Physiologically Based Method for Partitioning Flux-Tower NEE Measurements in Grassland and Agricultural Ecosystems into Photosynthesis and Respiration

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Introduction

Net CO_2 fluxes, F_c, provided by terrestrial flux-tower measurements represent the difference between two fundamental (and often close in magnitude) processes of gross photosynthesis (P_g) and ecosystem respiration (R_e):

$$F_c = P_g - R_e. \tag{1}$$

In general, factors of photosynthesis and respiration are not the same (though overlap), and the patterns of their response to a given factor are not identical. Therefore, to understand the dynamics of CO_2 exchange and predict its response to climatic change or anthropogenic management, decomposition of the F_c data into gross photosynthesis and respiration (1) is a necessary part of tflux data processing, known as partitioning of F_c into P_g and R_e components. While in the earlier period of flux data analysis partitioning was usually based on estimation of *day-time* respiration from *night-time* fluxes, derivation of **day-time** respiration from **day-time** measurements became a dominant approach (Gilmanov et al. 2003, 2005, 2007, 2010; Reichstein et al. 2005; Lasslop et al. 2010). An essential feature of the daytime CO_2 exchange utilized in partitioning algorithms based on light-period measurements, is that the decrease of F_c is directly associated with the increase of respiration R_e, which, in its turn, is closely related to temperature. The problem is that the decrease of F_c may also be caused by decreasing photosynthesis P_g, e.g. resulting from water stress. A number of methods to incorporate water-stress were proposed in the literature (e.g., Gilmanov et al. 2003, Lasslop et al. 2010). In this presentation we describe a **physiologically based approach** incorporating combined effects of **photosynthetically active radiation** (Q), **soil temperature** (T_s), and **vapor pressure deficit** (*VPD*).

Light-Soil temperature-VPD-response of the ecosystem CO_2 exchange

Analysis of the tower CO_2 exchange data in a wide range of grassland and crop ecosystems led us to the partition equation:

$$F_c(Q,\ T_s,\ VPD) = P_g(Q,\ VPD) - R_e(T_s), \tag{2}$$

provided that for the net flux F_c, radiation Q, soil temperature T_s, and vapor pressure deficit *VPD* only the 30-min data for single days are used. This assumption excludes the need to introduce factors which change slowly within a day (e.g., soil water content, soil nutrients concentrations, leaf area). A popular approach to describe photosynthetic response is to use the rectangular hyperbolic:

$$P_g(Q;\ \alpha,\ A_{max}) = A_{max}\ \alpha\ Q/(A_{max} + \alpha\ Q) \tag{3}$$

or the Mitscherlich-type

$$P_g(Q;\ \alpha,\ A_{max}) = A_{max}\ (1 - Exp(-\ \alpha\ Q/A_{max})), \tag{4}$$

equations, where α is the initial slope (apparent quantum yield), and A_{max} is the plateau (photosynthetic capacity) of the light-response. To incorporate VPD-limitation, these equations are multiplied by a function $\varphi(VPD)$, describing inhibition of photosynthesis by *VPD*. E.g., rectangular hyperbola with *VPD* limitation was used by Lasslop et al. 2010. Unfortunately, both equations can not describe light-response curves of varying convexity, including the ramp-type Balckman functions. This leads to significant biases in estimation of parameters, particularly for C_4 plants such as maize, which often demonstrate Blackman-type response to light. To allow variation of the convexity of the light-response we have selected nonrectangular hyperbolic light-response function with convexity parameter θ:

$$P_g(Q,VPD;\alpha,A_{\max},\theta,\sigma_{VPD}) = \frac{\varphi(VPD;\ \sigma_{VPD})}{2\theta}\left(\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max}\theta Q}\right), \tag{5}$$

where the $\varphi(VPD;\sigma_{VPD})$ depends on the curvature σ ($2 \le \sigma_{VPD} \le 16$) with lower values describing strong water-stress effect, and the higher values - weak effect (Fig. 1).

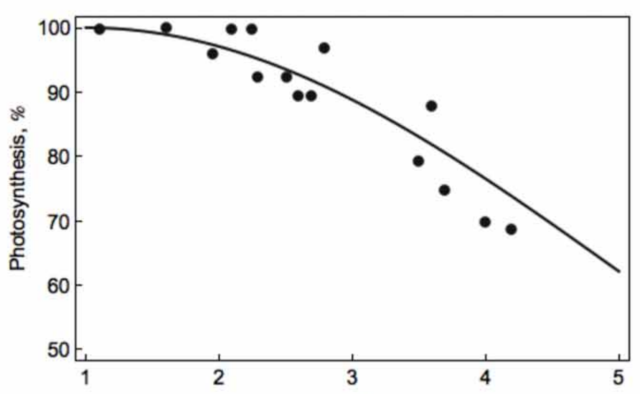

Figure 1. Photosynhesis VPD-response function φ(VPD; σ_{VPD}) with curvature parameter σ_{VPD} = 5.4 kPa (after El-Sharkawey et al. 1984).

Because soil respiration is not closely linked to *VPD*, it was possible to describe ecosystem respiration by only temperature-dependent term $R_e(T)$. In contrast to authors using air temperature T_a as predictor for R_e, we found top-soil temperature T_s as a more numerically robust driver for R_e, because while *VPD* and T_a are closely correlated resulting in numerical difficulties in parameter estimation, T_s is less directly related to *VPD*, leading to more robust estimates. Following Tornley and Johnson(2000), we retained for $R_e(T_s)$ the classical Vant-Hoff's equation in its exponential form:

$$R_e(T_s;\ r_0,\ k_T) = r_0\ Exp(k_T\ T_s), \tag{6}$$

where $r_0 = R_e(0)$, and k_T is the temperature sensitivity coefficient. Combining (5) and (6), we obtain the general equation for the net CO_2 exchange in the form:

$$F_C(Q,T_S,VPD;\alpha,A_{\max},\theta,r_0,k_T,\sigma_{VPD}) = \frac{\varphi(VPD;\sigma_{VPD})}{2\theta}\left(\alpha Q + A_{\max} - \sqrt{(\alpha Q + A_{\max})^2 - 4\alpha A_{\max}\theta Q}\right) - r_0 Exp(k_T T_S). \tag{7}$$

Study Sites

The light-soil temperature-*VPD* method of flux partitioning was applied to many grassland and agricultural sites worldwide from the AMERIFLUX, AGRIFLUX and other FLUXNET-member-networks, as well as to the data from non-affiliated researchers (cf. references in Gilmanov et al. 2007, 2010; Li Zhang et al. 2011), with particular emphasis to the AMERIFLUX sites in South Dakota: a C_3 grassland (Brookings) dominated by C_3 species (Fig. 2) and a C_4 maize crop (Lennox/Sioux Falls) (Fig. 3).

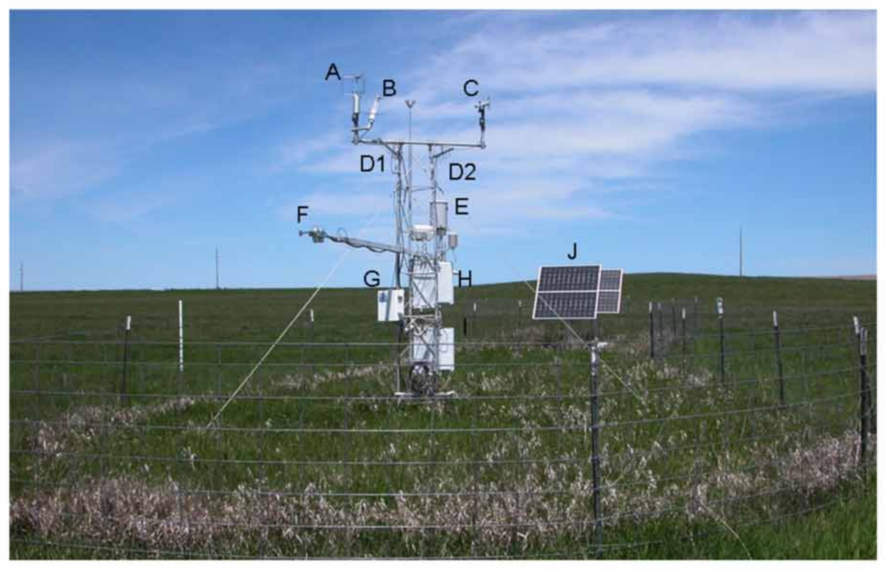

Figure 2. Eddy-covariance tower on a grassland near Brookings, SD: A – ultrasonic anemometer; B – CO_2/H_2O sensor; C – wind monitor; D1, D2 – telemetry antennas; E – micromet. module (temperature, humidity, atmospheric pressure, precipitation); F – radiometers; G – LiCor 7500 infrared gas analyzer; H – communication block and computer; I – data logger; J – solar panels.

Figure 3. Eddy-covariance tower on a continuous maize crop near Lennox/Sioux Falls, SD.

Both stations are members of the AMERIFLUX network with continuous measurements since April 2004 at the Brookings site and since November 2007 at the Lennox site. Original 30-min aggregated raw data of the observations at these towers processed according the standard protocol are available as the Level-1 data at the AMERIFLUX database (http://cdiac.ornl.gov/).

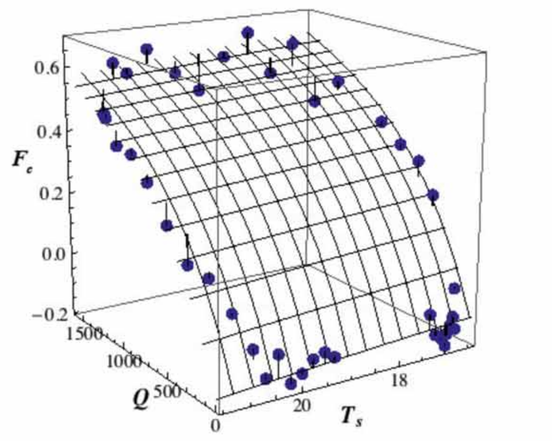

Figure 4. CO_2 flux F_c (mg CO_2 m^{-2} s^{-1}) at the Brookings grassland site, DOY 182-2009, in relation to photosynthetically active radiation Q (mmol m^{-2} s^{-1}) and soil temperature T_s (°C). Response surface shows fluxes corresponding to average daily VPD value. Estimated flux values $F_c(Q,T_s,VPD)$ are closer to the experimental data (dots) than shown by the response surface.

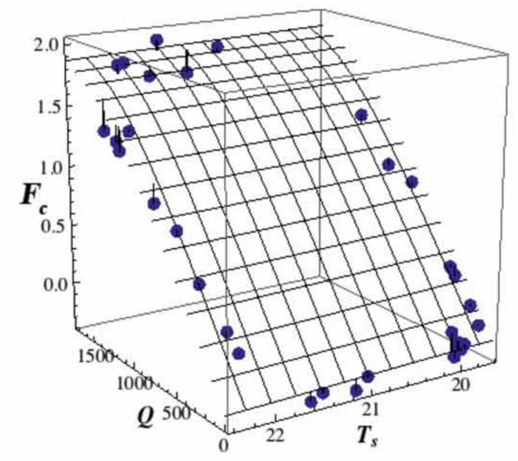

Figure 5. CO_2 flux F_c (mg CO_2 m^{-2} s^{-1}) at the Lennox maize site, DOY 191-2009, in relation to photosynthetically active radiation Q (µmol m^{-2} s^{-1}) and soil temperature T_s (°C). Response surface shows fluxes corresponding to average daily VPD. Estimated flux values $F_c(Q,T_s,VPD)$ are closer to the experimental data (dots) than shown by the surface.

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Estimation of the parameters

Parameters α, A_{max}, θ, σ_{VPD}, r_0, and k_T of the function $F_c(Q,\ T_s,\ VPD)$ were numerically estimated for every day of the year with available Q, T_s, *VPD*, and F_c data. Using the Global Optimization Package of the "Mathematica" system, for every day's $\{Q(i),\ T_s(i),\ VPD(i),\ F_c(i),\ i = 1, 2, \ldots, n\}$ data set of $n \le 48$ values with 30-min time step we identified best-fit parameter values $\{\alpha,\ A_{max},\ \theta,\ \sigma_{VPD},\ r_0,\ k_T\}$. For example, Figure 4 shows the 3-D projection of the 4-D hyperspace corresponding to the average *VPD* value for day 182 of the year 2009 at the Brookings grassland site.

Numerical estimates and statistics of the equation (7) parameters that best fit the DOY 182-2009 Brookings data (Table 1).

Table 1. Numerical values and the goodness-of-fit characteristics of the parameters of equation (7) for day 182-2009 at the Brookings grassland site.

Parameter	α mg CO2/µmol	A_{max} mg CO_2/ m²/s	θ ratio	r_0 mg CO_2/ m²/s	k_T (°C)$^{-1}$	σ_{VPD} kPa
Value	0.00128	1.15	8.6*10^{-9}	0.0383	0.0683	2.675
St. error	0.000114	0.092	0.0075	0.0299	0.0409	1.483
t-value	8.896	12.477	1.14*10^{-6}	1.284	1.67	1.804
p-value	6.42*10^{-11}	6.22*10^{-15}	0.5	0.1037	0.052	0.04

Table 2. Numerical values and the goodness-of-fit characteristics of the parameters of equation (7) for day 191-2009 at the Lennox maize site.

Parameter	α mg CO_2/µmol	A_{max} mg CO_2/ m²/s	θ ratio	r_0 mg CO_2/ m²/s	k_T (°C)$^{-1}$	σ_{VPD} kPa
Value	0.00164	2.471	0.953	0.0674	0.0642	3.135
St. error	0.000135	0.5907	0.0909	0.0988	0.0709	1.058
t-value	12.15	4.78	10.48	0.68	0.905	2.964
p-value	1.6*10^{-12}	0.00014	3.92*10^{-11}	0.25	0.187	0.003

Comparison of parameter estimates for various days and sites shows that while the numerical optimization routine practically always finds physiologically reasonable sets of parameters, there are differences in the uncertainties of these estimates. As exemplified by the *t*- and *p*-values in the above tables, parameters of apparent quantum yield α, photosynthetic capacity A_{max}, and *VPD*-response curvature σ_{VPD} have considerably lower uncertainties than parameters of light-response convexity θ and temperature-response parameters r_0 and k_T. Because of that, for comparative purpose we have also calculated average daytime respiration rate $r_{day} = r_0\ Exp(k_T T_s)$ which has much lower uncertainty.

Significance of the VPD control of the net CO_2 exchange.

Significance of the *VPD* as a factor controlling the net CO_2 flux may be characterized by the histogram of the estimated curvature parameters σ_{VPD}. Estimated σ_{VPD} values typically lie in the interval from 2 to 16 kPa, the lower range characterizing strong *VPD* effect (rapid decrease of F_c with *VPD* increasing to values higher than 1 kPa), while higher values of σ_{VPD} describe functions $\varphi(VPD;\ \sigma_{VPD})$ which decrease only gradually with increasing aerial drought.

In the Brookings grassland, 2009 there were 66 days with VPD-response curvature $\sigma_{VPD} < 3$ kPa, and 27 days with $3 \le \sigma_{VPD} < 5$ kPa, when substantial reduction of photosynthesis due to aerial drought was observed. In contrast, at the Lennox maize field in 2009 there were only 33 days with $\sigma_{VPD} < 3$ kPa, and 31 days with $3 \le \sigma_{VPD} < 5$ kPa, indicating lower limitation of photosynthesis by drought relative to grassland. For comparison, in the more southern Freeman Ranch, TX grassland in 2006 the number of days with $\sigma_{VPD} < 3$ kPa was 159, and the number of days with $3 \le \sigma_{VPD} < 5$ kPa was 49, indicating stronger VPD-effect on photosynthesis in this ecosystem.

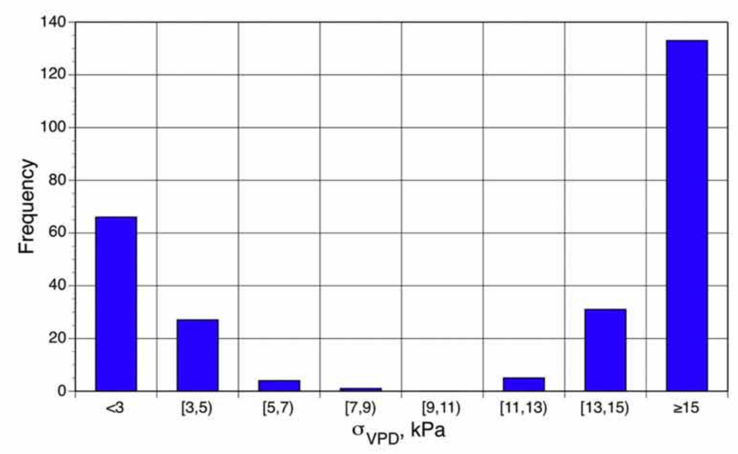

Figure 6. Histogram of values of the curvature σ_{VPD} for the VPD-response function of the Brookings grassland during the 2009.

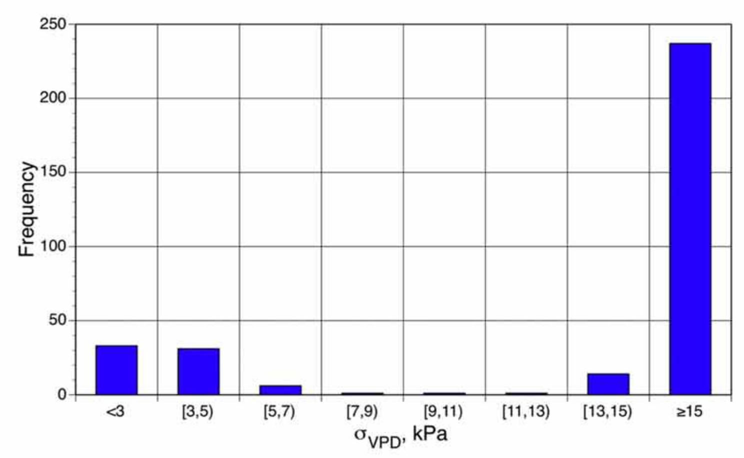

Figure 7. Histogram of values of the curvature σ_{VPD} for the VPD-response function of the Lennox/Sioux Falls maize crop during the 2009.

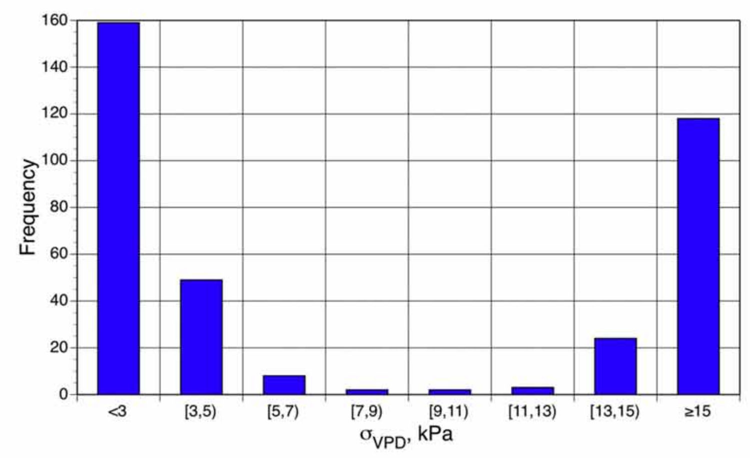

Figure 8. Histogram of values of the curvature σ_{VPD} for the VPD-response function of the Freeman Ranch, TX grassland during the 2006.

Dynamics of photosynthesis and respiration parameters

Parameters estimated by flux partitioning demonstrate seasonal and year-to-year patterns highly important for understanding, gap-filling, predictive modeling, and scaling-up of the whole-ecosystem CO_2 exchange. Considerable day-to-day variability makes it necessary to use the 7-day (weekly) averages of parameters and their errors providing more consistent and comparable results. Maximum weekly values $\alpha_{max,wk}$ of the quantum yield in the grassland during 6 years remained in the range of 30 to 40 mmol/mol as the $\alpha_{max,wk}$ values for the maize crop (Fig. 9A, 10A), while the photosynthetic capacity of grassland ($0.6 < A_{max,wk} < 1.5$ mg CO_2 m^{-2} s^{-1}) remained lower than in maize (2.2 mg CO_2 m^{-2} s^{-1}) resulting in the overall lower light-use efficiency compared to the crop ($12 < \varepsilon_{g,wk} < 30$ mmol mol^{-1} for grassland compared to $\varepsilon_{g,wk} = 33$ mmol mol^{-1} for the maize, Fig. 9D, 10D).

As expected, in both ecosystems ecological light-use efficiency was lower than quantum yield (Fig. 9A,D, Fig. 10A,D). Nevertheless, in maize with its C_4 photosynthesis the difference between α and ε_g values was substantially lower than in the C_3 grassland, which is in part due to the convexity of the maize close to $\theta = 1$ characteristic to the Blackman-type light response (cf. Fig. 4, 5, Table 1, 2).

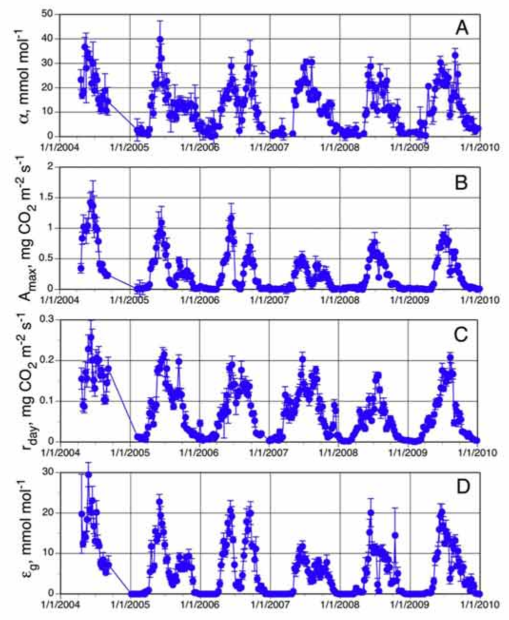

Figure 9. Dynamics of photosynthesis and respiration parameters of the Brookings grassland, 2004-2009: A - quantum yield, B – photosynthetic capacity, C – day-time ecosystem respiration, D - light-use efficiency.

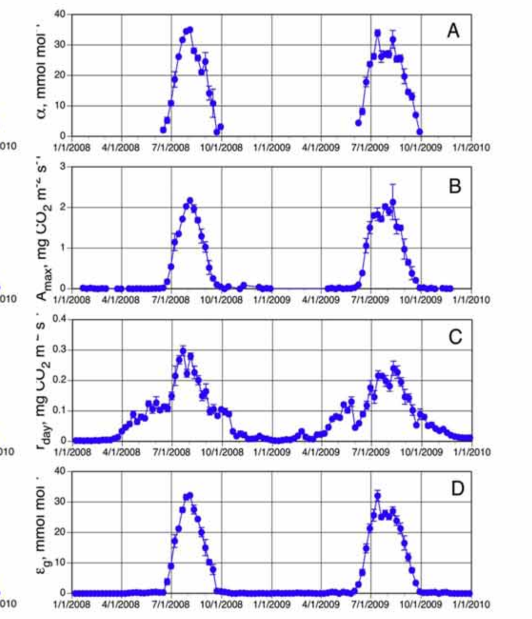

Figure 10. Dynamics of photosyn-thesis and respiration parameters of the Lennox/Sioux Falls maize crop, 2008-2009: A - quantum yield, B - photosyn-thetic capacity, C - daytime ecosystem respiration, D - light-use efficiency.

Conclusions

▪ Net flux partitioning using light, soil temperature and *VPD* factors provides robust estimates of photosynthesis, respiration, and eco-physiological parameters applicable to a wide range of grassland and crop ecosystems.

▪ On a significant number of days photosynthesis is limited by drought, making introduction of the *VPD* factor necessary to prevent overestimation of respiration during light-response analysis.

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