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Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis

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Abstract

Tower CO_2 flux measurements from 20 European grasslands in the EUROGRASSFLUX data set covering a wide range of environmental and management conditions were analyzed with respect to their ecophysiological characteristics and CO_2 exchange (gross primary production, P_g, and ecosystem respiration, R_e) using light-response function analysis. Photosynthetically active radiation (Q) and top-soil temperature (T_s) were identified as key factors controlling CO_2 exchange between grasslands and the atmosphere at the 30-min scale. A nonrectangular hyperbolic light-

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response model $P(Q)$ and modified nonrectangular hyperbolic light–temperature-response model $P(Q, T_s)$ proved to be flexible tools for modeling CO_2 exchange in the light. At night, it was not possible to establish robust instantaneous relationships between CO_2 evolution rate r_n and environmental drivers, though under certain conditions, a significant relationship $r_n = r_0\,e^{k_T T_s}$ was found using observation windows 7–14 days wide. Principal light-response parameters—apparent quantum yield, saturated gross photosynthesis, daytime ecosystem respiration, and gross ecological light-use efficiency, $\varepsilon = P_g/Q$, display patterns of seasonal dynamics which can be formalized and used for modeling. Maximums of these parameters were found in intensively managed grasslands of Atlantic climate. Extensively used semi-natural grasslands of southern and central Europe have much lower production, respiration, and light-use efficiency, while temperate and mountain grasslands of central Europe ranged between these two extremes. Parameters from light–temperature-response analysis of tower data are in agreement with values obtained using closed chambers and free-air CO_2 enrichment. Correlations between light-response and productivity parameters provides the possibility to use the easier to measure parameters to estimate the parameters that are more difficult to measure. Gross primary production (P_g) of European grasslands ranges from 1700 g CO_2 m^{-2} $year^{-1}$ in dry semi-natural pastures to 6900 g CO_2 m^{-2} $year^{-1}$ in intensively managed Atlantic grasslands. Ecosystem respiration (R_e) is in the range $1800 < R_e < 6000$ g CO_2 m^{-2} $year^{-1}$. Annual net ecosystem CO_2 exchange (NEE) varies from significant net uptake (>2400 g CO_2 m^{-2} $year^{-1}$) to significant release (<−600 g CO_2 m^{-2} $year^{-1}$), though in 15 out of 19 cases grasslands performed as net CO_2 sinks. The carbon source was associated with organic rich soils, grazing, and heat stress. Comparison of P_g, R_e, and NEE for tower sites with the same characteristics from previously published papers obtained with other methods did not reveal significant discrepancies. Preliminary results indicate relationships of grassland P_g and R_e to macroclimatic factors (precipitation and temperature), but these relationships cannot be reduced to simple monofactorial models.

Keywords: Grassland ecosystems; Eddy covariance-measured CO_2 flux; Net CO_2 flux partitioning; Gross primary production; Ecosystem respiration; Nonrectangular hyperbolic model

1. Introduction

European grasslands occupy more than 90 million ha (~40% of agricultural area) and constitute an important economic and environmental resource (Dziewulska, 1990; Follett and Schuman, 2005; Lüscher et al., 2005). Expert estimates and model-based calculations indicate that global atmospheric change and management may be substantially affect grasslands (Parton et al., 1993; Coughenour and De-Xing, 1997; Thornley and Cannell, 1997; Kundzewicz and Parry, 2001; Fuhrer, 2003; Rounsevell et al., 2005). At the same time, through a number of feedback mechanisms grasslands influence the carbon, water, and energy budgets of the atmosphere and may mitigate the greenhouse effect (Allen-Diaz et al., 1996; Follett et al., 2001). The fundamental role in determining the sensitivity and feedbacks of grasslands to global environmental changes belongs to the interaction of photosynthetic assimilation (characterized by gross primary productivity, P_g) and total ecosystem respiration (R_e). Quantitative description of these ecosystem-scale characteristics is a necessary condition for understanding, prediction and management of ecosystems (Odum, 1971). At present, estimates of P_g and R_e based on long-term measurements are available for several grassland communities (Dirks et al., 1999; Gilmanov et al., 2002, 2003a,b, 2004, 2005a,b; Jacobs et al., 2003; Novick et al., 2004; Xu and Baldocchi, 2004; Wohlfahrt et al., 2005b), but there are no systematic generalizations concerning the ranges of these variables and their relationships to environmental and management factors in grasslands. Results of the International Biological Program, which have greatly contributed to our understanding of carbon cycling and energetics of grasslands (Coupland, 1979; Breymeyer and Van Dyne, 1981), did not cover the gross productivity and total respiration processes in detail because of the lack of adequate methods at the time. Only with the advancement of micrometeorological studies of the ecosystem-scale CO_2 exchange (Baldocchi et al., 1996; Baldocchi, 2003) combined with the development of methods for partitioning net ecosystem CO_2 exchange into gross assimilation and respiration components (Norman and Arkerbauer, 1991; Wofsy et al., 1993; Ruimy et al., 1995; Goulden et al., 1996; Gilmanov, 2001; Gilmanov et al., 2003a, 2004, 2005a,b; Bowling et al., 2003), it became possible to obtain measurement-based estimates of gross primary productivity and total ecosystem respiration.

Tower flux measurements in grasslands of Europe initiated in Austria (Cernusca, 1991; Tappeiner and Cernusca, 1996) and The Netherlands (Hensen et al., 1996;) were subsequently expanded in a series of nationally supported studies and under the auspices of European projects like ECOMONT/CARBOMONT (Cernusca et al., 1998; Cernusca, 2004), GreenGrass (Soussana et al., 2004) and CarboEurope-IP/Grassland-Wetland section (CarboEurope-IP, 2003). In this study we used the EUROGRASSFLUX dataset assembled by T. Gilmanov during his CarboEurope-IP-supported 11 month visit at the French National Institute of Agronomy Research (INRA) in Clermont-Ferrand, France (2004–2005). Resulting from the true spirit of cooperation among participating scientists, the data set includes 28 site-years of long-term measurements of the net CO_2 exchange of grassland ecosystems collected at 20 flux-tower sites in 9 European countries representing a wide range of climatic and management regimes. These net tower fluxes were partitioned into gross assimilation and ecosystem respiration components to perform comparative analysis of their relationships to ecological and management factors.

2. Materials and methods

2.1. Study sites

Grassland CO_2-flux stations used in this study are shown on Fig. 1 and described in Tables 1 and 2. They cover a wide range of climatic conditions in the latitudes from Finland to Spain, and the longitudes from Ireland to Hungary, and elevations from sea level to 1800 m at the mountain grasslands of the Pyrenees Mountains. With respect to management, the data set covers the gradient from semi-natural to intensively managed (grazing, hay-mowing, fertilization) grasslands. For 15 out of 20 tower flux stations, original 30-min data sets of net CO_2 exchange data were analyzed using the light-response function method described in Gilmanov (2001) and Gilmanov et al. (2003a, 2003b, 2005b). For the Rigi-Seebodenalp and Neustift sites light-response analysis was performed by site investigators (Rogiers and Eugster, and Wohlfahrt, respectively), and for the Cabauw, Hegyhátsál, and Monte Bondone sites available estimates of ecophysiological and CO_2 budget parameters were utilized.

2.2. Methods of tower CO_2 flux measurements

At present, all the 20 European grassland CO_2 flux sites are equipped with eddy-covariance systems, though in mid-1990s at the Caubauw site an aerodynamic gradient method was used. General principles of the eddy-covariance flux measurement methodology adopted by the CarboEurope IP community are described in detail by Aubinet et al. (2000, 2003), and based on this methodology, at different sites different software packages and data screening procedures were used where necessary (Table 2). Each site was equipped with an eddy covariance sensor array measuring data at 10 or 20 Hz that were used to calculate mean 30 min fluxes of CO_2, sensible heat, latent heat and momentum. The device included a fast response sonic anemometer and an open or closed path CO_2–H_2O analyzer installed on each plot taking into account footprint considerations. With open path sensors, fluxes were adjusted for the variation in air density due to the concurrent sensible heat and water vapor fluxes (Webb et al., 1980). At most sites, open-path CO_2 sensors are used as they combine precise flux measurements with robustness, high signal stability, and low maintenance and calibration needs. However, several groups have found that due to rain and dew formation, quite a large amount of data from open-path sensors has to be discarded. Therefore, it seems that for rather moist environments closed-path sensors (or a combination of both) are preferable. Different types of software are used to calculate fluxes (Table 2). Within various projects participating sites have initially checked their software against "gold files" (standard files for intercomparison of flux software within a network) and adjustments have been made to ensure compatibility of the results.

Quality check of the data was done following CarboEurope IP guidelines (Aubinet et al., 2003). Additional filtering

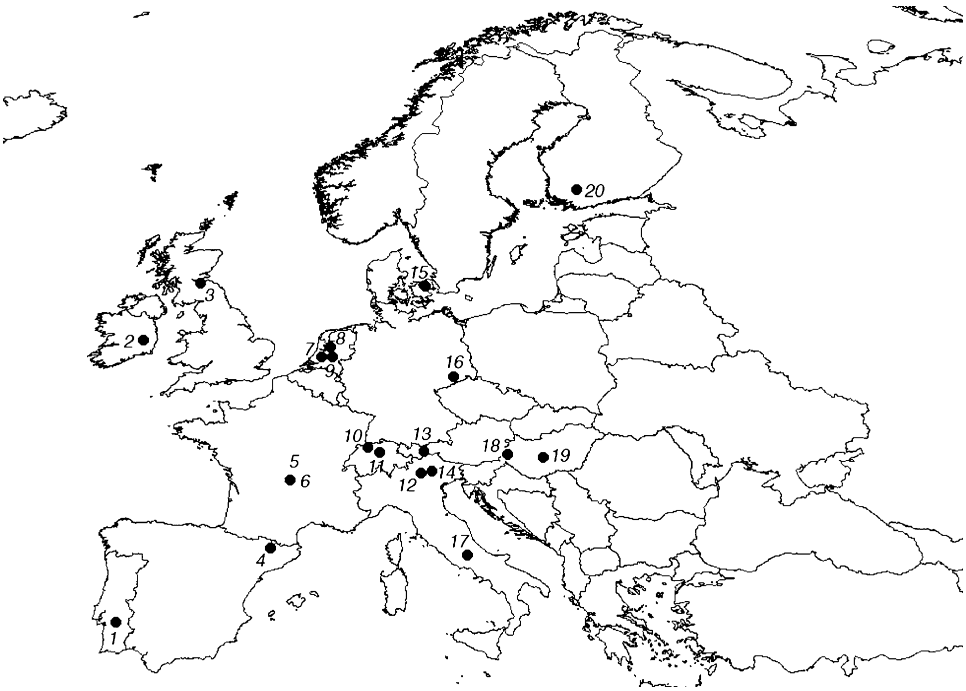


Fig. 1. Geographical distribution of the study sites: (1) Tojal, Portugal; (2) Carlow, Ireland; (3) Easter Bush, U.K.; (4) Alinyà, Spain; (5) Laqueuille (extensive), France; (6) Laqueuille (intensive), France; (7) Cabauw, The Netherlands; (8) Lelystad, The Netherlands; (9) Haarweg, The Netherlands; (10) Oensingen (extensive), Switzerland; (11) Rigi-Seebodenalp, Switzerland; (12) Monte Bondone, Italy; (13) Neustift, Austria; (14) Malga Arpaco, Italy; (15) Lille Valby, Denmark; (16) Grillenburg, Germany; (17) Amplero, Italy; (18) Hegyhátsál, Hungary; (19) Bugacpuszta, Hungary; (20) Jokioinen, Finland.

Table 1
Site characteristics of the European grassland CO_2 flux-tower stations

No.	Site, country	Year	Latitude (°)	Longitude (°)	Elevation (m)	Annual temperature (°C)	Annual precipitation (mm year^{-1})	Max leaf area index (m^2 m^{-2})	Grassland type	Soil	Mineral N input (kg N ha^{-1} year^{-1})	Grazing/cut herbage (g C m^{-2} y^{-1})	C import (manure) (g C m^{-2} year^{-1})
1	Tojal, Portugal	2004–2005	38.4744	−8.0236	190	14.6	387	<1.0	Semi-natural grassland	Luvisol	0	Grazed	0
2	Carlow, Ireland[a]	2003	52.85	−6.90	50	10.1	974	4.09	Sown grass-clover	Calci-gley luvisol, medium texture	200	1 cut; extensive grazing July–September to maintain 8–10 cm grass height	0
3	Easter Bush, U.K.[a]	2003	55.8660	−3.2058	190	9.0	870	2.47	Intensive permanent	Sandy-clay loam	147	Cut/grazed	3
4	Alinyà, Spain[b]	2003–2004	42.1522	1.4485	1770	6.1	1064	–	Extensive nonmanaged	Lithic cryrendoll	0	Grazing (mid-June to October)	0
5	Laqueuille ext., France[a]	2002–2003	45.6431	2.7358	1040	8.62	1064	3.0	Semi-natural extensively managed	Andosol	0	Grazed	0
6	Laqueuille int., France[a]	2002–2003	45.6431	2.7358	1040	8.62	1013	3.0	Semi-natural intensively managed	Andosol	170	Grazed	0
7	Caubauw, The Netherlands	1993–1994	51.971	4.927	−0.7	9.8	786	2.0	Intensive permanent	Alluvial clay on peat	–	Cut/grazed	–
8	Lelystad, The Netherlands[a]	2003	52.5	5.5	0	10	780	2.0	Intensive permanent	Clay polder soil	237	Cut/grazed	92
9	Haarweg, The Netherlands	2002	51.97	5.63	7	9.5	760	3.4	Sown grassland	Heavy alluvial clay	0	Cut (not removed)	0
10	Oensingen ext., Switzerland[a]	2002–2003	47.2833	7.7333	450	9.2	1109	5.9	Extensively managed grassland	Stagnic cambisol	0	3 cuts (295)	0
11	Rigi-Seebodenalp, Switzerland[b]	2003	47.05838	8.45736	1025	7.32	1327	4.4	Subalpine grassland	Stagnic cambisol	0	Cut, followed by grazing	0
12	Monte Bondone, Italy[b]	2004	46.014	11.045	1550	5.5	1189	2.8	Subalpine grassland	Humic umbrisols	0	1 cut	0
13	Neustift, Austria[b]	2001	47.1167	11.3167	970	6.5	852	4.6	Mountain grassland	Fluvisol	0	3 cuts (317)	284
14	Malga Arpaco, Italy[a]	2003	46.1167	11.7028	1699	5.49	1816	3.9	Semi-natural mountain	Alfisol, sandy-loam	45	Grazed	0
15	Lille Valby, Denmark[a]	2004	55.7	12.1167	15	8.53	1119	6.87	Barley-grass	Sandy-loam	176	2 cuts (333)	1400
16	Grillenburg, Germany	2004	50.9496	13.5125	385	7.2	853	3.9	Managed grassland	Speudo-gley	0	3 cuts	0
17	Amplero, Italy[b]	2004	41.8667	13.6333	900	9.49	1243	2.3	Semi-natural mountain	Haplic phaeozem	0	Cut/grazed	0
18	Hegyhátsál, Hungary	1999–2000	46.95	16.65	248	8.9	750	–	Semi-natural grass field	Alfisol	0	2 cuts	0
19	Bugacpuszta, Hungary[a]	2003	46.6911	19.6013	111	9.83	450	1.5	Semi-natural dry grassland	Sandy chernozem	0	Grazed	0
20	Jokioinen, Finland	2002	60.8989	23.5144	104	3.9	581	5.3	Sown grassland	Terric histosol	141	2 cuts (373)	0

[a] Belongs to the GreenGrass network (http://clermont.inra.fr/greengrass/).

[b] Belongs to CARBOMONT network (http://carbomont.uibk.ac.at/).

Table 2
Technical characteristics of tower CO_2 flux measurements and initial data processing at European grassland sites

No.	Site, country	Method[a]	Measurement height (m)	CO_2 sensor	Software	Data coverage (%)	Data retained (%)	u^* correction use, threshold	Frequency correction	Footprint calculation	Quality check of fluxes
1	Tojal, Portugal	EC	2.5	Open-path	Eddysoft	90	53	$u^* < 0.08$	No	Yes	CarboEurope IP
2	Carlow, Ireland	EC	2.0	Closed-path	Edisol-Edire	84	45	$u^* < 0.2$	Yes	Yes	CarboEurope IP
3	Easter Bush, U.K.	EC	2.15	Open-path	LabView in-house flux program	93	47	$u^* < 0.1$	Yes	No	CarboEurope IP
4	Alinyà, Spain	EC	2.25	Open-path	Eddylogp (SC-DLO de Fastcom)	64	41	$u^* < 0.1$	Yes	Yes	CarboEurope IP
5	Laqueuille ext., France	EC	2.0	Open-path	Edisol-Edire	70	53	$u^* < 0.08$	No	Yes	CarboEurope IP
6	Laqueuille int., France	EC	2.0	Open-path	Edisol-Edire	80	42	$u^* < 0.1$	No	Yes	CarboEurope IP
7	Caubauw, The Netherlands	Aerodynamic gradient, EC	10	Ultramat 5e, Siemens	–	–	–	–	–	–	–
8	Lelystad, The Netherlands	EC		Closed-path	In-house ECN	64	50	Yes	No	No	
9	Haarweg, The Netherlands	EC	4	Open-path	Van den Hurk, 1996	84	46	$u^* < 0.1$	Yes	No	Power and co-spectra, energy balance closure
10	Oensingen ext., Switzerland	EC	1.2	Open-path	FAL/PVWave	97	34	No	Yes	Yes	CarboEurope–IP, only high-quality data retained
11	Rigi-Seebodenalp, Switzerland	EC	2.4	Open-path	In-house ETH	46	42	When $u'w' \geq 0$	Yes	Yes	3 σ-outliers; relative humidity check; momentum flux direction
12	Monte Bondone, Italy	EC	2.5	Open-path	Edisol-Edire	92	66	No	Yes	Yes	CarboEurope-IP
13	Neustift, Austria	EC	3.0	Closed-path	Edisol-Edire	47	33	$u^* < 0.1$	Yes	Yes	Outlier removal; IRGA pressure CV; third rotation angle; turbulence/stationarity test
14	Malga Arpaco, Italy	EC	2.8	Open-path	In-house software	95	80	No	No	Yes	CarboEurope IP
15	Lille Valby, Denmark	EC	2.5	Open + closed-path	In-house software	98	93	No	No	Yes	CarboEurope IP
16	Grillenburg, Germany	EC	3.0	Open-path	In-house software	95	59	$u^* < 0.1$	Yes	Yes	CarboEurope IP
17	Amplero, Italy[3]	EC	4.0	Open-path	MASE by Manca	89	65	No	Yes	Yes	CarboEurope IP
18	Hegyhátsál, Hungary	EC	3.0	Closed-path	In-house software	64	94	No	Yes	Yes	5 σ-outliers; instrumental noise caused by weather
19	Bugacpuszta, Hungary	EC	4.0	Open-path	In-house software	75	63	$u^* < 0.1$	Yes	No	CarboEurope IP
20	Jokioinen, Finland	EC	3.0	Closed-path	LabView/BARFLUX	89	49	$u^* < 0.1$	Yes	No	Outlier removal; raw data spike test; variance test; anemometer temperature test

[a] EC—eddy covariance.

criteria were applied based on friction velocity (u^*) values. Critical values of u^* below which CO_2 flux is strongly dependant of u^* were determined empirically for each site (Table 2). They were invariably associated with nighttime measurements and were systematically discarded. The footprint of the flux in most of the plots was evaluated as a function of wind speed and direction and stability as part of the CarboEurope IP project (M. Göckede, personal communication). Preliminary identification of gaps and bad quality data was conducted according to the FLUXNET/CarboEurope IP methodology (Falge et al., 2001; Reichstein et al., 2005) with subsequent gap-filling using light-response functions, factorial regression, and time-series-based methods. A weather station coupled with a data logger was installed in each site. It provided 30 min averaged values of global radiation, net radiation, incident photosynthetic photon flux density, soil temperature (typically at soil surface and at 5–10–30–50 cm depth), soil water content (at 5–10–30–50 cm depth), air temperature and vapor pressure, wind speed and direction, and rainfall.

2.3. Net CO_2 exchange partitioning into gross primary production and total ecosystem respiration components

Partitioning of the net ecosystem CO_2 exchange (F_{NEE}) into its P_g, R_e, and storage change rate components using the data of flux and concentration measurements at the tower is illustrated by Fig. 2. Let $S_{CO_2}(t)$ denote the storage of CO_2 in the air layer between the soil surface ($z = 0$) and the CO_2 flux sensor located at height z_m.

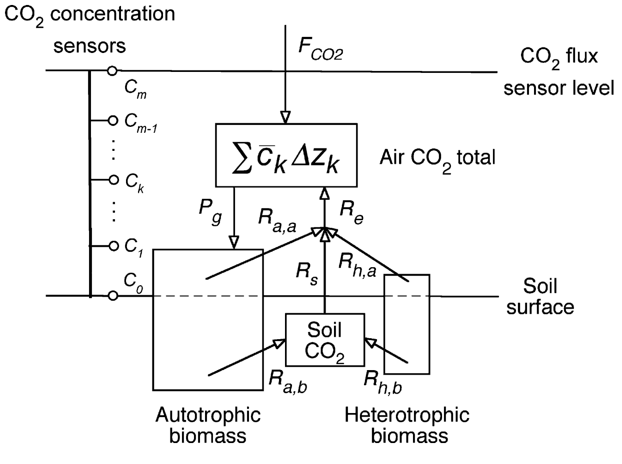


Fig. 2. Conceptualization of the tower CO_2 flux measurements in grasslands. CO_2 exchange between grassland ecosystem and the external atmosphere, F_{CO_2}, is measured by the eddy covariance sensor located at height z_m above the soil surface $z_0 = 0$. To estimate CO_2 storage, concentrations $C_k = C(z_k)$ are sampled at heights, z_k ($k = 0, 1, \ldots, m$). Major processes determining dynamics of CO_2 include uptake with gross primary production, P_g, exchange of CO_2 with atmosphere, F_{CO_2} (using physiological sign convention, flux to the ecosystem is considered positive), and release of CO_2 through ecosystem respiration, R_e, which includes respiration of aboveground autotrophic ($R_{a,a}$) and heterotrophic organisms ($R_{h,a}$) and soil respiration (R_s). The later consists of respiration of belowground autotrophs ($R_{a,b}$) and belowground heterotrophs ($R_{h,b}$) (modified after Gilmanov et al., 2005b).

Assuming no advection and using "ecological" sign convention (when plant uptake of CO_2 from the atmosphere to ecosystem is positive), the amount $S_{CO_2}(t)$ is increased by the influx of CO_2 from the atmosphere, F_{CO_2}, and by total ecosystem respiration, R_e, and is decreased by photosynthetic uptake, P_g, leading to the equation of the rate of CO_2 storage change as:

$$\frac{dS_{CO_2}}{dt} = F_{CO_2} + R_e - P_g. \qquad (1)$$

Introducing the net ecosystem CO_2 exchange rate, $F_{NEE} = P_g - R_e$, we obtain:

$$F_{NEE} = P_g - R_e = F_{CO_2} - \frac{dS_{CO_2}}{dt}. \qquad (2)$$

For modeling purposes, it is convenient to separate Eq. (2) into daytime (incoming photosynthetically active radiation $Q > 0$) and nighttime ($Q = 0$) parts. Introducing the notation P for F_{NEE} during daytime, R_{day} for ecosystem respiration during daytime, and R_{night} for ecosystem respiration at night, we obtain:

$$P = P(Q, X_1, \ldots, X_n) = P_g - R_{day}$$
$$= F_{CO2} - \frac{dS_{CO2}}{dt} \quad (\text{when } Q > 0) \qquad (3)$$

and

$$R_{night} = R_{night}(X_1, \ldots, X_n)$$
$$= -\left(F_{CO2} - \frac{dS_{CO2}}{dt}\right) \quad (\text{when } Q = 0). \qquad (4)$$

Eqs. (3) and (4) form the foundation of the light-response function method of net CO_2 exchange partitioning because relating experimentally measured F_{NEE} to photosynthetically active radiation, Q, and, possibly, other relevant factors X_i (air or soil temperature, air relative humidity, etc.) in the framework of appropriate multivariate response functions allows numerical identification of the P_g and R_e components of F_{NEE}.

2.4. Multivariate time series analysis of the CO_2 flux data sets

Data sets of 30-min values of F_{CO_2} (or F_{NEE}, when storage data were available) and the accompanying factors X_i (photosynthetically active radiation, Q; global incoming radiation, R_g; air temperature, T_a, soil temperature, T_s, relative humidity, RH; wind speed, U; precipitation, PCPN and other factors) were analyzed using methods of multidimensional time series analysis, including estimation of the sample covariance matrix $\boldsymbol{\Gamma}(\tau) = (\gamma_{kj}(\tau))$ and the smoothed spectral density matrix $\boldsymbol{f}(\omega) = (f_{kj}(\omega))$, where $f_{kj}(\omega)$ is the cross spectrum of variables X_k and X_j (Priestley, 1981; Yu and He, 1995; Reinsel, 1997). Referring index 1 to F_{CO_2}, index 2 to Q, and index 3 to soil temperature, T_s, $f_{12}(\omega)$ becomes the cross spectrum between CO_2 flux and photosynthetically active radiation at frequency ω, and $f_{13}(\omega)$ is the cross spectrum of CO_2 flux and soil temperature at ω. An important task of time series analysis is the identification of relationships among variables in both the time and frequency domains. Because in the general case the cross-spectrum $f_{kj}(\omega)$ is a complex number, $f_{kj}(\omega) = c_{kj}(\omega) + iq_{kj}(\omega)$, it is convenient to consider its amplitude spectrum, $a_{kj}(\omega)$ and phase spectrum, $\varphi_{kj}(\omega)$:

$$f_{kj}(\omega) = a_{kj}(\omega)\,\mathrm{e}^{\mathrm{i}\varphi_{kj}(\omega)}, \tag{5}$$

where the function $a_{kj}(\omega) = \sqrt{c_{kj}^2(\omega) + q_{kj}^2(\omega)}$ is known as cross-amplitude spectrum or cospectrum, and $\varphi_{kj}(\omega) = \tan^{-1}[-q_{kj}(\omega)/c_{kj}(\omega)]$ is the phase spectrum or quadrature spectrum (Priestley, 1981). These functions convey important information about properties of the CO_2 flux and other variables in the frequency domain. In particular, the graphs of the cross-amplitudes $a_{ij}(\omega)$ accompanied by the graphs of autospectra $f_{ii}(\omega)$ and $f_{jj}(\omega)$ show in which frequency bands the highest amplitudes of CO_2 flux and environmental factors affecting it are observed. While such time series analyses are very common for raw (i.e. 10 or 20 Hz) data, it should be noted that we will apply these methods to 30-min averages in order to assess correlations among variables as a function of frequency of occurrence.

Especially interesting in this context is the coherency function, $K_{kj}(\omega)$, between variables k and j at frequency ω:

$$K_{kj}^2(\omega) = \frac{|f_{kj}(\omega)|^2}{f_{kk}(\omega)\,f_{jj}(\omega)} \tag{6}$$

that is considered as a measure of linear relationship between $X_k(t)$ and $X_j(t)$ (Priestley, 1981). Statistically significant maxima of coherency between CO_2 exchange and ecological factors may be used to identify factors most strongly affecting F_{CO_2} dynamics (e.g., Gallegos et al., 1977). Significance of the observed maxima of the squared coherence is evaluated using the F-criterion (Priestley, 1981).

2.5. Types of response functions

During the earlier period of tower flux data analysis, NEE light response was usually described by the rectangular hyperbola (Tamiya, 1951), which was considered a ‘‘universal’’ tool for light-response fitting (Ruimy et al., 1995; Luo et al., 2000):

$$P(Q;\alpha,A_{\max},r_{\mathrm{d}}) = \frac{\alpha Q A_{\max}}{\alpha Q + A_{\max}} - r_{\mathrm{d}}. \tag{7}$$

It was later shown that nonrectangular hyperbolic equation (Rabinowitch, 1951):

$$P(Q;\alpha,A_{\max},r_{\mathrm{d}},\theta) = \frac{1}{2\theta}\left(\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max}\theta Q}\right) - r_{\mathrm{d}} \tag{8}$$

represents a much more flexible and convenient fitting tool than hyperbola (7) (Thornley, 1976; Lieth and Reynolds, 1987; Boote and Loomis, 1991). Parameters in Eq. (8) applied to ecosystem-scale light response are: α, apparent quantum efficiency (initial slope of the light-response curve); $A_{\max}$, maximum gross photosynthesis; r_{d}, average daytime ecosystem respiration; θ, curvature of the light-response.

To describe the temperature dependence of ecosystem respiration, either Q_{10}-type (or equivalent exponential), Van’t Hoff, or Arrhenuis-type equations were used successfully at temperatures below 25 °C, though modified Arrhenius equation or even more flexible asymmetric bell-shaped functions were applied with better success (Gilmanov, 1977; Lloyd and Taylor, 1994; Frank et al., 2002; Reichstein et al., 2005).

For a number of grassland and shrubland ecosystems exhibiting hysteresis of the light-response, it was demonstrated that temperature-dependent modification of the nonrectangular hyperbola (Gilmanov et al., 2003b) provides a more tight fit for empirical light–temperature response:

$$\begin{aligned} &P(Q,T;\alpha,A_{\max},r_d,\theta,r_0,k_T)\\ &\quad= \frac{1}{2\theta}\left(\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max}\theta Q}\right)\\ &\qquad - r_0\,\mathrm{e}^{k_T T}, \end{aligned} \tag{9}$$

where T is temperature (soil or air, whichever is more appropriate); k_T, coefficient of temperature response; r_0, ecosystem respiration at $T = 0$ °C. Parameters on Eqs. (7)–(9) that provide best fit for daytime NEE measurements at the flux towers may be estimated using advanced nonlinear regression packages, e.g., the ‘‘Global Optimization’’ of the Mathematica® (Loehle Enterprises, 2004). Seasonal patterns typically revealed at the time-domain plots, especially for $\alpha(t)$, $A_{\max}(t)$, and $r(t)$, allow estimation of these parameters for days with absent measurements and can be used in gap-filling.

2.6. Quality control and gap filling

Original 30-min data sets of CO_2 fluxes and accompanying variables from the sites were already subjected to standard screening procedures according to the CarboEurope IP protocol (Aubinet et al., 2000, 2003). Only minor additional screening was performed at the stage of light-response analysis, mostly through visual inspection of the (Q,P) or (Q,T_s,P) scatter plots for individual days. Gap filling generally followed recommendations by Falge et al. (2001) and Reichstein et al. (2005), and in particular included the following stages. Linear or spline interpolation was used for short ($\leq$2 h) gaps. Gaps during daytime period were filled using the response functions $P(Q)$ or $P(Q,T_s)$ for the same day, if available. Otherwise, light-response parameters were interpolated using adjacent days, and response function for the day was used with interpolated parameters. Large gaps during nighttime were filled as follows. If it was possible to establish significant exponential temperature dependence for the nighttime fluxes using 30-min data with window up to 14 days wide, these relationships were used for gap filling. Otherwise, exponential respiration term of the modified nonrectangular model for daytime fluxes (9) available for the current day or interpolated from adjacent days was used to estimate nighttime respiration. Gap filling using the mean diurnal variation or median smoothing were used as the choice of last resort.

2.7. Light-use efficiency

There are two major light-use efficiency characteristics used in literature: *physiological* light-use efficiency $\varepsilon_{phys} = P_g/Q_{abs}$ calculated as a ratio of gross primary productivity to absorbed photosynthetically active radiation (Larcher, 1995), and *ecological* light-use efficiency $\varepsilon_{ecol} = P_g/Q$ calculated as the ratio of gross primary productivity to total incident photosynthetically active radiation (Cooper, 1970; Austin et al., 1978). While ε_{phys} is most adequate in studies at the individuum and population levels, ε_{ecol} has obvious advantages in at the ecosystem scale because it reflects not only physiological–biochemical properties of individual plants but also additional ecosystem-scale characteristics such as plant population density, aboveground biomass and leaf area index. This is especially evident in comparing ecosystems with similar life forms and species composition (which leads to similar ε_{phys} values) but different plant population densities and leaf area indices resulting in substantially different ε_{ecol} values. In this paper we will use only gross ecological efficiency, ε_{ecol}, *hereinafter expressed as* ε (mmol CO_2 per mol incident photosynthetically active radiation) to compare use of radiation resources by grassland ecosystems.

3. Results

3.1. Spectral coherency

For 14 sites of the EUROGRASSFLUX data set, the measurement periods with the least possible missing data were selected, occasional gaps were filled using interpolation and regression techniques, and the resulting data sets were subjected to multidimensional spectral coherency analyses. Squared coherency $K^2_{F_{CO_2},X_k}(\omega)$ graphs were constructed for every environmental factor X_k such as PAR, total radiation, air temperature, soil temperature, etc. Maximum squared coherency values and corresponding frequencies ω_{max} were identified for each of the sites, mean squared coherencies and standard deviations for factors across the sites were calculated, and the factors X_k were ranked in the order of decreasing mean maximum squared coherency. Fig. 3 shows ranking of the environmental factors in terms of their mean squared coherency with net CO_2 flux averaged over the study sites.

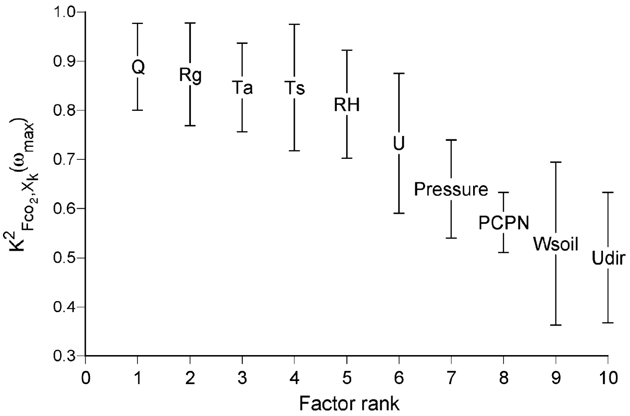


Fig. 3. Ranking of the average maxima of the squared coherencies between F_{CO_2} and environmental factors X_k (Q, photosynthetically active radiation; R_g, global radiation; T_a, air temperature (2 m); T_s, soil temperature (5 cm); RH, relative humidity; U, wind speed; Pressure, atmospheric pressure; PCPN, precipitation; W_{soil}, topsoil moisture; U_{dir}, wind direction); error bars describe standard deviations of squared coherencies for a given factor over the study sites.

3.2. Empirical light-response functions

The nonlinear regression procedure to identify parameters of light-response functions (8) and (9) was applied to every daily set of 30-min data at every site for which necessary information $\{Q(t), T_s(t), F_{CO_2}(t)\}$ was available. Convergence of the algorithm was different at different sites, but overall in more than 4 out of 5 of all days with available data it was possible to identify physiologically acceptable parameters of light-response (8) with less than 1000 iterations. From approximately 66 to 75% of these cases (i.e., 50–60% of all days with data) it was also possible to find parameters of the light–temperature response (9) providing a better fit than nonrectangular hyperbola (8). The simple rectangular hyperbolic model (7) was occasionally found to work for European grasslands for selected days (Fig. 4, Table 3). Nevertheless, the rectangular model provides rather biased estimates of light-response parameters, with errors in estimation of α, A_{max}, and r_d becoming more significant as the curvature of the light response curve increases approaching the Blackman-type light-response (Gilmanov et al., 2003a,b).

We have found that radiation plays a dominant role (i.e. explains >90% of the CO_2 flux variation during daytime), and the nonrectangular hyperbola (8) is a very effective fitting tool, equally well describing (Q,P)-scatterplots of different patterns, from low curvature (close to rectangular) case of Grillenburg (2004), day 139 ($\theta = 0.12$) (Fig. 5, Grillenburg) to high curvature (close to Blackman type) case of Malga Arpaco 2003, day 200 ($\theta = 0.97$) (Fig. 5, Malga Arpaco). Goodness of fit of the nonrectangular hyperbolic model applied at the ecosystem-scale may be illustrated by

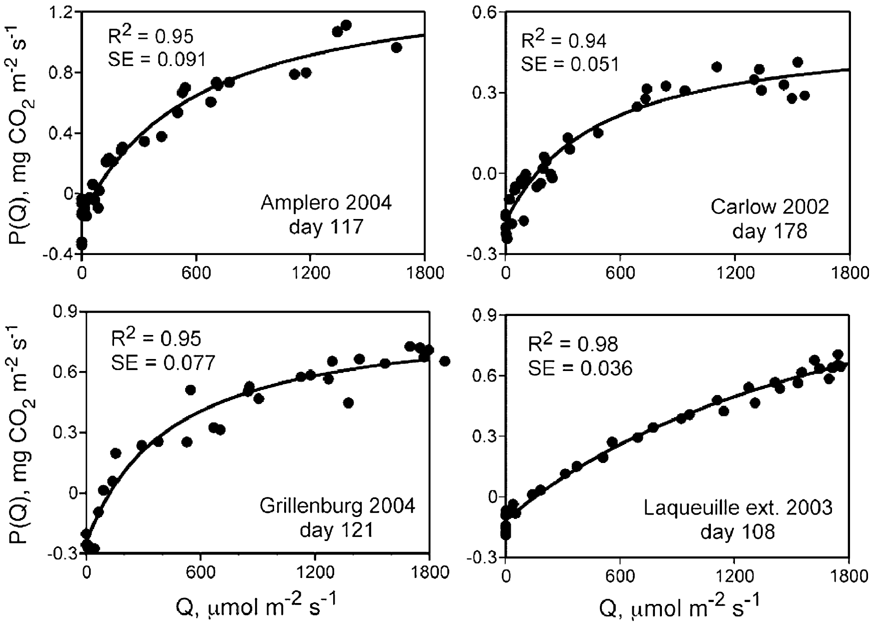


Fig. 4. Rectangular hyperbolic light-response functions for selected sites and days, P (mg CO_2 m^{-2} s^{-1}); Q, incoming PAR (μmol m^{-2} s^{-1}); dots, 30-min tower flux data; curves represent functions described by model (7).

data for Carlow grassland, 2002 day 144: it explains 97% of the variance of the daytime carbon dioxide flux and has a standard error <0.1 mg CO_2 m^{-2} s^{-1}, with all parameters being significant with t-value greater than 2 and respective p-values in the order of 0.01 or much lower (Table 4).

In spite of a success of the PAR-dominated hyperbolae under certain conditions, in general for European grasslands for days with pronounced hysteresis of the (Q, P) scatter plot, monofactorial light-response function $P(Q)$ becomes inadequate and should be replaced by a bifactorial light–temperature function $P(Q,T_s)$, e.g., by the modified nonrectangular hyperbolic model (9) (Gilmanov et al., 2003a,b, 2004, 2005a,b). Scatter plots with morning to afternoon hysteresis and light–temperature-response surfaces described by Eq. (9) for several representative sites and days are presented on Fig. 6. Table 5 illustrates statistical characteristics of the resulting nonlinear models.

3.3. Temperature response of nighttime respiration

To investigate dependence of nighttime ecosystem respiration rate (r_n) on soil temperature (T_s), datasets of $\{T_s, F_{CO_2}\}$ values for various site-years were screened for patterns using a biweekly wide window. Our results for European grasslands confirmed earlier findings for grasslands and shrublands of North America that typical scatter plots of $\{T_s, F_{CO_2}\}$ data with 30 min time step do not display patterns one might expect from the classical exponential relationship of metabolic rates to temperature (Dugas, 1993; Gilmanov et al., 2003b). Only in less than one quarter of all cases was it possible to identify statistically significant relationships $r_n(T_s) = r_0\,e^{k_T T_s}$ with physiologically meaningful values of the temperature coefficient k_T, as shown on Fig. 7. Consequently, it was often necessary to gap fill nighttime fluxes using the estimates of the respiration term from light-response analyses (8) and (9) or recurring to interpolation methods that do not take into account dependence of respiration on environmental factors.

3.4. Evaluation of daytime respiration estimates from light-response analysis

Testing the realism of the estimation of daytime ecosystem respiration, r_d, provided by light-response functions analysis, is crucial for evaluation of the daily gross photosynthetic uptake, P_g (g CO_2 m^{-2} d^{-1}) calculated as $P_g = P_d + R_d$, where P_d is daytime integral of the net CO_2 flux provided by the tower measurements, and $R_d = r_d \times \mathrm{DL}$, where DL

Table 3
Estimates of the light-response function parameters for Amplero grassland, 2004, day 117, described by rectangular hyperbolic model (7), standard error of approximation S.E. = 0.091 mg CO_2 m^{-2} s^{-1}, R-squared coefficient $R^2 = 0.95$

Parameter	α (mg CO_2 μmol^{-1})	A_{max} (mg CO_2 m^{-2} s^{-1})	r_d (mg CO_2 m^{-2} s^{-1})
Estimate	0.0026	1.63	0.149
Standard error	0.0004	0.149	0.026
t-Value	6.88	10.94	5.73
p-Value	<0.00001	<0.00001	<0.00001

Table 4
Estimates of the light-response function parameters for Carlow grassland, 2002, day 144, described by nonrectangular hyperbolic model (8), S.E. = 0.095 mg CO_2 m^{-2} s^{-1}, $R^2 = 0.97$.

Parameter	α (mg CO_2 μmol^{-1})	A_{max} (mg CO_2 m^{-2} s^{-1})	θ (dimensionless)	r_d (mg CO_2 m^{-2} s^{-1})
Estimate	0.0026	1.77	0.66	0.29
Standard error	0.0005	0.22	0.28	0.037
t-Statistic	5.10	8.03	2.33	7.97
p-Value	<0.0001	<0.0001	0.0132	<0.0001

(s day^{-1}) is the actual length of the light period of the particular day. It is difficult to directly measure daytime respiration at the ecosystem scale, but there are at least two indirect methods to evaluate estimated r_d values. First, r_d estimates from light-response may be compared with r_n rates directly measured at the tower during the same day. Second, we may compare ecosystem respiration estimates, R_e (which include daytime rates as their major component during the growing season) with independently measured soil respiration, R_s.

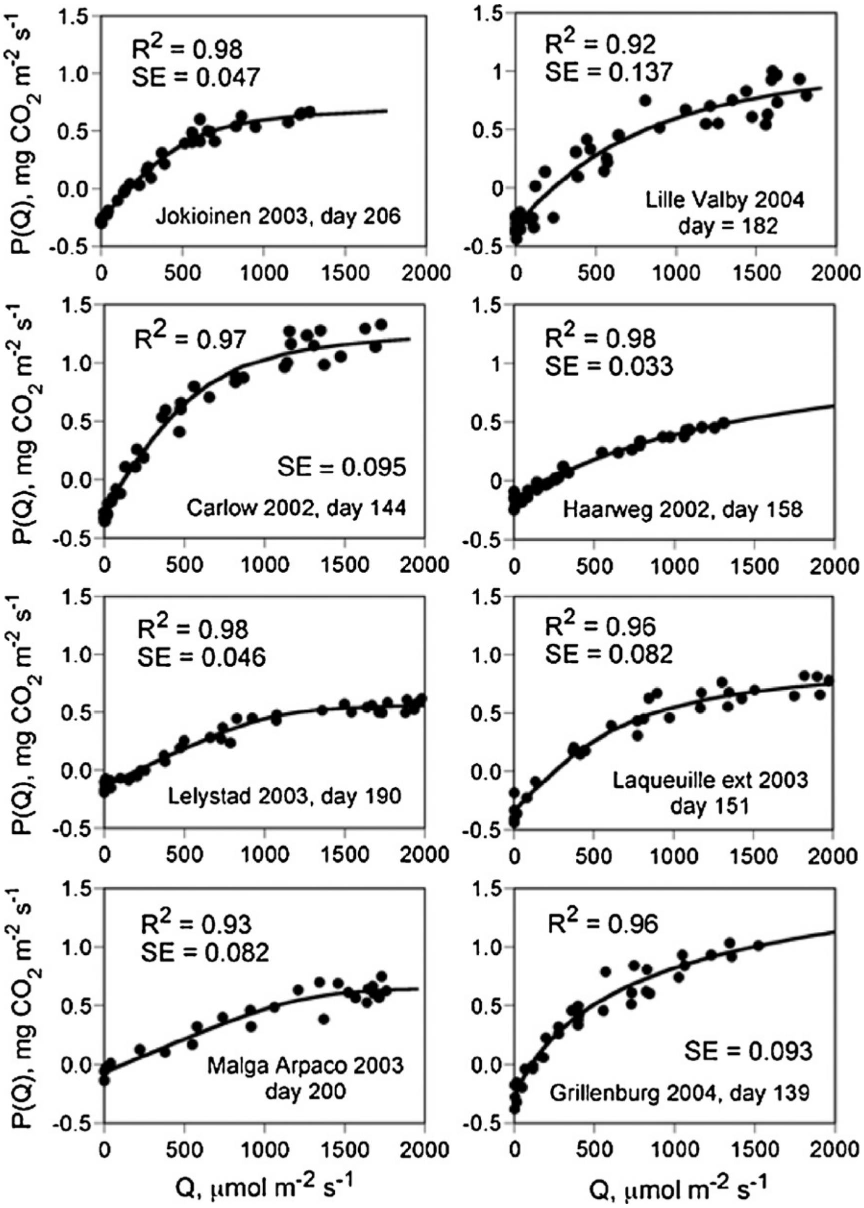


Fig. 5. Nonrectangular hyperbolic light-response functions for selected sites and days, *P* (mg CO_2 m^{-2} s^{-1}); *Q*, incoming PAR (μmol m^{-2} s^{-1}); dots, 30-min tower flux data; curves represent functions described by model (8).

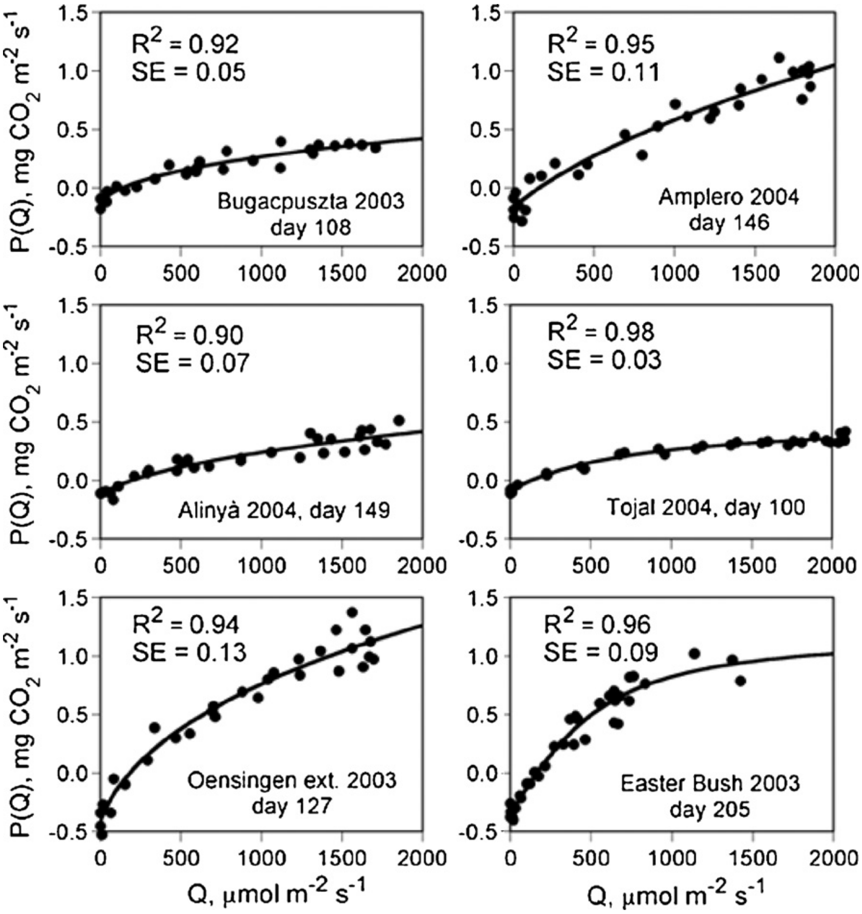


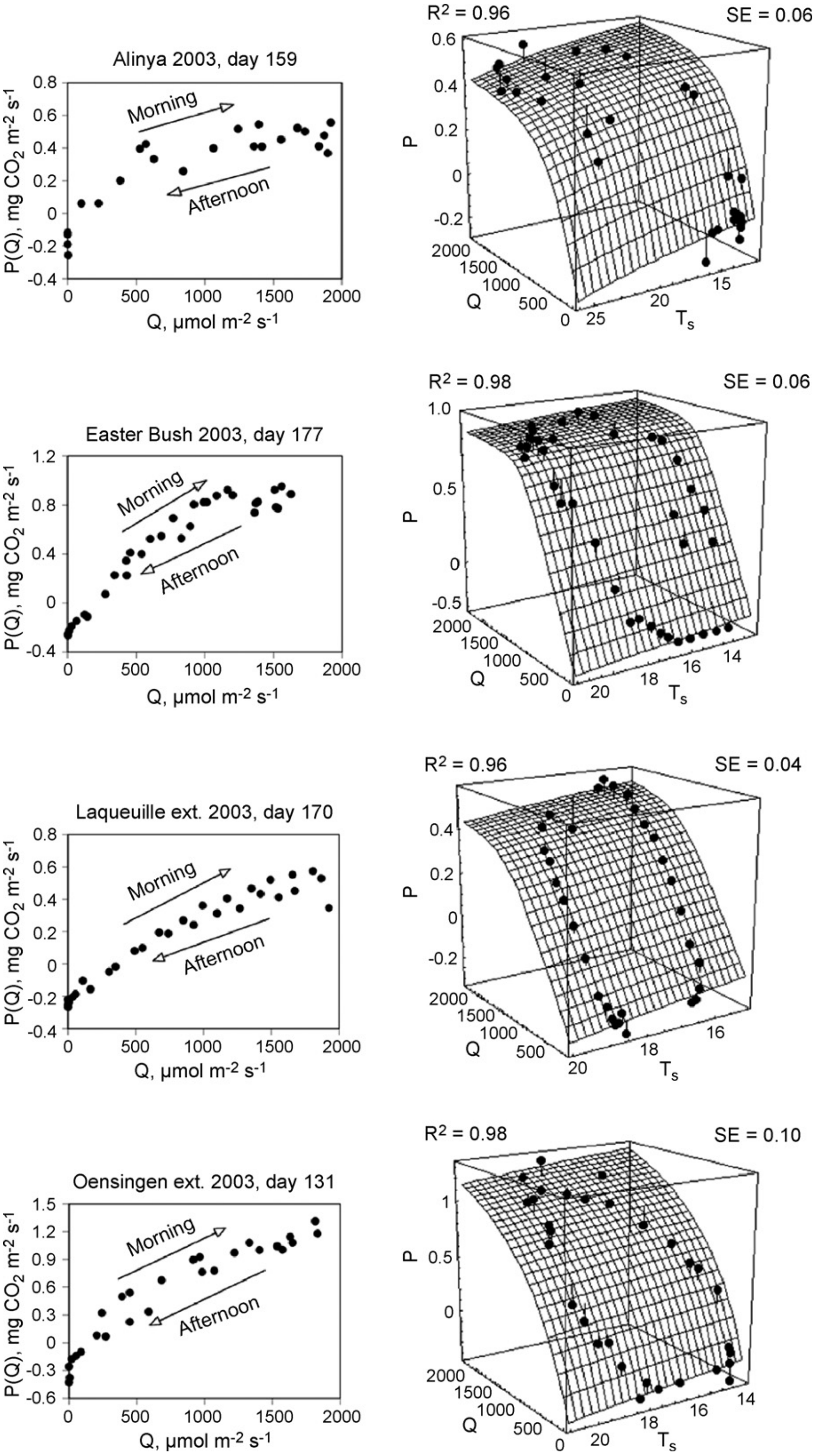
Fig. 5. (*Continued*).

To smooth the high frequency fluctuations, we have calculated weekly averages (subscript "wk" below) of estimated r_d and measured r_n values and plotted them as the scatter diagrams of $r_{d,wk}$ against $r_{n,wk}$ (Fig. 8). Not unexpected, the results demonstrate significant linear relationship between daytime and nighttime respiration. In most cases, $r_{d,wk}$ is statistically higher than $r_{n,wk}$, and the regression line on the scatter plot lies above the 1:1 line. A more thorough analysis is required to identify specific mechanisms leading to $r_d > r_n$, though, as it was shown by Gilmanov et al. (2003a) for grasslands of southern Great Plains of North America, higher daytime temperatures acting through a $Q_{10} = 2.0$ mechanism may be one of the direct contributors to higher r_d values.

For one site, the sown grass-clover sward at Carlow, long-term chamber measurements of soil respiration taken during daytime (mostly, around noon) were available (M.L. Williams, personal communication). Estimates of the 24-h soil respiration totals, R_s, derived through extrapolation of these measurements, were compared with the 24-h R_e totals calculated from light-response (Fig. 9). Despite occasional outliers that may result from chamber effects, patterns of the two curves (Fig. 9a) are in agreement, on the average R_s contributing 75% of the total ecosystem respiration R_e (Fig. 9b). For comparison, Hunt et al. (2004) estimated that in a tussock grassland in New Zealand with LAI considerably lower than at Carlow, soil respiration contributed 85% of the ecosystem respiration.

Table 5
Estimates of the light–temperature response parameters for Alinyà grassland, 2003, day 159, described by the modified nonrectangular hyperbolic model (9), S.E. = 0.06 mg CO_2 m^{-2} s^{-1}, $R^2 = 0.96$

Parameter	α (mg CO_2 μmol^{-1})	A_{max} (mg CO_2 m^{-2} s^{-1})	θ (dimensionless)	r_0 (mg CO_2 m^{-2} s^{-1})	k_T (°C)$^{-1}$
Estimate	0.0014	0.771	0.699	0.048	0.067
Standard error	0.0005	0.100	0.375	0.016	0.018
t-Value	3.01	7.74	1.86	2.94	3.66
p-Value	0.0030	<0.0001	0.0371	0.0035	0.0006


Alinya 2003, day 159

Easter Bush 2003, day 177

Laqueuille ext. 2003, day 170

Oensingen ext. 2003, day 131

Fig. 6. Light–temperature response functions for days with hysteresis of the light-response: dots, 30-min daytime CO_2 flux data from tower measurements, *P* (mg CO_2 m^{-2} s^{-1}); *Q*, incoming PAR (μmol m^{-2} s^{-1}); T_s, soil temperature at 5 cm depth (°C); response surfaces fitted by modified nonrectangular hyperbolic Eq. (9).

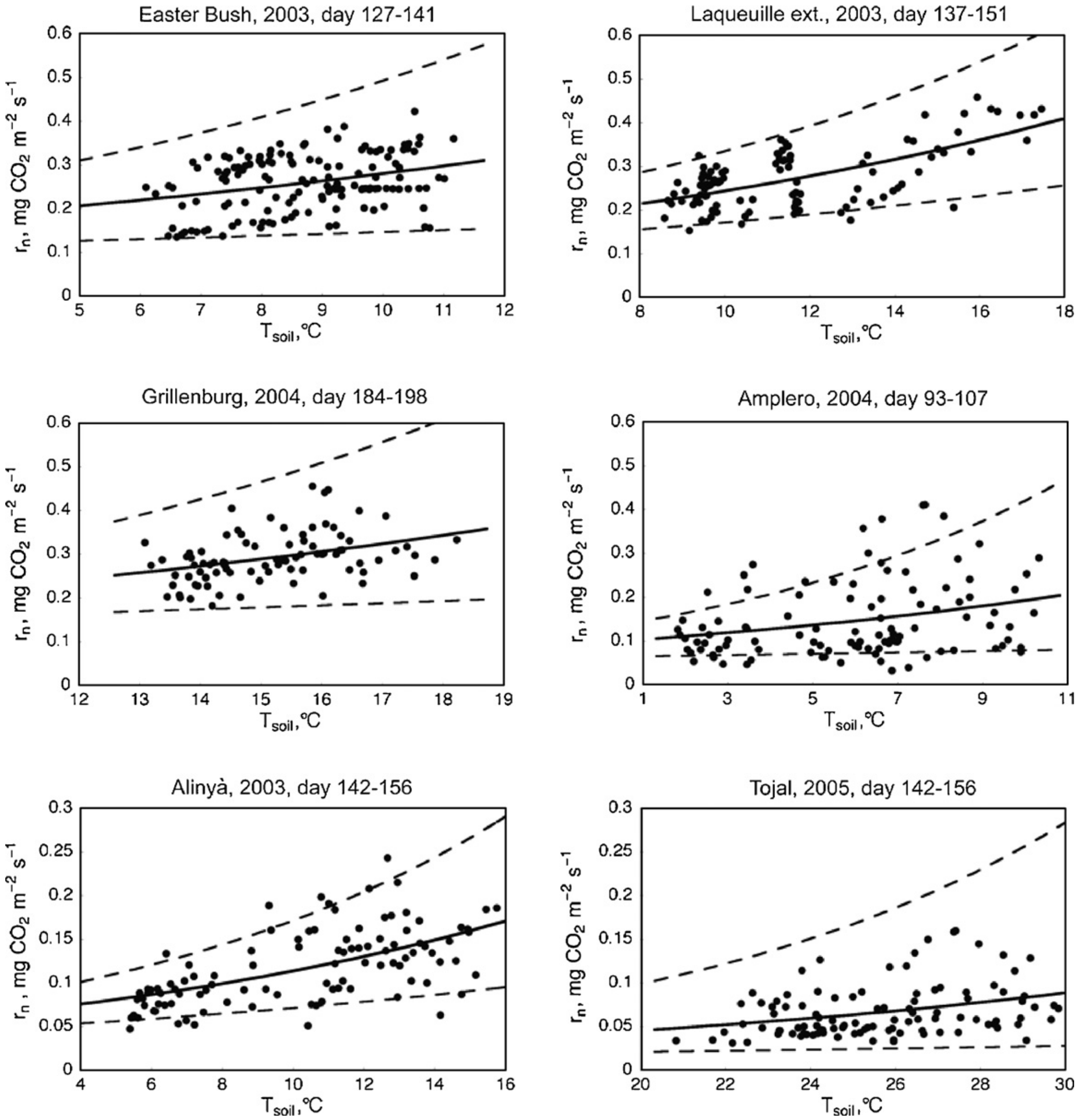


Fig. 7. Temperature response of nighttime respiration for selected sites of the EUROGRASSFLUX data set. Parameters r_0 and k_T (Table 6) of the exponential function $r_n(T_s) = r_0\,e^{k_T T_s}$ (solid line) were fitted for the biweekly windows of 30-min nighttime $\{T_s, F_{CO_2}\}$ data (dots); dashed lines show 95% confidence interval for $r_n(T_s)$.

3.5. Seasonal patterns of light-response parameters

Identification of the light-response parameters for all days with convergence of the fitting procedure shows the seasonal dynamics of α, A_{max}, and r_d. To smooth day-to-day fluctuations, for every week of the observation period, mean values α_i, $A_{max,i}$, and r_d (and their standard errors, s_α, $s_{A_{max}}$, and s_r) were calculated (Fig. 10).

Table 6

Parameters r_0 (standard error s_{r_0}) and k_T (standard error s_{k_T}) of temperature response of nighttime respiration (r_n) for selected grassland ecosystems estimated for the biweekly data windows by fitting the exponential function $r_n(T_s) = r_0\,e^{k_T T_s}$

Site, year, period (days)	r_0 (mg CO$_2$ m^{-2} s^{-1})	s_{r_0} (mg CO$_2$ m^{-2} s^{-1})	k_T (°C^{-1})	s_{k_T} (°C^{-1})	n	R^2	S.E. (mg CO$_2$ m^{-2} s^{-1})
Easter Bush, 2003, 127–141	0.152	0.022	0.061	0.016	142	0.10	0.061
Laqueuille ext., 2003,137–151	0.127	0.012	0.065	0.007	102	0.40	0.054
Grillenburg, 2004, 184198	0.121	0.030	0.058	0.016	85	0.14	0.053
Amplero, 2004, 93–107	0.096	0.017	0.069	0.024	103	0.08	0.085
Alinyà, 2003,142–156	0.057	0.007	0.068	0.01	100	0.35	0.035
Tojal, 2005,142–156	0.012	0.006	0.067	0.20	103	0.11	0.028

Goodness of fit is characterized by the R-squared coefficient R^2 and standard error S.E.

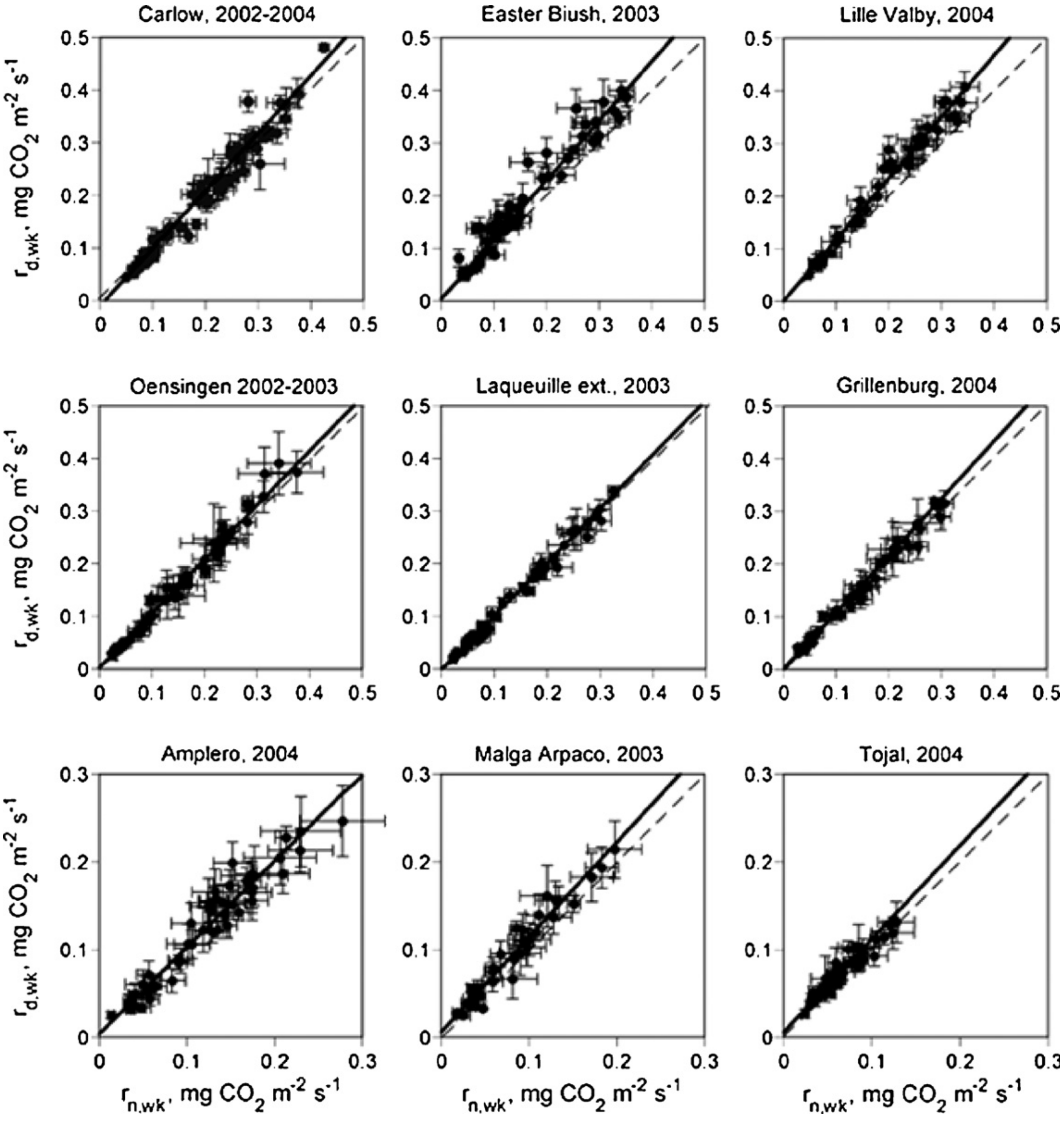


Fig. 8. Daytime and nighttime respiration in selected sites: mean weekly daytime respiration, $r_{\mathrm{d,wk}}$ from light-response plotted against average weekly nighttime respiration, $r_{\mathrm{n,wk}}$ from tower measurements; error bars indicate standard errors of the means; solid line—linear regression; dashed line—1:1 relationship.

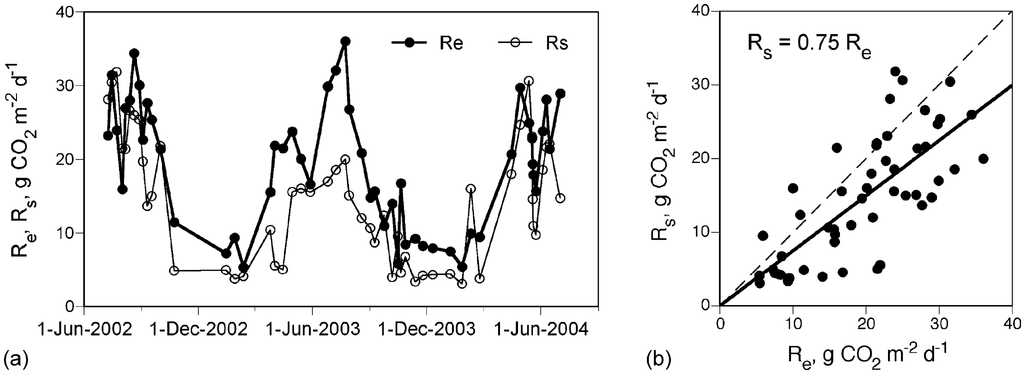


Fig. 9. Dynamics of total ecosystem respiration (R_e) and soil respiration (R_s) at Carlow site, 2002–2004: (a) time domain plot; (b) scatter diagram. Linear regression $R_s = 0.75 \times R_e$ (solid line on (b)) is statistically significant ($p < 10^{-9}$) and has $R^2 = 0.56$; the dashed line shows a 1:1 diagonal.

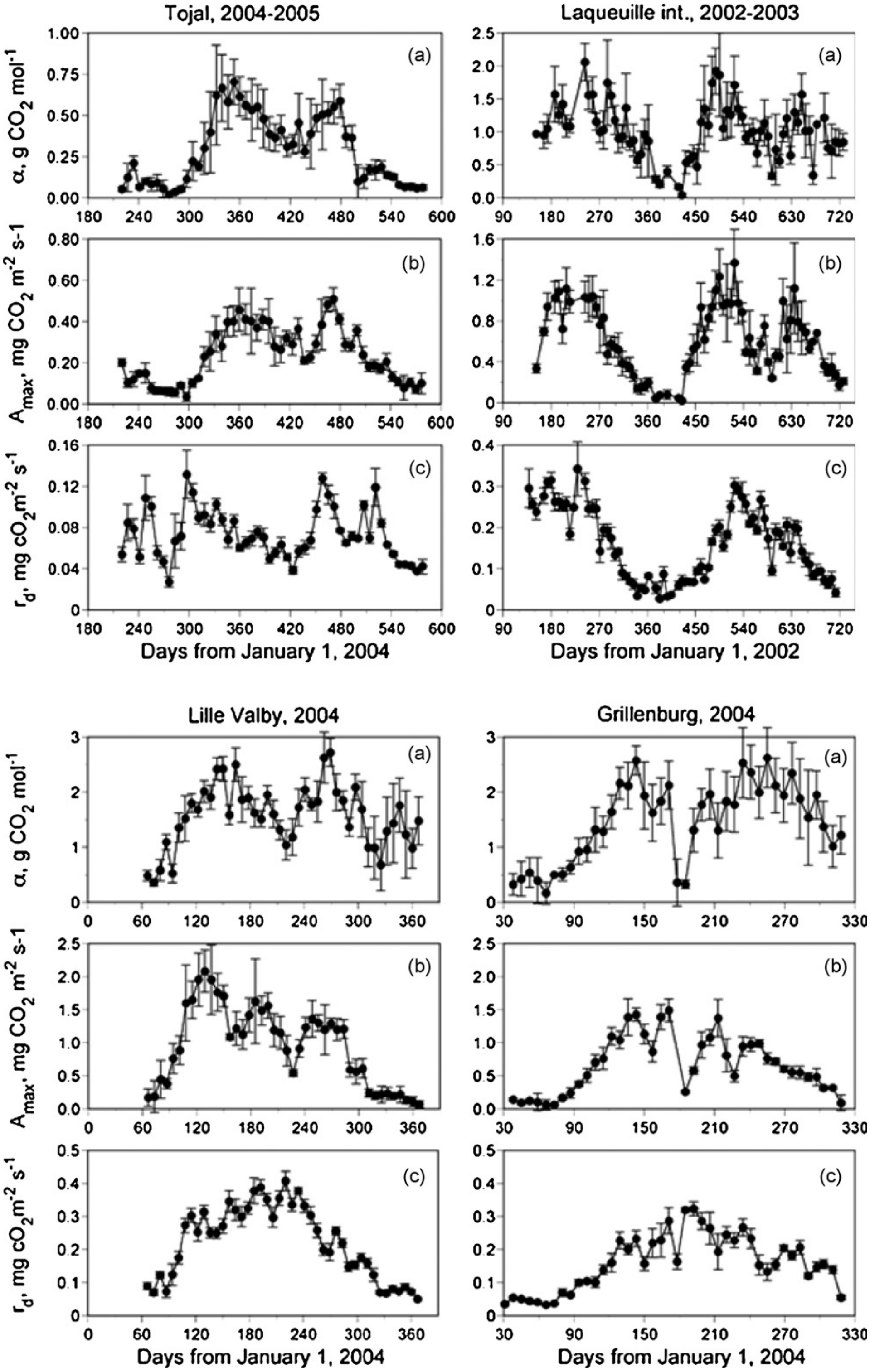


Fig. 10. Seasonal dynamics of light-response parameters in selected sites: (a) apparent quantum efficiency, α, g CO_2 mol^{-1}; (b) saturated gross photosynthesis, A_{max}, mg CO_2 m^{-2} s^{-1}; (c) daytime respiration, r_d, mg CO_2 m^{-2} s^{-1}. Dots—weekly means; bars—standard errors of the means.

As expected, all three parameters demonstrate seasonal patterns, reflecting both the changes of the amount and activity of biomass, and the effects mowing and grazing.

3.6. Light-use efficiency

Ecological light-use efficiency, ε, shows considerable variation both within the year and from site to site (Fig. 11,

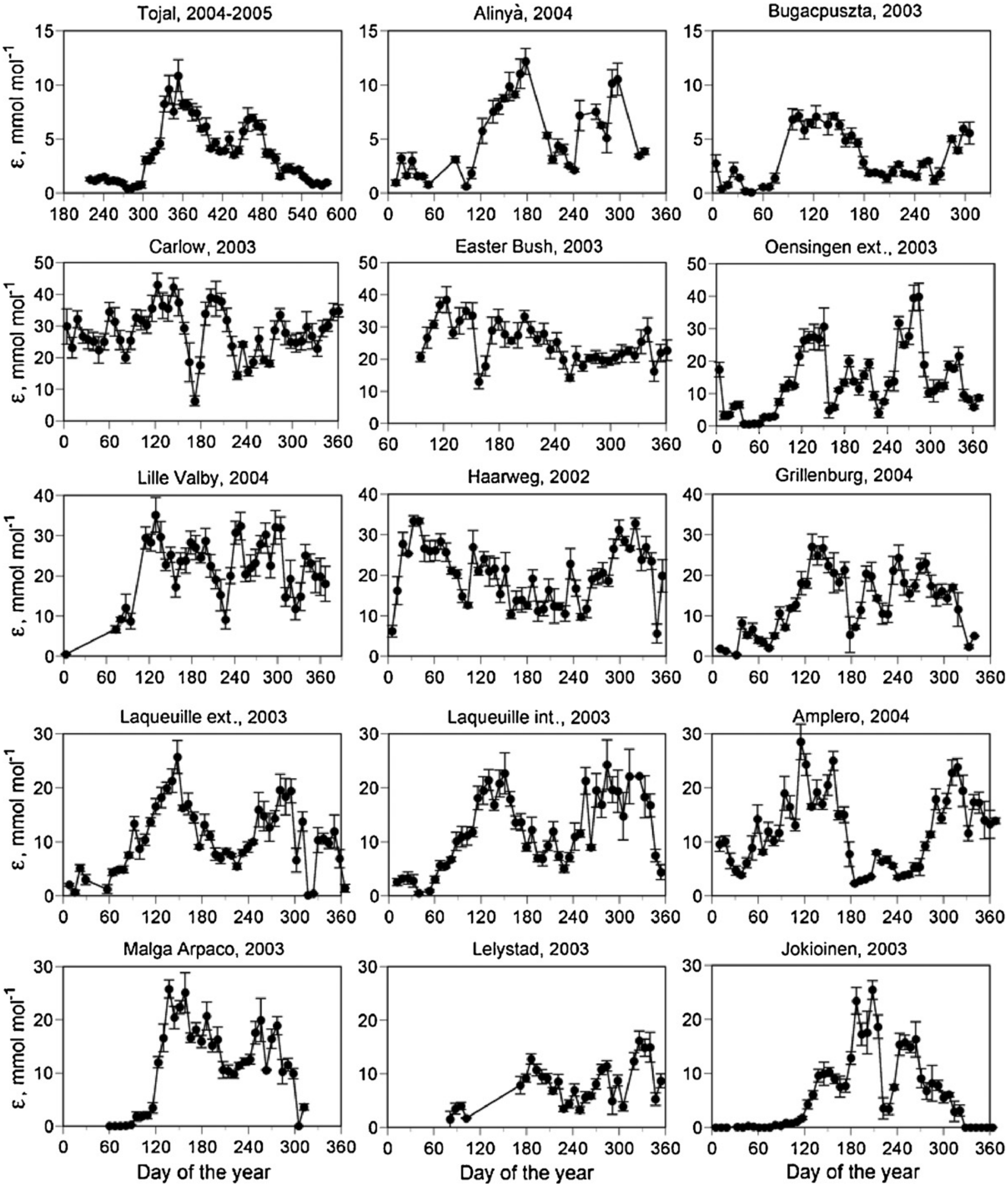


Fig. 11. Seasonal dynamics of gross ecological light use efficiency ε, mmol CO_2 (mol quanta)$^{-1}$ in selected grasslands.

Table 7). Lowest ε values are observed not only during fall, winter, and spring periods, but also after hay-mowing events and intensive grazing. Because of considerable variability of ε values for individual days, it is more informative to calculate weekly averages of ε and to compare maximum weekly $\varepsilon_{wk,max}$ estimates for different sites (Table 7). As expected, grasslands from different ecoregions have significantly different $\varepsilon_{wk,max}$ values: from 7 to 12 mmol mol^{-1} in semiarid grasslands of Hungary, Spain and Portugal (Bugacpuszta, Tojal, Alinyà) to 35–43 mmol mol^{-1} in fertilized Atlantic grasslands of Ireland, U.K., Denmark and The Netherlands.

3.7. Comparison of ecophysiological parameters

The wide range of environmental and management regimes and corresponding productivity and metabolic characteristics of grasslands in EUROGRASSFLUX dataset make it possible to conduct a first comparison of their major ecophysiological parameters at the ecosystem scale. This is

Table 7
Ecosystem-scale ecophysiological parameters of European grasslands

Site, year	$\alpha_{\mathrm{wk,max}}$ (g CO_2 mol^{-1})	$A_{\mathrm{maxwk,max}}$ (mg CO_2 m^{-2} s^{-1})	$r_{\mathrm{dwk,max}}$ (mg CO_2 m^{-2} s^{-1})	$P_{\mathrm{g,max}}$ (g CO_2 m^{-2} d^{-1})	$R_{\mathrm{e,max}}$ (g CO_2 m^{-2} d^{-1})	$\varepsilon_{\mathrm{wk,max}}$ (mmol mol^{-1})
Tojal, 2004–2005	0.70	0.51	0.13	16.9	18.2	10.9
Carlow, 2002–2004	3.10	2.11	0.45	57.9	40.3	43.0
Easter Bush, 2003	2.79	1.96	0.41	63.6	46.9	38.4
Alinyà, 2003–2004	1.11	0.94	0.17	25.7	18.3	12.9
Laqueuille ext., 2002–2003	2.36	1.32	0.33	42.8	33.5	24.7
Laqueuille int., 2002–2003	2.04	1.25	0.32	39.0	35.5	33.0
Cabauw, 1993–1994	3.30	2.60	0.45	–	–	–
Lelystad, 2004	1.31	1.3	0.28	43.4	29.3	23.9
Haarweg, 2002	1.90	1.77	0.28	57.5	46.8	26.9
Oensingen ext., 2002–2003	2.44	1.85	0.37	50.2	36.7	35.1
Rigi-Seebodenalp, 2003	2.20	1.35	0.20	39.2	38.58	–
Monte Bondone, 2004	1.57	1.26	0.35	53.2	40.59	–
Neustift, 2001	3.08	1.97	0.45	47.9	38.44	30.6
Malga Arpaco, 2003	1.7	1.66	0.21	48.0	29.0	25.8
Lille Valby, 2004	2.72	2.08	0.41	55.3	44.1	35.2
Grillenburg, 2004	2.63	1.49	0.32	49.7	40.7	27.0
Amplero, 2004	2.00	1.82	0.25	41.0	32.8	28.5
Hegyhátsál, 2002	2.10	1.79	0.25	–	–	–
Bugacpuszta, 2003	1.23	0.58	0.15	20.3	15.7	7.2
Jokioinen, 2002	1.60	1.14	0.28	35.7	27.6	26.2
Mean	2.17	1.55	0.30	43.7	34.06	26.8
Standard deviation	0.74	0.52	0.10	12.9	9.49	9.8

Notes: subscript "wk" denotes weekly aggregated values; "–" denotes unavailability of parameter estimate.

expected to be a substantial addition to our current knowledge from previously published reviews of grassland ecophysiology (Caldwell, 1975; Ripley and Rdmann, 1976; Tieszen and Detling, 1983; Risser, 1985; Long and Hutchin, 1991; Ruimy et al., 1995; Campbell et al., 2000; Reich et al., 2003) that did not all have the possibility of using direct ecosystem-scale tool like a flux-tower which only became abundant in recent years. Table 7 presents a summary of numerical values of some of the major ecophysiological parameters of grasslands in the EUROGRASSFLUX data set.

The maximum average weekly apparent quantum efficiency, $\alpha_{\mathrm{wk,max}}$, obtained from light-response analyses, in European grasslands has a mean value $\bar{\alpha}_{\mathrm{wk}} = 2.09$ g CO_2 mol^{-1} (48 mmol mol^{-1}) and varies in the broad range from 0.7 g CO_2 mol^{-1} (16 mmol mol^{-1}) in a dry semi-natural Tojal grassland in Portugal to 3.3 g CO_2 mol^{-1} (75 mmol mol^{-1}) in the Cabauw grassland in Netherlands. For European grasslands the mean $\bar{A}_{\max} = 1.52$ mg CO_2 m^{-2} s^{-1} and the range of $A_{\max}$ values $0.5 < A_{\max} < 2.6$ mg CO_2 m^{-2} s^{-1}. Our estimate of the mean $\bar{r}_{\mathrm{d}} = 0.29$ mg CO_2 m^{-2} s^{-1} and the range $0.13 < r_{\mathrm{d}} < 0.45$ mg CO_2 m^{-2} s^{-1} of the daytime ecosystem respiration is also in agreement with the few available daytime ecosystem respiration data for temperate grasslands (Franzluebbers et al., 2002; Li et al., 2003; Novick et al., 2004; Chimner and Welker, 2005).

In agreement with the light-response parameters, a wide range of values of the maximum total daily photosynthesis ($16.9 \leq P_{\mathrm{g,max}} \leq 63.6$ g CO_2 m^{-2} day^{-1}) and maximum daily ecosystem respiration ($15.7 \leq R_{\mathrm{e,max}} \leq 46.9$ g CO_2 m^{-2} day^{-1}) was found in European grasslands (Table 7), illustrating high diversity of the regimes of carbon cycling. Our estimate $P_{\mathrm{g,max}} = 63.6$ g CO_2 m^{-2} day^{-1} is still lower than the record value of $P_{\mathrm{g,max}} = 93$ g CO_2 m^{-2} d^{-1} obtained by Thomas and Hill (1949) for alfalfa experimental plots, but is comparable to the value $P_{\mathrm{g,max}} = 55$ g CO_2 m^{-2} day^{-1} considered by Olson (1964) as representative for terrestrial vegetation. Actually, Olson's estimate was surpassed by the net daily flux value $F_{\mathrm{n}} = 57$ g CO_2 m^{-2} day^{-1} measured by Toda et al. (2000) using aerodynamic method on a mixed C_3/C_4 temperate grassland in Japan, implying an even higher $P_{\mathrm{g,max}}$ value.

Reflecting the P_{g} variability, the gross ecological light-use efficiency also varies greatly from maximum weekly mean of $\varepsilon_{\mathrm{wk,max}} = 7.2$ mmol mol^{-1} in the dry semi-natural grassland Bugacpuszta to $\varepsilon_{\mathrm{wk,max}} = 43.0$ mmol mol^{-1} in the intensively managed Carlow grassland.

Scatter plots (Fig. 12) demonstrate significant positive correlations between major ecophysiological parameters. Correlations between the ecosystem-scale $A_{\max}$ (which may often be estimated using on-site and remotely sensed measurements) and the more "intensive" parameters $\alpha_{\max}$, $r_{\mathrm{d,max}}$, and $\varepsilon_{\max}$ is especially significant from the modeling point of view as a means to estimate important ecophysiological parameters for process-based ecosystem models. The scatter plot of $R_{\mathrm{e,max}}$ against $P_{\mathrm{g,max}}$ with a high $R^2 = 0.87$ value seems to be especially interesting. It should be noticed that determination of $R_{\mathrm{e,max}}$ value includes not only effects of daytime respiration (from light-response analysis) but also independently measured nighttime CO_2 fluxes. Thus, close correlation between the

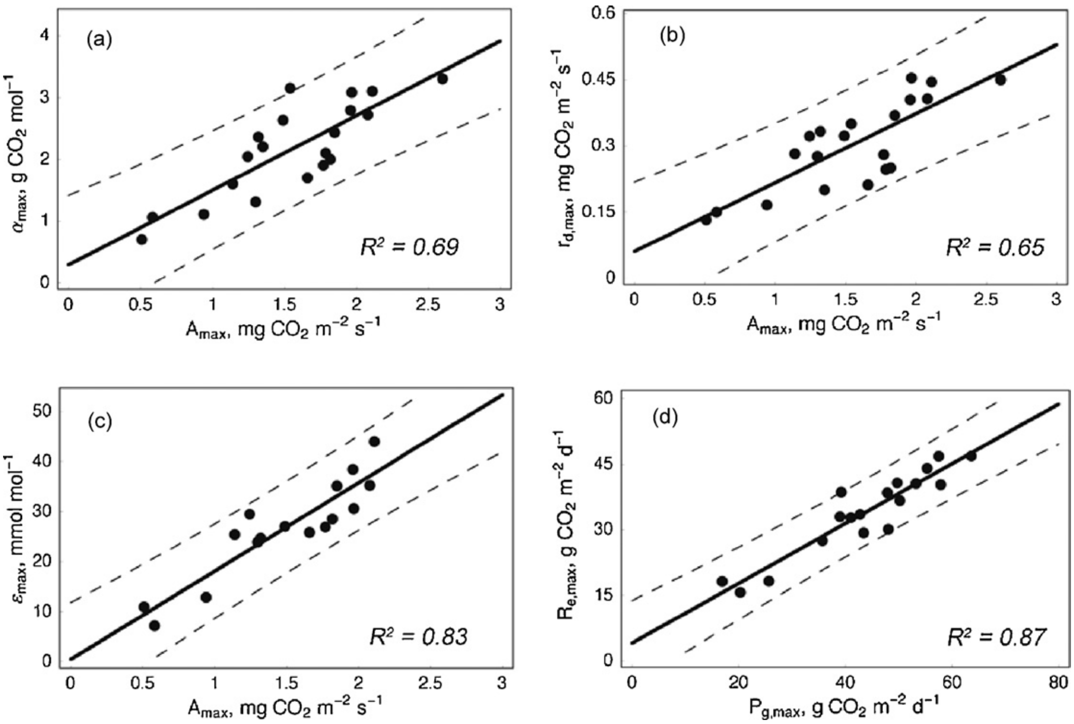


Fig. 12. Correlations between ecophysiological parameters of European grasslands: (a) maximum average weekly gross photosynthesis (A_{max}) and maximum average weekly apparent quantum yield (α_{max}); (b) maximum average weekly gross photosynthesis (A_{max}) and maximum average weekly daytime ecosystem respiration rate (r_d); (c) maximum average weekly gross photosynthesis (A_{max}) and maximum average weekly gross light-use efficiency (ε_{max}); (d) maximum daily gross primary productivity ($P_{g,max}$) and maximum daily ecosystem respiration ($R_{e,max}$). Dots—data (Table 7); solid line—linear regression; dashed lines show 95% confidence interval of regression fit.

two variables does not seem to be an artifact and reflects the consistency of the data set. The fact that in all sites except Tojal (where the measurement year was very dry), $R_{e,max}$ was less than $P_{g,max}$, indicates higher intensities of the CO$_2$ uptake processes (which are concentrated on shorter time intervals both within the day and during the year) compared to the CO$_2$ release through respiration.

3.8. Year-round dynamics and budget of CO$_2$ exchange

Identification of the seasonal patterns of light-response parameters allow their interpolation for periods with missing measurements and gap filling of the data sets, leading to reconstruction of the long-term dynamics of the CO$_2$ exchange. Resulting curves of seasonal and year-to-year dynamics of gross productivity, ecosystem respiration, net ecosystem exchange, and cumulative net ecosystem exchange for selected European grasslands are shown on Fig. 13. In contrast to forests (especially, deciduous) where maxima of assimilation and respiration are clearly separated in time resulting in a distinct seasonal pattern of F_{CO_2}, in grasslands curves of gross primary productivity (P_g) and ecosystem respiration (R_e) remain pretty much in phase, so that the early summer maximum on net CO$_2$ exchange is less pronounced (Fig. 13). In grazed grasslands where only small part of ecosystem production is exported, annual CO$_2$ budget remains either neutral or moderately positive (Fig. 13a and b). In contrast, grasslands managed for hay demonstrate predominantly increasing curves of cumulative net CO$_2$ exchange and act as local sinks for atmospheric carbon dioxide (though their carbon exported with hay will be mineralized elsewhere) (Fig. 13c and d). In Table 8 and on Fig. 14 we present average annual gross primary production, ecosystem respiration, and net ecosystem exchange data for all analyzed grassland sites. The highest P_g (6800 g CO$_2$ m^{-2} year^{-1}) and NEE (1200–2400 g CO$_2$ m^{-2} year^{-1}) values were observed in intensively managed hay meadows (including N-fertilization) and moderately grazed grasslands of Atlantic climate with sufficient precipitation like Carlow (Ireland), Easter Bush (U.K.), Lille Valby (Denmark), and Haarweg (The Netherlands). Lowest levels of annual photosynthetic CO$_2$ uptake were found in grazed semiarid grasslands of Hungary, Portugal, and Spain (Bugacpuszta, Tojal, and Alinyà, respectively), with P_g values around 2000 g CO$_2$ m^{-2} year^{-1} and neutral or even negative NEE budget (Table 8). Lowland and low to medium mountain grasslands of various management types in France, Italy, Switzerland, Austria, Germany, Hungary and Finland are characterized by more moderate P_g and NEE values, which is primarily caused by their shorter growing season and to a lesser extent by their ecophysiological potential (Table 7).

3.9. Sink–source activity of grasslands

Our data for European grasslands confirm earlier estimates for North American grasslands (Follett et al., 2001) that these ecosystems predominantly act as a sink for CO_2. Based on NEE data for two measurement years, Soussana et al. (2007) showed that nine grassland plots were a net sink for atmospheric CO_2. Examination of the (R_e, P_g) scatter plot (Fig. 14) shows that most of the points lie below the 1:1 diagonal, indicating that these grasslands are moderate to strong sinks for carbon dioxide. Of the four sites with R_e slightly exceeding P_g, two sites (Jokioinen and Rigi-Seebodenalp) have high organic soils with a significant peat horizon, while the semiarid grazed grasslands of the Tojal and Bugacpuszta sites experienced drought stress during the years of measurements. Apparently, sufficient water supply, fertilization, and management by cutting act as the promoters of net CO_2 uptake in grasslands.

3.10. Production and respiration in response to macroclimatic variables

Materials of our study covering wide range of climatic conditions shed new light on the old problem of relationship of the ecosystem productivity and respiration to macroclimatic parameters (cf. Walter, 1939; Olson, 1964; Lieth, 1975; Box, 1978; Webb et al., 1983; Esser et al., 1994; Raich and Tufekcioglu, 2000; Raich et al., 2002; Xiao and Moody, 2004). In agreement with previous studies, our data show strong positive effect of precipitation on both the gross primary production and the ecosystem respiration in the range $300 < \mathrm{PCPN} < 800\ \mathrm{mm\ year}^{-1}$ (Fig. 15). In the higher precipitation range ($\mathrm{PCPN} > 800\ \mathrm{mm\ year}^{-1}$), in contrast to findings of Sala et al. (1988) for grasslands of North America, we did not observe positive response to precipitation, but rather a switch in controlling factors, because in this factorial domain both the P_g and R_e become

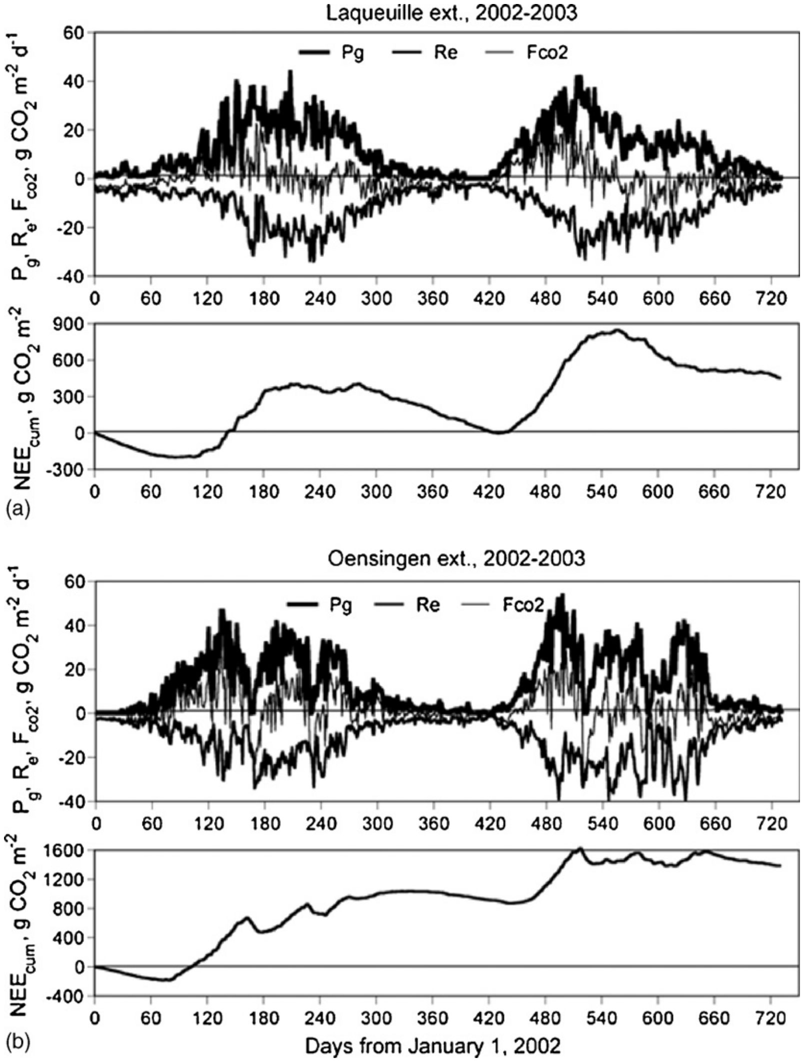


Fig. 13. Long-term dynamics of gross primary productivity (P_g), ecosystem respiration (R_e), net CO_2 exchange (F_{CO_2}), and cumulative net ecosystem production (NEE_{cum}) in selected grasslands: (a) Laqueuille extensive, 2002–2003; (b) Alinyà, 2003–2004; (c) Oensingen extensive, 2002–2003; (d) Carlow, 2002–2004.

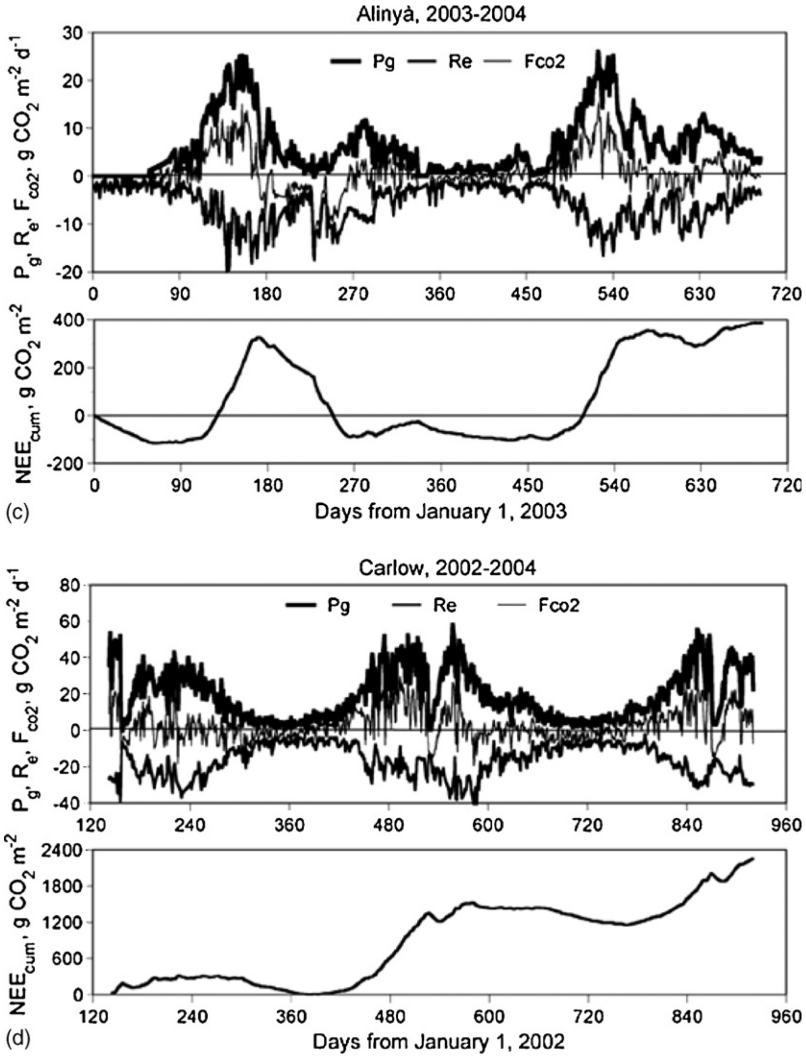


Fig. 13. (*Continued*).

Table 8

Average annual gross primary production (P_g), ecosystem respiration (R_e), and net ecosystem CO_2 exchange (NEE) in European grasslands for the period indicated

Site, year	P_g (g CO_2 m^{-2} $year^{-1}$)	R_e (g CO_2 m^{-2} $year^{-1}$)	NEE (g CO_2 m^{-2} $year^{-1}$)
Tojal, 2004–2005	1936	2200	−264
Carlow, 2002–2004	6807	5622	1185
Easter Bush, 2003	6793	5451	1324
Alinyà, 2003–2004	2221	2049	172
Laqueuille (ext.) 2002–2003	4418	4193	225
Laqueuille (int.) 2002–2003	4649	4160	509
Lelystad, 2003	3974	3448	526
Haarweg, 2002	5915	3521	2394
Oensingen (ext.), 2002–2003	5123	4426	697
Rigi-Seebodenalp, 2003	5320	5947	−627
Monte Bondone, 2004	4527	4253	274
Neustift, 2001	5748	5726	22
Malga Arpaco, 2003	3972	2346	1626
Lille Valby, 2004	6873	5730	1143
Grillenburg, 2004	4742	4206	536
Amplero, 2004	4778	3994	784
Hegihatsal, 2002	5867	5668	199
Bugacpuszta, 2003	1713	1809	−96
Jokioinen, 2002	2486	2642	−156

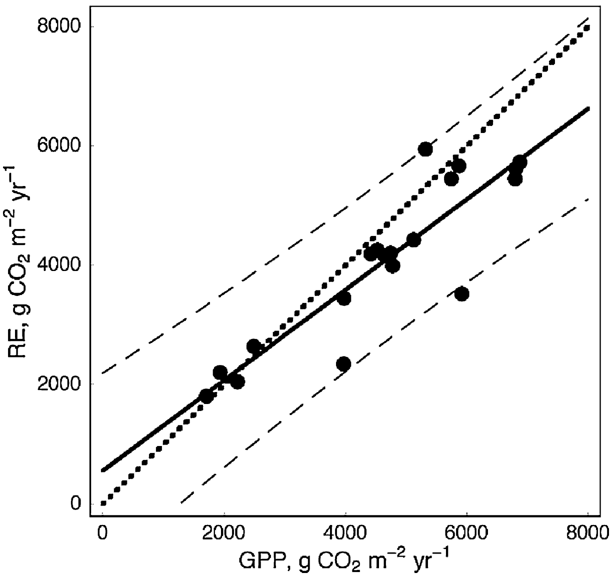


Fig. 14. Comparison of gross primary production (P_g) and ecosystem respiration (R_e) for European grasslands (Table 8). Dots—average data; solid line—regression $R_e = 551 + 0.76P_g$ ($n = 19$, $R^2 = 0.80$; $F_{\text{ratio}} = 67.5$; p-value $= 2.5 \times 10^{-7}$); dashed lines show 95% confidence zone for expected "new" estimates; dotted line shows the 1:1 diagonal.

apparently controlled by other environmental factors, e.g., temperature. Due to limited amount of data, these conclusions have preliminary character and may be subjected to change, as new site-years of flux measurements are included into the analysis.

4. Discussion

Results of the cross-spectral analysis show that radiation factors (photosynthetically active radiation, Q, and total global radiation, R_g) have the highest coherency with the net CO_2 flux, with squared coherency maxima observed at frequencies corresponding to the 24 and 12-h cycles. This conclusion is not unexpected and is in agreement with the role of radiation in the photoassimilation process. The factors of air and soil temperature (T_a, T_s) are following radiation in the ranked sequence of coherence with the CO_2 flux (Fig. 3), air temperature having higher squared coherence in some sites (Lelystad, Lille Valby, Oensingen), soil temperature—in other sites (Alinyà, Amplero), or T_a and T_s having rather similar correlations with F_{CO_2} (Tojal, Malga Arpaco, Haarweg, Jokioinen). Other factors included in our analysis (relative humidity, wind speed, atmospheric pressure, precipitation, soil moisture, and wind direction) have lower coherencies with net CO_2 flux, and their maxima occur not only at 24 and 12-h cycles but also in the higher and lower frequencies. Thus, selection of photosynthetically active radiation and soil temperature as factors-predictors for CO_2 fluxes at the 30-min time scale does not contradict to the results of spectral coherency analysis.

Though the classic rectangular hyperbola was found to be applicable for light-response of grasslands on individual days, more often the nonrectangular hyperbola worked better, while on days with hysteresis of the (Q,P) scatter plot, the modified nonrectangular model (9) provided the best fit. In the most physiologically driven, "demonstration" cases exemplified by the plots on Fig. 7, the exponential temperature coefficient k_T gravitates to the "classical" value 0.069 °C^{-1} corresponding to $Q_{10} = 2$. One might speculate that on such days environmental conditions did not cause substantial stress (e.g., drought), so that the classical Q_{10}-type temperature dependence becomes transparent. To the contrary, values of k_T higher than 0.069 °C^{-1} occasionally produced by light–temperature-function fits on certain days might indicate water stress and stomatal limitation of

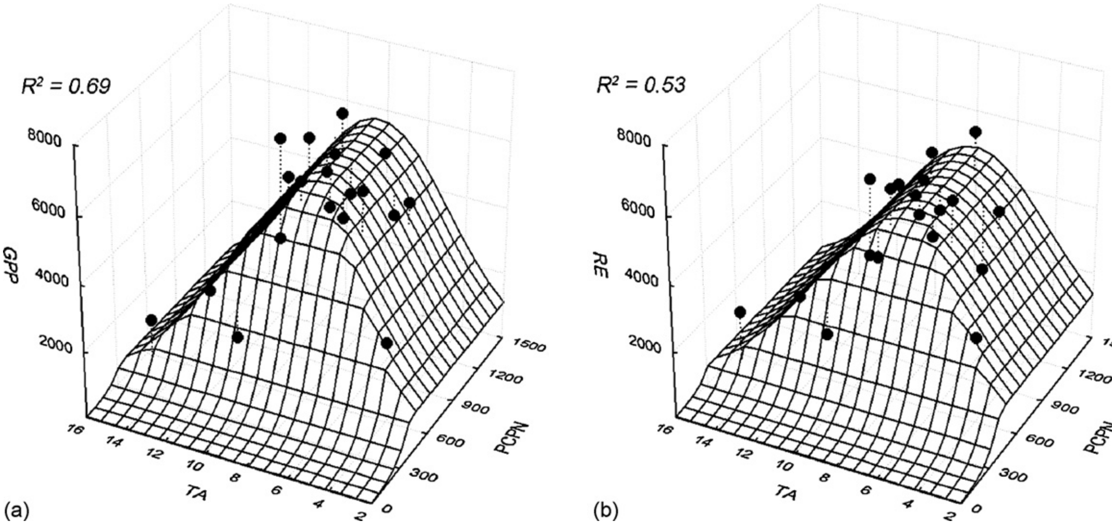


Fig. 15. Gross primary production P_g (g CO_2 m^{-2} year^{-1}) (a), and ecosystem respiration R_e (g CO_2 m^{-2} year^{-1}) (b) of European grasslands in relation to precipitation (PCPN, mm year^{-1}) and mean annual temperature (TA, °C). Dots—data points; response surfaces P_g(PCPN, TA) and R_e(PCPN, TA) are fitted using the model $y = \min\{f_P(\text{PCPN}), f_T(\text{TA})\}$, where f_P(PCPN) is a sigmoidal function of precipitation, and f_T(TA) is a bell-shaped function of temperature.

CO_2, that formally translate into a higher than "physiological" values of k_T during fitting of surface (9). Resulting models (9) still can be used for gap-filling of daytime fluxes, but using the exponential term $r_0\,e^{k_T T_s}$ to estimate daytime (and nighttime) respiration would lead to overestimation. In such cases, it is recommended to use a more conservative, but robust estimate of the respiration term r_d from nonrectangular hyperbolic model (8). Comparing r_n estimates for a mountain meadow in Austria, based on eddy covariance, chamber, and modeling methods, Wohlfahrt et al. (2005a) found that they remained within uncertainties of the methods estimated as 35%. We conclude that both comparison with nighttime measurements and soil chamber measurements did not indicate large overestimation of daytime ecosystem respiration using light-response function method.

The range of α in Table 7 include majority of the quantum yield values found in the literature for temperate grasslands (e.g., Ehleringer and Bjorkman, 1977; Baker et al., 1988; Long et al., 1993; Ehleringer et al., 1997; Dirks et al., 2002; Hanan et al., 2002; Li et al., 2003; Kubien and Sage, 2004). On this occasion, it should be noticed that moderate α values for otherwise highly productive stands encountered in the literature, e.g., $\alpha = 2.20$ g CO_2 mol^{-1} (50 mmol mol^{-1}) for a tallgrass prairie in Oklahoma (Hanan et al., 2002) or $\alpha = 2.42$ g CO_2 mol^{-1} (55 mmol mol^{-1}) for a temperate C_3 and C_4 grassland in Japan (Li et al., 2003) may result from fitting the light-curves to the (Q,P)-scatterplots with pooled data for several days of measurement. Experience clearly shows that pooling data from days with different α results in considerable underestimation of this parameter. Occasionally, maximum α estimates for C_3 grasslands with values higher than bioenergetically constrained value of $\alpha_{max} = 1/8$ mol mol^{-1} may be found in the literature (e.g., Ruimy et al., 1995 cite several α estimates in the range of 177–224 mmol mol^{-1}). Our maximum α estimates are close to and do not surpass the values $\alpha_{max} = 80$ mmol mol^{-1} proposed by Peisker and Apel (1981) and Campbell and Norman (1998) and $\alpha_{max} = 90$ mmol mol^{-1} estimated by Bugbee and Monje (1992), respectively.

Maximum weekly average of the saturated gross photosynthesis for European grasslands is $A_{max} = 2.60$ mg CO_2 m^{-2} s^{-1} (Cabauw grassland, The Netherlands) is lower but rather close to the estimate $A_{max} = 3.16$ mg CO_2 m^{-2} s^{-1} cited by Ruimy et al. (1995). Taking into account that the later estimate is not for weekly averages, the agreement between the two values seems to be rather close. For comparison, the highly productive C_4 aquatic grass *Echinochloa polystachya* in the Amazon floodplain with LAI = 3.40 is characterized by $A_{max} = 4.42$ mg CO_2 m^{-2} s^{-1} (Morison et al., 2000). In one of the most recent comparative studies of the issue, Ellsworth et al. (2004) presented data on the assimilation capacity of a number of herbaceous species determined in FACE experiments. For the light-saturated net CO_2 assimilation at $pC_a = 36$ Pa per unit leaf area, $F_{n,max}$, they provide the mean $F_{n,max} = 0.66$ mg CO_2 (m leaf area)$^{-2}$ s^{-1} and the range $0.42 \le F_{n,max} \le 1.0$ mg CO_2 (m leaf area)$^{-2}$ s^{-1}. Assuming that flux per unit ground is directly proportional to LAI, for maximum LAI = 4 m^2 m^{-2}, this would translate into mean $F_{n,max} = 2.66$ (range 1.67–4.0) mg CO_2 m^{-2} s^{-1}. On the other hand, taking account that $F_{n,max} = A_{max} - r_{canopy} < A_{max}$, the nonlinear relationship between A_{max} and LAI (leading to $A_{max} < A_{max,L} \times \text{LAI}$), as well as the fact that Ellsworth et al. (2004) estimated maximum daily values, and not weekly means of daily maxima, the agreement between FACE-based and tower-based estimates of maximum photosynthesis parameters of herbaceous plants seems to be acceptable.

Estimate of the maximum average weekly daytime ecosystem respiration $r_{d,max} = 0.45$ mg CO_2 m^{-2} s^{-1} achieved at three European grasslands (Carlow, Cabauw, and Neustift) is substantially higher than $r_{max} = 0.31$ mg CO_2 m^{-2} s^{-1} cited in the survey by Ruimy et al. (1995). Interpreting the difference, one should take into account lower diversity of grasslands included into the sample analyzed by the latter authors. At the same time, our maximum of r_d is very close to the estimate $r_{d,max} = 0.44$ mg CO_2 m^{-2} s^{-1} obtained by Hanan et al. (2002) for tallgrass prairie in Oklahoma using weekly moving window.

Our observation that daytime ecosystem respiration rates (r_d) are closely correlated with and are systematically higher than nighttime rates (r_n) (Fig. 9) are in agreement with findings by Chimner and Welker (2005) who established close correlation ($R^2 = 0.91$) between the mid-day and total daily ecosystem respiration rates in a Wyoming mixed grass prairie, mid-day respiration being consistently higher than the 24-h respiration. Using the light-response functions method, Suyker and Verma (2001) also showed that for rates <0.3 mg CO_2 m^{-2} s^{-1}, daytime respiration in an Oklahoma tallgrass prairie is on the average higher than nighttime, though $r_d < r_n$ was more frequently observed in the $r_n > 0.3$ mg CO_2 m^{-2} s^{-1} range. In contrast, results of the network-wide synthesis by Falge et al. (2002) including a variety of ecosystem types within FLUXNET suggest a relationship $r_n = 0.0106 + 0.94 r_d$ (mg CO_2 m^{-2} s^{-1}), indicating that nighttime respiration is higher than daytime in the lower range (<0.18 mg CO_2 m^{-2} s^{-1}), but r_n becomes lower than r_d in the higher respiration range. To further complicate the picture, for a California grassland with wintertime precipitation maximum, Xu and Baldocchi (2004) found that light-curve derived r_d were on the average lower than r_n from nighttime tower measurements, though it should be emphasized that the authors used biweekly pooled data to identify the light-curve parameters. Apparently, more detailed studies of the factors determining magnitudes of the day- and nighttime respiration in grasslands are required.

Though the problem of quantification of the light-use efficiency of grasslands is attracting attention of ecologists for nearly half a century (Cooper, 1970), it still remains rather controversial (Demetriades-Shah et al., 1992, 1994).

It is only recently that the new flux-tower and remotely sensed data provided the impetus for the progress in this field (Turner et al., 2003; Gilmanov et al., 2005b). The quantum yield of one molecule of CO_2 per 8 quanta of absorbed light provides the upper boundary of $\varepsilon < 125$ mmol mol^{-1} because even in closed canopies not all light is absorbed by photosynthetic tissues and used for photosynthesis. Numbers presented by Bélanger et al. (1994) who estimated gross photosynthesis and PAR in low (80 kg N ha^{-1}) and high (240 kg N ha^{-1}) fertilized stands of tall fescue (*Festuca arundinacea*) in southern France using biomass accumulation method provide us with an opportunity to compare their data with tower-based ε estimates for the Laqueuille site in central France. During summer regrowth period with 19.8 MJ m^{-2} day^{-1} of global radiation low fertilized stand showed P_g = 28.32 g DM m^{-2} day^{-1}, while high fertilized stand achieved P_g = 35.78 g DM m^{-2} day^{-1}. Assuming 42% C content of dry matter, 50% PAR in global radiation, and 1 MJ ~ 4.6 mol photons, we obtain $\varepsilon_{ecol,80}$ = 22 mmol mol^{-1} for low-fertilized, and $\varepsilon_{ecol,240}$ = 27 mmol mol^{-1} for high-fertilized variants. These estimates are not too far from values 24.7 and 33.0 mmol mol^{-1} we obtained for the extensively and intensively (143 kg N ha^{-1} year^{-1} fertilizer) managed Laqueuille grasslands (Table 7). According to Goudriaan and Van de Laar (1994), real maximum of the conversion efficiency of C_3 plants is estimated as 11 μg CO_2 J^{-1} or approximately 54 mmol mol^{-1}. Comparing with this figure, we may conclude that with fertilization and adequate moisture supply, temperate European grasslands, demonstrating maximum average weekly ε in the range 30–40 mmol mol^{-1}, on certain days were actually performing near the maximum level of C_3 photosynthetic efficiency, as is confirmed by the data for Carlow, Easter Bush, and Lille Valby grasslands.

Prior to the development of the flux-tower methodology and whole-ecosystem light-response analysis, measurement-based estimation of the ecosystem-scale P_g and R_e totals was rather difficult. Nevertheless, in those rare cases where P_g and R_e estimates obtained using other than flux tower methods are available, their comparison with tower-based data is highly desirable. For example, using chamber measurements Maljanen et al. (2001) estimated P_g of a grassland field with organic soil in eastern Finland as 2292 g CO_2 m^{-2} year^{-1}, which is remarkably close to our estimate of 2486 g CO_2 m^{-2} year^{-1} for Jokioinen grassland in southern Finland. Paustian et al. (1990) used a comprehensive array of harvest and physiological techniques to determine a carbon budget for a well fertilized grass ley (*Festuca pratensis* Huds.) in south-central Sweden. Their estimate of the net canopy carbon assimilation (=$P_g - R_{canopy}$) is 3084 g CO_2 m^{-2} year^{-1}, root respiration 374 g CO_2 m^{-2} year^{-1}, and heterotrophic respiration 917 g CO_2 m^{-2} year^{-1}. Assuming that respiration is proportional to production and using an estimate of root:shoot production for the grass ley site 285/454, we come to P_g = 3640 g CO_2 m^{-2} year^{-1} and R_e = 1847 g CO_2 m^{-2} year^{-1}. This P_g value fits well into the range of tower-based estimates in Table 8. With respect to the R_e estimate, it seems lower than tower-based estimates for comparable sites, though one should take into account the unusually high harvesting (equivalent to 1309 g CO_2 m^{-2} year^{-1}) and the fact that accumulation of carbon in phytomass and dead organic matter compartments was observed in this ecosystem during the experiment (Paustian et al., 1990).

Aeschlimann et al. (2005) conducted a comprehensive study of the CO_2 exchange in a managed *Lolium perenne* grassland at Eschikon near Zürich, Switzerland, using the FACE (Free Air Carbon dioxide Enrichment) technology. The FACE methodology cannot measure P_g, but provides net canopy carbon assimilation $P_g - R_{canopy}$ that for this grassland (receiving 140 kg N ha^{-1} year^{-1} in the low N treatment variant) was found to be 3890 g CO_2 m^{-2} year^{-1}. Estimate of R_{canopy} was not available, but it can be roughly estimated from the available annual nighttime respiration $R_{e,night}$ = 1261 g CO_2 m^{-2} year^{-1}. For the Oensingen grassland we found that the ratio of annual totals of daytime and nighttime respirations is equal to 3:2, which gives for the Eschikon grassland $R_{e,day}$ = 1892 g CO_2 m^{-2} year^{-1}. Taking into account the rather high value of aboveground biomass at the site (356 g DW m^{-2}), at least one third of $R_{e,day}$ may be attributed to canopy respiration, leading to a P_g estimate of 4520 g CO_2 m^{-2} year^{-1}. This lies within the 12% margin of the P_g = 5123 g CO_2 m^{-2} year^{-1} estimated for the Swiss site at Oensingen using light-response method (Table 8).

Casella and Soussana (1997) have estimated P_g of a *Lolium perenne* mesocosm with outdoor climatic conditions of central France (Clermont-Ferrand, 365 m a.s.l.) combining net assimilation measured in a canopy enclosure with shoot respiration estimated from temperature corrected nocturnal respiration measurements. For low-fertilized plots (160 kg N ha^{-1}), for the period from April to October, P_g = 5463 g CO_2 m^{-2}, while for the high-fertilized plots (530 kg N ha^{-1}), P_g reached 6930 g CO_2 m^{-2}. The above estimate for low-fertilized variant can be compared to the tower-based P_g = 4649 g CO_2 m^{-2} year^{-1} for the intensively managed grassland at Laqueuille, located on the mountain plateau above Clermont-Ferrand. Although the tower-based P_g value is less than the low-fertilized plot value by Casella and Soussana, such difference is reasonable considering differences in elevation, meteorology, and grazing between the two sites.

The tower-based P_g = 5915 g CO_2 m^{-2} year^{-1} estimate for the Haarweg site in The Netherlands is extremely close to a value 5988 g CO_2 m^{-2} year^{-1} which is an average of two years of measurements in the *Lolium perenne* microcosm near Wageningen, The Netherlands, located in close geographical proximity to the Haarweg site (Schapendonk et al., 1997).

Yet another approach to evaluate tower-based P_g estimates consists in comparing them with some (though rarely available) data on the total ecosystem net primary production ($NPP = P_g - R_a$, where R_a is autotrophic respiration) using the concept of ecosystem-scale carbon use efficiency $CUE = NPP/P_g$ (cf. Gifford, 1994; Choudhury, 2000; Amthor and Baldocchi, 2001). For grasslands, CUE typically ranges from about 0.35 to 0.65 (Amthor and Baldocchi, 2001), but under stress (e.g., grazing, hay-mowing) values close to the lower end may be expected (Gifford, 2003). Taking a conservative CUE = 0.5 and assuming 42% phytomass carbon content, for the fertilized *Festuca–Agrostis* grassland in western Germany with NPP = 1189 g DW m^{-2} $year^{-1}$ (Speidel and Weiss, 1972; Speidel, 1976; Rychnovska, 1993) we obtain P_g = 3662 g CO_2 m^{-2} $year^{-1}$. With similar coefficients, for an *Allopecurus* grassland in Czechoslovakia with NPP = 1423 g DM m^{-2} $year^{-1}$ (Rychnovska, 1993), P_g will be 4383 g CO_2 m^{-2} $year^{-1}$. These two values compare rather well with our tower-based estimate P_g = 4742 g CO_2 m^{-2} $year^{-1}$ obtained for the Grillenburg site in eastern Germany, taking into account that field methods of NPP measurements usually underestimate root exudates, while tower measurements inherently include them.

Overall, estimates of P_g and R_e for European grasslands remain within the limits available in the literature for natural and managed nonforest ecosystems of temperate climate (cf. Gilmanov et al., 2003a, 2004, 2005a,b; Novick et al., 2004; Wohlfahrt et al., 2005b). Nevertheless, possibly due to higher levels of N-fertilization in intensively managed European grasslands in Atlantic climate, they achieve higher P_g levels than, e.g., unfertilized North American grasslands in comparable climate. Pronounced effect on N-fertilization on productivity of grasslands is not only well established in direct experiments (cf. Casella and Soussana, 1997), but can also be seen in flux-tower measurements. For example, for an unfertilized warm-temperate Duke grassland in North Carolina (T_{year} = 15.5 °C, PCPN = 1145 mm $year^{-1}$) Novick et al. (2004) reported P_g = 4407 g CO_2 m^{-2} $year^{-1}$ which is 1000–2000 g CO_2 m^{-2} $year^{-1}$ lower than in highly fertilized (though not as warm) European grasslands. For comparison, for the moderately fertilized grassland of the Haller site, Pennsylvania (T_{year} = 9.3 °C, PCPN = 900 mm $year^{-1}$, 90 kg N ha^{-1} $year^{-1}$), application of the light-response method to the eddy-covariance tower data resulted in P_g range of 4600–5300 g CO_2 m^{-2} $year^{-1}$ (Skinner, 2005; Skinner et al., 2007), which is higher than in Duke grassland and considerably closer to European grassland data.

The $\{P_g, R_e\}$-scatter plot for European grasslands (Fig. 14) illustrating predominance of the CO_2 sink performance in this ecosystem type apparently suffers the same problem of overrepresentation of highly productive sites (see Körner, 2003) as the rather similar $\{P_g, R_e\}$-scatterplot for the 34 FLUXNET sites presented by Falge et al. (2002), where in only 3 out of 34 ecosystems respiration is higher than gross production. In comparison, Gilmanov et al. (2005b) have demonstrated that the source type of activity is not an exception for the mixed prairie ecosystems of the Northern Great Plains of North America, especially during years with lower than normal precipitation. Hopefully, the on-going efforts in continuation and expansion of the European network of grassland flux tower sites will in the nearest future provide additional materials to document the role of grasslands in the estimated 30% reduction in P_g and substantial release of carbon to the atmosphere by European ecosystems as the result of the European heatwave of 2003 predicted recently by a simulation model (Ciais et al., 2005).

5. Conclusion

Application of the methods of cross-spectral and non-linear regression analyses to the EUROGRASSFLUX data set of CO_2 flux measurements on eddy covariance stations in the wide range of environmental conditions and management regimes have confirmed earlier views that photosynthetically active radiation (Q) and top-soil temperature (T_s) are imperative factors controlling CO_2 exchange between grassland ecosystems and atmosphere at the 30-min time scale. Nonrectangular hyperbolic light-response model $P(Q)$ and modified nonrectangular hyperbolic light–temperature-response model $P(Q, T_s)$ proved to be an adequate and flexible tool for modeling diurnal dynamics of CO_2 exchange in the light at the ecosystem scale. At nighttime, it was not possible to establish robust instantaneous (30 min scale) relationships between CO_2 evolution rate r_n and environmental drivers, though under certain conditions, statistically significant relationship $r_n = r_0 e^{k_T T_s}$ was confirmed using a 7–14 day observation window. The key ecosystem-scale light-response parameters—apparent quantum yield, α, maximum gross photosynthesis, A_{max}, mean daytime ecosystem respiration, r_d, as well as the coefficient of gross ecological light-use efficiency, $\varepsilon = P_g/Q$, display patterns of dynamics during the year which can be formalized and used for gap-filling and comparative analysis. Maximum estimates of these parameters were found in intensively managed and fertilized temperate grasslands of Atlantic climate. Semi-natural grasslands of southern and central Europe with extensive grazing have much lower production, respiration, and light-use efficiency characteristics, while temperate and mountain grasslands of central Europe are characterized by intermediate parameter values. Ecophysiological parameters of European grasslands derived from light–temperature-response analysis of flux-tower data are in good agreement with values obtained using other methods (e.g., closed chambers, FACE chambers). Correlations between the light-response and productivity parameters at the ecosystem scale provide opportunities to estimate some of them using available information about the others during the modeling process. Annual gross primary production (P_g) of European grasslands has a wide range, from 1700 g CO_2 m^{-2} $year^{-1}$ in dry semi-natural pastures of south-central Europe to 6900 g CO_2 m^{-2} $year^{-1}$ in intensively managed grasslands in Atlantic climate. Annual totals of ecosystem respiration (R_e) at European tower sites is in the range $1800 < R_e < 6000$ g CO_2 m^{-2} $year^{-1}$. Annual net ecosystem CO_2 exchange (NEE) varies from significant net uptake (>2400 g CO_2 m^{-2} $year^{-1}$) to significant release (<−600 g CO_2 m^{-2} $year^{-1}$), though in 15 out of 19 cases grasslands acted as net sinks for atmospheric CO_2. In our selection of grasslands, source behavior was associated with organic rich soils, grazing, heat stress, or combination of these factors. Comparison of P_g, R_e, and NEE estimates for grassland tower sites with the same characteristics for European grasslands obtained with other methods did not reveal significant differences, though more representative samples are highly desired. Interestingly, patterns demonstrated by the European grassland data in the three-dimensional {PCPN, TA, P_g} and {PCPN, TA, R_e} spaces (Fig. 15) are quite different from analogous scatter plots for European forest flux data (Valentini et al., 2000): while in grasslands both production and respiration are primarily under control of precipitation (at least for PCPN $\leq$ 800 mm $year^{-1}$), in forests both P_g and R_e are more closely related to annual temperature, especially in the TA < 10° range. Overall, our results suggest significant relationships of the P_g and R_e of European grasslands to macroclimatic parameters such as annual precipitation and temperature, but apparently these relationships cannot be reduced to simple monofactorial models.

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