistically compare both daily photosynthesis and respiration maxima, the difference between the estimates of Suyker et al. (2005) and our estimates lies within the ± 2 SE range and therefore may be considered not significant. According to Verma et al. (2005) and Peng and Gitelson (2012) for the rainfed soybean crop at the Mead site in 2002, $P_{g,\text{max}} = 53.9$ g CO₂ m⁻² d⁻¹ and $F_{\text{max}} = 23.8$ g CO₂ m⁻² d⁻¹, which are also rather close to our estimates for the same site-year of $P_{g,\text{max}} = 55.7$ g CO₂ m⁻² d⁻¹ and $F_{\text{max}} = 26.2$ g CO₂ m⁻² d⁻¹.

In terms of the annual totals, which reflect not only the intensive physiological parameters of species and cultivars but also such extensive parameters as length of the period of active photosynthesis during the year, the situation is as follows: the mean annual GPP (Eq. [9]) from flux-tower sites in maize fields was 4480 g CO₂ m⁻² yr⁻¹, in wheat fields it was 2393 g CO₂ m⁻² yr⁻¹ (Gilmanov et al., 2013), and in legume fields it was 3056 g CO₂ m⁻² yr⁻¹ (this study). The corresponding values for ecosystem respiration RE (Eq. [10]) are 3269 for maize, 2276 for wheat, and 3159 g CO₂ m⁻² yr⁻¹ for legume crops. As a result, the mean annual net ecosystem production NEP (Eq. [11]) amounts to 1211 g CO₂ m⁻² yr⁻¹ for maize, 116 g CO₂ m⁻² yr⁻¹ for wheat

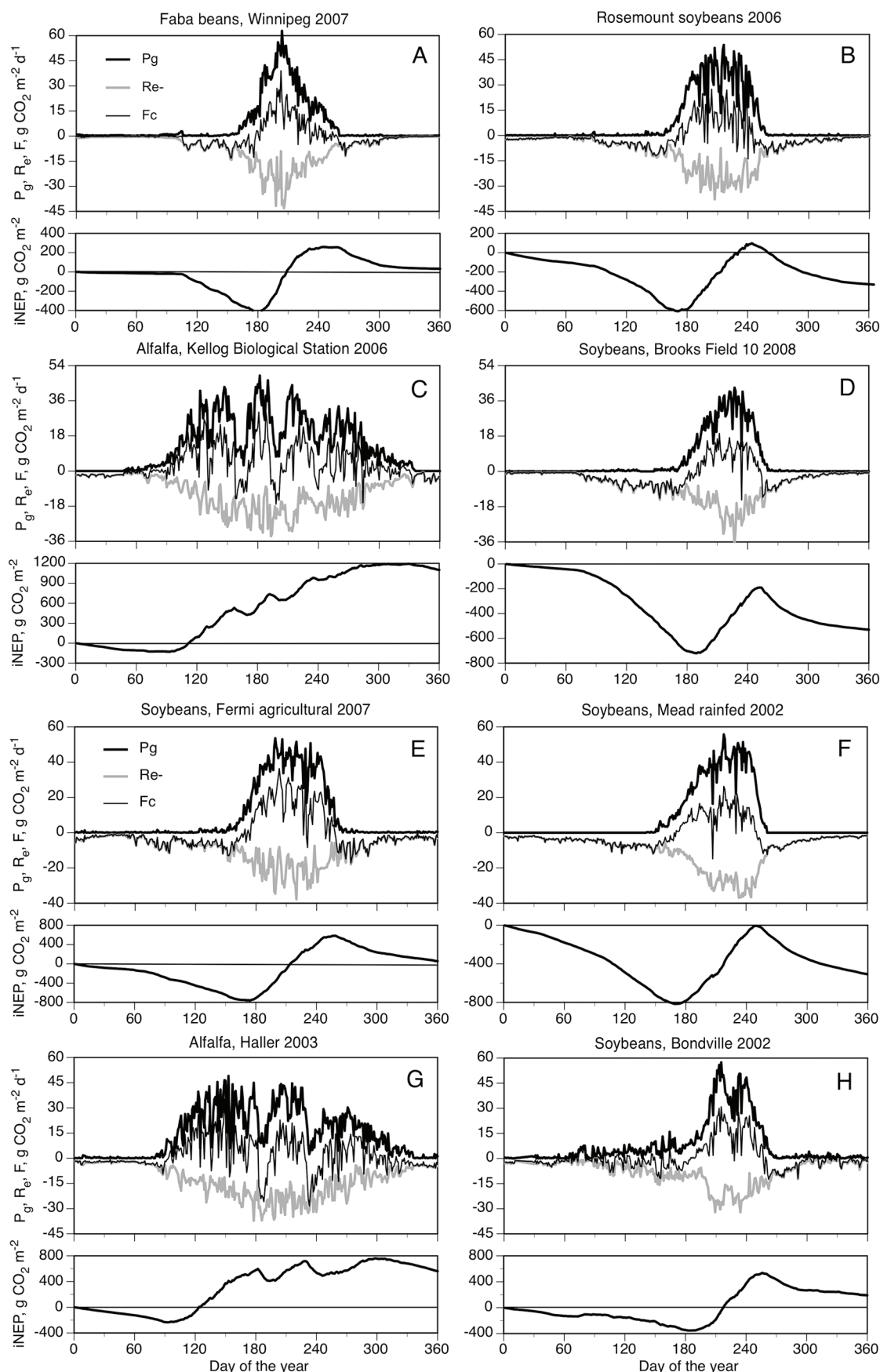


Fig. 5. Seasonal dynamics of gross photosynthesis P_g , ecosystem respiration R_e , net ecosystem CO_2 exchange F , and accumulated net ecosystem production $iNEP$ in selected legume fields: (A) faba bean, Trace Gas Manitoba, 2007; (B) soybean, Rosemount conventional, 2006; (C) alfalfa, Kellogg Biological Station, 2006; (D) soybean, Brooks Field 10, 2008; (E) soybean, Fermi agricultural site, 2007; (F) soybean, Mead rainfed, 2002; (G) alfalfa, Haller, 2003; and (H) soybean, Bondville, 2002.

Table 7. The daily maxima of gross photosynthesis ($P_{g,max}$), ecosystem respiration ($R_{e,max}$), and net ecosystem exchange (F_{max}) and the annual totals of photosynthetic production (GPP), respiration (RE), and net ecosystem production (NEP) for the site-years of the study.

Site	Crop	Year	T_{air}^{\dagger} °C	PCPN [‡] mm yr ⁻¹	LGSS [§] d	Tsum5 [¶] °C d	$P_{g,max}$ g CO ₂ m ⁻² d ⁻¹	$R_{e,max}$ g CO ₂ m ⁻² d ⁻¹	F_{max}	GPP	RE	NEP
Edmonton, AB, Canada	alfalfa	2010	4.18	381	189	1545	56.31	29.74	35.56	3460	2300	1160
Trace Gas Manitoba, MB, Canada	faba bean	2007	2.88	464	192	1887	62.83	43.08	38.95	2503	2470	32
Oensingen-2, Switzerland	pea	2010	8.39	1142	238	1996	67.98	62.58	28.52	3174	5240	-2066
Mandan H5, North Dakota	alfalfa	2010	5.34	605	206	2088	56.25	39.61	37.58	4332	3419	913
Rosemount alternative, Minnesota	soybean/rye	2004	7.31	766	219	2288	50.97	36.90	30.09	3228	2983	245
Rosemount conventional, Minnesota	soybean	2004	7.31	766	219	2288	41.90	24.16	24.73	2070	2434	-364
Rosemount conventional, Minnesota	soybean	2006	9.20	669	214	2548	53.75	37.89	25.59	2710	3041	-331
Avignon, France	pea	2005	14.01	491	298	3476	60.72	34.56	32.43	1966	2578	-612
Lennox, SD	soybean	2012	10.47	336	239	2999	40.15	17.82	23.62	1360	2032	-672
Kellogg Biological Station, Michigan	alfalfa	2006	10.05	1156	233	2496	48.87	33.38	30.52	4932	3845	1086
Brooks Field-10, Iowa	soybean	2008	7.78	1179	212	2538	42.74	37.15	19.33	1961	2495	-534
Fermi agricultural site, Illinois	soybean	2007	9.92	1166	231	2940	53.53	37.81	36.31	3288	3250	38
Fermi agricultural site, Illinois	soybean	2009	8.02	1162	226	2429	44.26	26.53	26.65	2131	2826	-695
Ames, IA	soybean	2003	9.01	718	225	2688	49.40	38.30	22.02	2353	3159	-806
Mead rainfed, Nebraska	soybean	2002	10.71	544	234	2958	55.73	36.91	26.19	2964	3483	-519
Mead rainfed, Nebraska	soybean	2004	10.35	670	248	2919	52.74	30.47	29.95	2913	3244	-331
Mead irrigated rotation, Nebraska	soybean	2002	10.55	831	231	2911	58.84	41.04	24.62	3165	3277	-112
Borgo Cioffi, Italy	alfalfa	2002–2003	16.31	787	356	3933	53.80	31.97	31.77	6771	5596	1175
Haller, PA	alfalfa	2003	8.87	1193	239	2383	48.98	37.16	35.11	5219	4673	546
Bondville, IL	soybean	1998	12.55	930	266	3290	40.61	27.76	26.87	2063	2712	-649
Bondville, IL	soybean	2000	10.71	582	249	3051	52.95	29.01	36.75	2724	3014	-291
Bondville, IL	soybean	2002	11.65	704	244	3063	57.42	32.12	30.83	2998	2821	177
Bondville, IL	soybean	2004	11.31	1010	266	3046	71.09	37.77	45.38	4032	3269	763
Bondville, IL	soybean	2006	11.83	1025	262	2887	55.36	33.67	30.53	3251	3394	-143
Lamont ARM main, Oklahoma#	soybean	2006	16.46	486	313	4385	15.09	19.93	12.58	389	985	-596
Winfred Thomas ARS, Alabama	soybean/winter wheat	2007	17.60	567	314	4806	36.09	21.23	16.07	2725	3096	-371
Winfred Thomas ARS, Alabama	soybean/winter wheat	2008	16.20	1310	307	4312	35.90	22.37	13.23	3364	3494	-130
Winfred Thomas ARS, Alabama	soybean/winter wheat	2009	16.78	1383	307	4381	33.75	27.75	14.33	3997	3925	72
Vienna, GA ^{††}	peanut	2005	16.77	1265	323	4386	46.34	24.59	25.89	2591	2554	37
Min.			2.88	336	189	1545	15.09	17.82	12.58	389	985	-2066
Max.			17.6	1383	356	4806	71.09	62.58	45.38	6771	5596	1175
Mean			10.78	838	252	2997	49.81	32.87	28.00	3056	3159	-103
SE			3.87	308	43	837	11.35	8.83	7.98	1231	914	697
CV			36	37	17	28	23	27	29	40	29	N/A
n			29	29	29	29	29	29	29	29	29	29

[†] Mean annual air temperature.

[‡] Annual precipitation.

[§] LGSS – number of days with mean daily temperature >5°C.

[¶] Annual sum of daily mean temperatures >5°C.

Productivity and respiration characteristics for Lamont ARM main site are given for the July–December period, when soybean was cultivated as the second crop after winter wheat harvested in June.

^{††} Out-of-season respiration estimated using respiration–temperature relationship.

(Gilmanov et al., 2013), and $-103 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ for legume crops. Within the legume group, the data show that perennial legumes (alfalfa) were on average a strong sink, with mean NEP of $976 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ (range $546\text{--}1175 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$), while annual legumes demonstrated a moderate to strong source activity, with mean NEP of $-327 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ (range -2066 to $763 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$), although it should be borne in mind that ecosystem respiration for annual legumes definitely includes decomposition of the net production (e.g., root residue) of the previous crop (Gebremedhin et al., 2012).

Our estimates of the GPP and RE for the rainfed (2964 and $3483 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) and irrigated rotation (3165 and $3277 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$) soybean crops at the Mead station in 2002 (Table 7) may be compared with tower-based estimates by Suyker et al. (2005) and model-based data by Grant et al. (2007). Suyker et al. (2005) obtained GPP and RE values of 3109 and $3175 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ and 3542 and $3670 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ for the rainfed and irrigated fields, respectively, showing differences $\sim 10\%$ in magnitude from our estimates, which are mostly due to differences in the estimation of daytime ecosystem respiration. Nevertheless, those differences are much smaller than the $>30\%$ differences between tower-based estimates by Suyker et al. (2005) cited above and estimates of 4257 and $4290 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ and 4653 and $4763 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, respectively, obtained by Grant et al. (2007) using the mechanistic simulation model. Gebremedhin et al. (2012) also observed the change in sink–source status of rainfed legumes (soybean): in a year with favorable atmospheric precipitation, the soybean crop was a sink, with a seasonal NEP = $242 \text{ g CO}_2 \text{ m}^{-2}$, while in a year with extreme drought (Palmer drought index = -4), the soybean crop acted as a CO_2 source, with seasonal NEP = $-154 \text{ g CO}_2 \text{ m}^{-2}$.

To graphically describe the general pattern of the source–sink activity of legume fields in comparison with cereals as another dominant group of North American crops (cf. Gilmanov et al., 2013), consider the (GPP, RE) diagram presented in Fig. 6. The advantage of this diagram is that for every point corresponding to a given site-year of measurements, it simultaneously shows all three components of the $\text{NEP} = \text{GPP} - \text{RE}$ equation: GPP as the abscissa, RE as the ordinate, and NEP as the algebraic distance in the horizontal direction from the main diagonal to the point under consideration (positive to the right, negative to the left). For example, for the point A corresponding to the legume crop with the highest NEP, the Borgo Cioffi alfalfa field in 2010, $\text{GPP} = 6771$ and $\text{RE} = 5596 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$. With correction for the organic matter input to the field by liquid sewage in the amount of $1 \text{ Mg ha}^{-1} \text{ yr}^{-1} = 367 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, point A moves to point A', corresponding to respiration of $\text{RE}' = 5229 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$. Because the point A' lies to the right of the main diagonal, the distance from the diagonal to A' in horizontal direction is positive, and $\text{NEP} = 6771 - 5229 = 1542 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$. The point B, describing the pea field at Oensingen in 2010 with $\text{GPP} = 3174$ and $\text{RE} = 5240$, has the lowest uncorrected NEP = $-2066 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, as shown by the negatively directed horizontal vector from the diagonal to point B; however, this high respiration (and the resulting low NEP) value includes $\sim 1600 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ from mineralization of the 10 Mg ha^{-1} of dry manure (7.4% water content, 47.4% C content) applied on the field in spring. With this correction, the modified NEP of the Oensingen pea

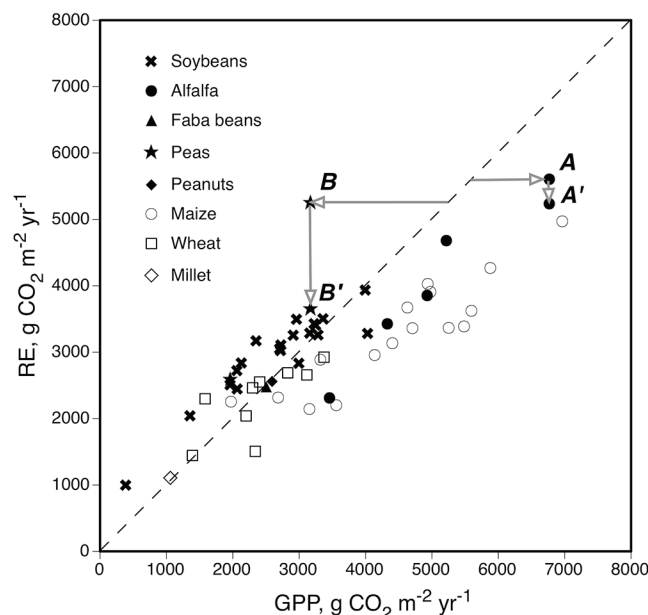


Fig. 6. Flux-tower-based estimates of annual gross primary production (GPP) and total respiration (RE) of various agroecosystems. Solid symbols show legume crops; open symbols are cereals (Gilmanov et al., 2013), presented for comparison.

crop in 2010 becomes only $-466 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, moving the corresponding point B' on the diagram much closer to the major cluster of legume crops.

Even though agronomically there are many phenological stages within a crop's cycle (emergence, vegetative production, reproduction, grain filling, senescence, fallow), we partitioned the annual CO_2 exchange from the legumes into two distinct periods: a relatively short period from emergence to harvest, when the curve of accumulated NEP is monotonically increasing (legume growing season), and the considerably longer period after harvest until the emergence of a new crop during the next year (fallow). Overall in Fig. 6, only six of the 29 legume points (including, not surprisingly, five alfalfa plots) are located significantly to the right of the diagonal, indicating strong CO_2 sink activity, while 14 (including 11 soybean crops) are clearly to the left of the diagonal, being net sources of CO_2 on an annual basis. Nine of the points lie close to the 1:1 line, indicating a zero C balance with respect to atmospheric CO_2 exchange. One of the reasons for the negative net ecosystem production in many annual legumes is their shorter growing season compared with cereals or perennial legumes grown for forage (according to the data in Table 5, ecophysiological parameters for alfalfa are not significantly different from annual legumes). Another reason is that legumes are usually cultivated in rotation or as the second seasonal crop following grain and/or cover crops, so that part of the NEP of the first crop is being metabolized during legume cultivation. The third reason, apparently applicable to all legumes, may be associated with the metabolic costs of symbiotic N_2 fixation. According to Werner (1992), fixing 1 g of N requires 12 g of carbohydrates. Assuming the average N_2 fixation rate as $125 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in soybean fields (Salvagiotti et al., 2008) and $250 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in alfalfa fields (Stacey et al., 1992), the annual CO_2 cost of N_2 fixation might be estimated as 220 to $440 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$. Taking into account that N_2 fixation costs are not the only reason for additional ecosystem respiration in

legume fields, at the qualitative level, these numbers compare well with the shift of $\sim 800 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ of the legume points to the left relative to the cereal points, as shown in Fig. 6, where the mean NEP for maize is $1211 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, $116 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ for wheat, and $-135 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ for legumes. In contrast to annual legumes, perennial legume crops (alfalfa) demonstrated pronounced CO_2 sink activity, with corresponding points on the GPP–RE diagram located to the right of the main diagonal. Nevertheless, on average, they also are shifted to the left compared with maize crops (Fig. 6), apparently reflecting the metabolic costs of N_2 fixation.

CONCLUSIONS

1. Ecosystem-scale physiological parameters of apparent quantum yield, photosynthetic capacity, ecosystem respiration, and photosynthetic light-use efficiency of the legume crops of North America estimated from flux-tower measurements using light-response function methods have intermediate values between the higher values for maize and lower values for wheat crops.
2. During the growing period, the parameters of quantum yield, photosynthetic capacity, respiration rate, and light-use efficiency exhibited pronounced patterns of seasonal variation, reflecting combined changes in intensive (physiological and phenological state) and extensive (biomass and leaf area) characteristics of the plant canopy, which have strong implications for the “light-use efficiency-based” models of ecosystem CO_2 exchange.
3. In periods of strong limitation of plant productivity due to water deficit, it is necessary to modify the classical nonrectangular hyperbolic equation of the canopy CO_2 exchange by introduction of VPD-dependent control of photosynthetic uptake. The curvature coefficient of the VPD response, σ_{VPD} (Eq. [5]), and characteristics derived from it, like the number of days when $\sigma_{\text{VPD}} < 4$ and $\text{VPD}_{\text{max}} \geq 1.0 \text{ kPa}$, may be used to quantify the level of VPD limitation of CO_2 exchange for comparative purposes.
4. Perennial legume crops (alfalfa) perform as strong sinks for atmospheric CO_2 , with mean NEP of 980 (maximum 1200) $\text{g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, but remain less productive than maize crops, with mean NEP of 1200 (maximum 2100) $\text{g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$, reduction in the alfalfa NEP being comparable to the costs of symbiotic N_2 fixation estimated at 220 to 440 $\text{g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$.
5. Annual RE controls a larger fraction of the GPP for annual legume crops than for cereals (Fig. 6), also reflecting generally lower NEP values and the potential for CO_2 –source activity, particularly for soybean and pea crops. This conclusion has four far-reaching implications. First, metabolic expenditures for N_2 fixation combined with the comparatively short growing season(s) may be among the factors contributing to lower annual NEP. Second, any management activity that affects C exchange during the period when legumes are not present can greatly change the annual C balance. These activities range from prolonging the fallow period (increasing the likelihood of an annual source) to multicropping systems (increasing the sink capacity), or other management activities, e.g., increased irrigation or fertilizer use. Third, any change in the abiotic drivers that affect the process rates (e.g.,

temperature, water availability, or light) will in turn affect the source–sink strength of these legume crops. A change in these drivers can be in the magnitude, quality, and periodicity, as well as the timing of seasonal changes, e.g., phenology, early-onset spring, or early-onset summer drought. Lastly, interactions among natural drivers, management choices, and agronomic economies are likely to change local to regional C balances of future legume cropping—but also bound within the ecophysiological parameters presented here.

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