

Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites

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[1] Pioneering work in the last century has resulted in a widely accepted paradigm that primary production is strongly positively related to temperature and water availability such that the northern hemispheric forest carbon sink may increase under conditions of global warming. However, the terrestrial carbon sink at the ecosystem level (i.e. net ecosystem productivity, NEP) depends on the net balance between gross primary productivity (GPP) and ecosystem respiration (TER). Through an analysis of European eddy covariance flux data sets, we find that the common climate relationships for primary production do not hold for NEP. This is explained by the fact that decreases in GPP are largely compensated by parallel decreases in TER when climatic factors become more limiting. Moreover, we found overall that water availability was a significant modulator of NEP, while the multivariate effect of mean annual temperature is small and not significant. These results indicate that climate- and particularly temperature-based projections of net carbon balance may be misleading. Future research should focus on interactions between the water and carbon cycles and the effects of disturbances on the carbon balance of terrestrial ecosystems. **Citation:** Reichstein, M., et al. (2007), Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites, *Geophys. Res. Lett.*, 34, L01402, doi:10.1029/2006GL027880.

1. Introduction

[2] The environmental controls of net primary production (NPP) and its spatial and temporal variability have been a topic of considerable interest in plant ecology for decades.

In 1939, Walter first documented a positive linear relationship between above ground NPP and mean annual precipitation [Walter, 1939]. Similar relationships were later found for many ecosystems around the world [Rosenzweig, 1968; Lieth, 1975; Knapp and Smith, 2001].

[3] However the carbon balance at the ecosystem level (net ecosystem production, NEP) is the difference between gross primary production (GPP), which is carbon uptake by photosynthesis, and carbon losses by autotrophic and heterotrophic respiration (terrestrial ecosystem respiration, TER) [Schulze et al., 2000]. Thus, the response of the carbon balance to climate is the combination of the responses of GPP and TER to climate. One of the first experimental studies on the overall ecosystem carbon balance demonstrated the important role of respiration in driving net carbon uptake along continental gradients [Valentini et al., 2000]. It is well established that both GPP and TER increase with temperature and both are limited by water availability [Kirschbaum, 2000; Reichstein et al., 2002]. The parallel behavior of these two processes already provides a hint to the fact that net ecosystem production (NEP) is less sensitive to climate than expected if climate-driven increases or decreases in GPP or TER are met with compensatory behavior in the other term. Indeed, ecosystem models, which primarily rely on climatic input as driving variables have more difficulties describing patterns of NEP than of NPP, partly due to simple assumptions about soil carbon pools, which affect the heterotrophic component of modeled TER [Thornton et al., 2002].

[4] The eddy covariance method has proven to be a valuable direct measure of net carbon and water fluxes between ecosystems and the atmosphere [Baldocchi et al., 1988; Aubinet et al., 2000] over hectares to about 1 km² and from short and long timescales (hours to years) [Schmid 1999]. Since the first continental-scale synthesis activities [Valentini et al., 2000; Law et al., 2002], the eddy covariance network FLUXNET has grown such that interannual variability and effects of climatic gradients on ecosystem production can be analyzed more thoroughly [Baldocchi et al., 2001]. Moreover, the possibility to statistically partition the net carbon fluxes into its major components gross primary production and ecosystem respiration [Reichstein et al., 2005] allows a better interpretation of the fluxes in terms of ecosystem processes. Here we analyze 93 site-years of eddy-covariance data from the EUROFLUX and CARBOEUROFLUX networks with respect to their annual sums of GPP, ecosystem respiration (TER) and NEP in relation to simple climatic indices. The goal of this empirical analysis is to determine the roles of temper-

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ature and water limitations on GPP and TER—and thereby NEP - across a range of European forest sites.

2. Methods

2.1. Sites and Data Processing

[5] We analyzed CO₂ and water flux data measured by the eddy covariance technique from 23 different sites in Europe from 1996 to 2003 that were submitted to the CARBOEUROFLUX database, resulting in a total of 93 annual data sets (see auxiliary material Table S1¹). The sites occupy climates from cold and wet boreal in northern Europe, maritime and sub-continental temperate in central Europe, and sub-humid and semi-arid Mediterranean climates in the southern Europe (see auxiliary material Figures S1 and S2) and include both managed and almost unmanaged forests of different age classes.

[6] These data sets were processed using a standardized methodology. The fluxes of CO₂ were first corrected for within-canopy CO₂ storage, then controlled for insufficient turbulence (u_* filtered) and outliers ('spikes'), and gap-filled and partitioned into gross primary productivity and ecosystem respiration [Reichstein et al., 2005; Papale et al., 2006]. Uncertainties of flux estimates due to the u_* -selection criterion, spike detection, storage correction, gap-filling, and flux-partitioning have been quantified as discussed in the above-mentioned publications. These combined uncertainties fall within the range of 13 and 92 g C m⁻² year⁻¹ (median 49 g C m⁻² yr⁻¹).

[7] Systematic errors in eddy covariance fluxes due to non-ideal observation conditions (e.g., advection [Aubinet et al., 2005] and the imbalance in the energy budget) are under intensive research and remain to be quantified exactly. However, total error is certainly below the value of 200 gC m⁻² yr⁻¹ that is conservatively assumed by the Monte-Carlo analysis of the regression results as discussed below.

2.2. Regression Analysis

[8] Mean annual temperature (MAT), an index of water availability (IWA) and annual potential radiation (R_{pot}) were related to the carbon dioxide fluxes derived from eddy covariance with a stratified linear regression. For this empirical analysis we split the data set into two populations by a threshold of potentially available radiation energy ($R_{pot,threshold}$) of 8.8 TJ m⁻² yr⁻¹, which corresponds to a latitude of approx. 52°N and which yielded the best overall regressions. The simple stratified linear regression model is:

$$y = \begin{cases} a_{MAT} \cdot MAT + b_{MAT}, & \text{if } R_{pot} < R_{pot,threshold} \\ a_{IWA} \cdot IWA + b_{IWA}, & \text{if } R_{pot} \geq R_{pot,threshold} \end{cases} \quad (1)$$

where a_{MAT} , b_{MAT} , a_{IWA} , and b_{IWA} are the regression coefficients, MAT (°C), IWA (dimensionless) and $R_{pot,threshold}$ are as defined above, and y represents annual GPP, TER or NEP, respectively. All flux units are kg C m⁻² yr⁻¹.

[9] Mean annual temperature was calculated as the mean over all half-hourly temperature observations. We define the

IWA as the ratio of annual actual to potential evapotranspiration (AET/PET), where AET is derived from the eddy covariance latent heat flux measurements and PET using the Penman-Monteith equation with a zero canopy resistance. Since AET does not depend on soil water availability alone but also on the vegetation (e.g., LAI) the IWA does not fully isolate limitation by water availability; this could be refined in the future. Apart from the direct application of this regression (equation 1) to the data, we evaluated the robustness of the results against potential errors in the annual sums of NEP, TER, and GPP. Therefore we performed a Monte-Carlo simulation by adding an error of either + or -200 g C m⁻² yr⁻¹ to the annual flux of each site and year. For each site and year the sign of the error was randomly and independently assigned. We performed the regression analysis on 500 simulated fluxes to obtain a distribution of the explained variance by the regression model. Clearly, the added error is much larger than expected in reality. Hence, our approach is conservative and the results robust against errors in annual carbon fluxes.

2.3. Analysis of Modeled and Observed Ecosystem Respiration

[10] Ecosystem respiration was modeled at three Mediterranean sites with seasonal drought and ample information on soil hydraulic properties with the BIOME-BGC model (version 4.11) [Thornton et al., 2002] driven by local meteorology. The standard parameterizations for evergreen broadleaf forest and shrubland were used and a spin-up run was performed until soil carbon pools reached equilibrium. Both daily model output of ecosystem respiration and daily ecosystem respiration estimates derived from eddy covariance measurements were analyzed using the same diagnostic regression model:

$$TER = f(T_{soil}, RSWC) \cdot g(RSWC) \quad (2)$$

with soil temperature (T_{soil}) and relative soil water content ($RSWC$) as predictors (for details see Reichstein et al. [2003a]). The apparent Q_{10} of ecosystem respiration was then calculated from the parameterized equation as a function of soil water content and soil water availability as

$$\ln(Q_{10}(T, RSWC)) = 10 \cdot \frac{\partial}{\partial T} \ln(f(T, RSWC)).$$

3. Results and Discussion

[11] The simple stratification of the data according to potential radiation yielded strongly different controls at northern and southern sites. Annual gross primary production (GPP) at the southern sites correlates positively and significantly with the index of water availability (IWA, Figure 1a) (F-test; $r = 0.71$, $p < 0.001$, $N = 61$), while variation in GPP at the northern sites can be explained to a large extent by mean annual air temperature (MAT, Figure 1b) ($r = 0.91$, $p < 0.001$, $N = 33$; see Figure S3 for plots of northern sites GPP versus IWA and southern sites GPP versus MAT). This different control on GPP is expected, since the Northern sites are rather cool (MAT between -2 and 11°C) and rarely water-limited, while the

¹Auxiliary material data sets are available at <ftp://ftp.agu.org/apend/gl/2006g1027880>. Other auxiliary material files are in the HTML.

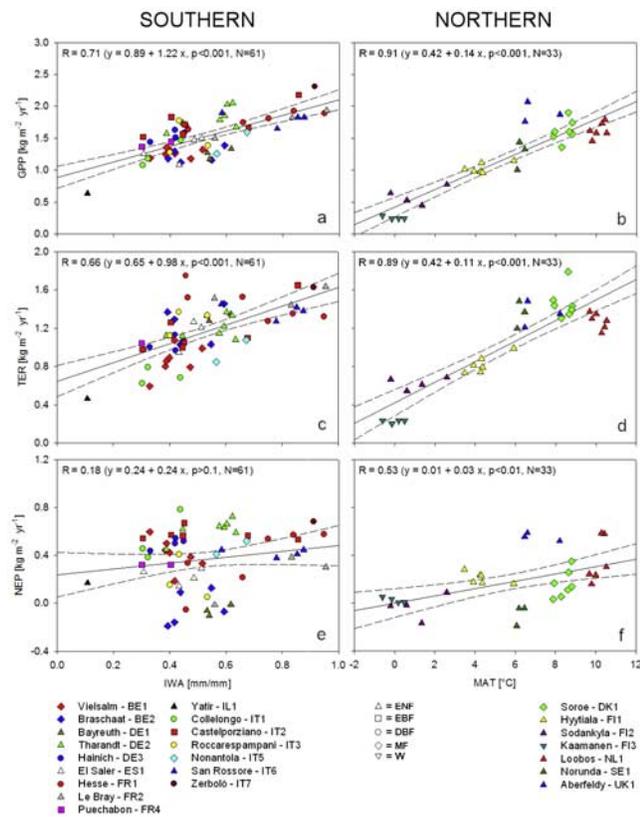


Figure 1. The correlation between the index of water availability (IWA) and annual (a) gross primary production (GPP), (c) terrestrial ecosystem respiration (TER) and (e) net ecosystem production (NEP), and between mean annual temperature (MAT) and annual (b) GPP, (d) TER, and (f) NEP. Solid and dashed lines represent the linear regression lines with associated 95% confidence bands. The linear correlation coefficient, the linear regression equation, and the significance level are reported in each plot. (ENF = Evergreen Needle Forest, EBF = Evergreen Broadleaf Forest, DBF = Deciduous Broadleaf Forest, MF = Mixed Forest, W = Wetland).

Southern sites are warmer and relatively more water-limited. Ecosystem respiration at both southern and northern sites correlates similarly with the IWA and MAT, respectively (Figures 1c and 1d). This response almost completely compensates for the GPP response and results in very weak correlation between net ecosystem production and climate indices (Figures 1e–1f).

[12] The simple stratified linear regression model described above (equation 1) explains more than two thirds of the continental-scale spatial and temporal variability of GPP (Figure 2 and auxiliary material Figure S4a), which is in accordance with the first hypotheses concerning climatic control of primary production [Rosenzweig, 1968; Lieth, 1975] and also recent analyses carried out on NPP [Knapp and Smith, 2001] and eddy covariance GPP data [Law et al., 2002].

[13] We found a relationship between TER and both MAT and IWA that nearly parallels the GPP response (Figures 1c and 1d). A similar proportion of spatio-temporal

variance of TER is explained by the simple empirical model equation (1) (Figure 2 and auxiliary material Figure S4b). However, it is evident that this concept of limiting climatic factors as a major determinant of production cannot be transferred to net ecosystem production as observed by the eddy covariance network: only 23% of its variation can be explained by the model (Figure 2, ‘24 hr NEP’). Figure 2 demonstrates that the good performance of equation (1) for explaining annual GPP and TER but not NEP is not a statistical artifact of the derivation of TER and GPP; direct eddy covariance observations of NEP during the hours of photosynthesis or during nighttime are similarly well explained by equation (1). Moreover, in Figure 2 we confirm that the results are robust against potential errors in the annual sums of NEP, since they prevail even with the very large errors introduced by the Monte-Carlo approach (cf. methods). We can exclude that this result is specific to the selected predictor variables IWA and MAT since we performed multiple regressions against many other meteorological variables which did not result in improved estimates of annual NEP (based on the adjusted r^2 -criterion). In addition, model residuals were not significantly correlated with other climatic variables (Table 1).

[14] While the current analysis is of course very simplified also biogeochemical models tend to have large problems to predict variation of annual NEP [Thornton et al., 2002]. Here we find, that in particular the complex temperature-water availability interaction on ecosystem respiration does not seem to be described correctly as we find from a subset of three Mediterranean sites where validated soil hydrological information was available [Reichstein et al., 2003b]. We analyzed the observed and modeled daily ecosystem respiration (cf. methods) with the identical empirical regression model that allows detecting an effect of soil moisture on the apparent Q_{10} of ecosystem respiration [Reichstein et al., 2002]. This analysis yielded similar magnitudes of Q_{10} for observed and modeled TER data, but opposite responses to soil water availability (Figure 3). The apparent Q_{10} of respiration from the observed data declines with decreasing water availability, as has previously been shown for soil respiration [Reichstein et al., 2003a]. The reasons for this behavior remain to be clarified but may include changes in substrate availability and microbial starvation, such that the rate-limitation of decomposition switches from temperature to C availability [Davidson et al., 2006]. Yet, the increase of the effective Q_{10} during drier conditions (Figure 3b) in the modeled data can be attributed to the growth-maintenance-respiration paradigm [Amthor, 2000]. When water becomes limiting, modeled assimilation decreases, leading to decreased (temperature insensitive) growth respiration, while the temperature sensitive maintenance respiration remains largely unaffected. Hence the proportion of temperature sensitive to temperature-insensitive respiration increases resulting in higher Q_{10} values under water limiting conditions. Since the growth-maintenance-respiration paradigm is implemented in most biogeochemical models including coupled climate-carbon-cycle simulations [Cox et al., 2000], a similar behaviour may be expected that is contrary to the ecosystem-level observational evidence.

[15] At the annual time scale the data suggests that water availability generally overrides the temperature effect on

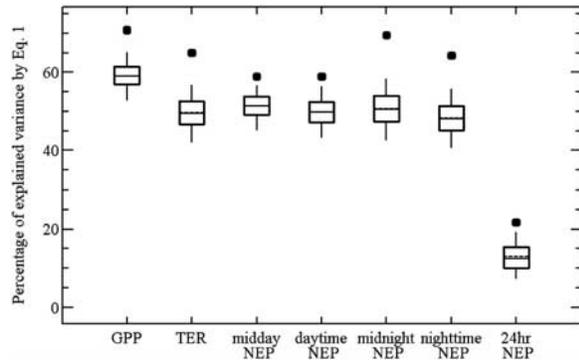


Figure 2. Coefficients of determination (r^2) of the simple regression model (equation 1) for the explanation of annual GPP, TER and NEP, where for NEP midday (11h–13h, daytime’, midnight (23h–1h), nighttime and 24-hour integrals were calculated. Black dots denote results for the original data, while standard box-and-whisker plots show the results of the Monte-Carlo simulation ($n = 500$) where annual flux estimates were randomly perturbed by either + or -200 gC m^{-2} to simulate a potentially large measurement error.

terrestrial ecosystem respiration, as reflected in the best-fit linear regression equations (units as in equation (1); parameter standard errors in parenthesis):

Northern sites:

$$\text{TER} = 0.42(0.11) + 0.55(0.11)\text{GPP} - 0.28(0.01) \cdot \text{IWA} + 0.02(0.02)\text{MAT}; r^2 = 0.90, p < 0.001 \quad (3a)$$

Southern sites:

$$\text{TER} = 0.27(0.15) + 0.36(0.12)\text{GPP} + 0.51(0.20) \cdot \text{IWA} + 0.01(0.01)\text{MAT}; r^2 = 0.50, p < 0.001 \quad (3b)$$

In both equations only the effect of GPP and IWA were statistically significant. Thus IWA has a statistical effect on TER additional to GPP, while MAT does not. Again, other temperature indices do not have a stronger effect than MAT.

[16] Similarly, variation in NEP appears more related to variation in GPP and water availability than to TER and MAT, contrasting *Valentini et al.* [2000]. Variation in TER explains only 1% of the variance in NEP, while GPP explains nearly 40% (auxiliary material Figure S5). Stratified regressions with northern and southern sites also determined that GPP and IWA were the most important predictors of NEP, while MAT has no statistically significant influence on NEP when GPP is included as predictor in the regression (equation (4a), (4b), units as in Figure 1):

Northern sites:

$$\text{NEP} = -0.42(0.11) + 0.45(0.11)\text{GPP} + 0.28(0.01) \cdot \text{IWA} - 0.02(0.02)\text{MAT}, r^2 = 0.59, p < 0.001 \quad (4a)$$

Southern sites:

$$\text{NEP} = -0.27(0.14) + 0.64(0.11)\text{GPP} - 0.53(0.19) \cdot \text{IWA} - 0.01(0.01)\text{MAT}, r^2 = 0.43, p < 0.001 \quad (4b)$$

On the contrary, the relationship between IWA and GPP is significant and shows latitudinal variation, with a positive effect on GPP at northern and a negative effect on southern sites. Consequently, given a fixed GPP, southern sites tend to have a lower NEP under moister conditions owing to a stimulation effect on respiration [*Xu et al.*, 2004]. This result highlights the possibility that with respect to changing climate a change in rainfall pattern may affect respiration more strongly than gross productivity, leading to a reaction of the net ecosystem carbon balance, that may be counter-intuitive given contemporary understanding of the relationships of NPP with climate.

[17] The failure of current paradigms to describe the spatio-temporal variability of NEP (Figure 1) and temperature-carbon-water interactions (Figure 3) should alert us to the fact that interactions with the components of NEP—namely GPP and TER—may be more important. The development of biogeochemical models should be revisited, particularly in the context of the global warming trend will be accompanied by a decreased water-availability and that already today more than 40% of the terrestrial ecosystems are considered partially water-limited. Moreover, prospects

Table 1. Residual Variance of the Empirical Model (Equation (1)) Explained by Seasonal Rather Than Annual Climatic Indices^a

| Climate variable | -NEP Residual = a * x + b | | ERV |
|---|---------------------------|-----------|-------|
| | a | b | |
| Length of carbon uptake period (days) | -0.3122 | 0.001453 | 0.224 |
| Soil water content 2nd layer (not available at all sites) (%) | -0.1058 | 0.005505 | 0.147 |
| Potential evapotranspiration Jan–Mar (mm) | -0.04509 | 0.00148 | 0.101 |
| Actual evapotranspiration Jul–Sep (mm) | -0.2572 | 0.001738 | 0.083 |
| Potential evapotranspiration Oct–Dec (mm) | -0.01439 | 0.001449 | 0.077 |
| Actual evapotranspiration Jan–Feb (mm) | -0.05815 | 0.001607 | 0.037 |
| Actual evapotranspiration Oct–Dec (mm) | -0.06217 | 0.001835 | 0.033 |
| Soil temperature (°C) | 0.08828 | -0.009916 | 0.03 |
| Potential evapotranspiration Jul–Sep (mm) | -0.09776 | 0.0003916 | 0.029 |
| Potential evapotranspiration Apr–Jun (mm) | -0.1271 | 0.0001459 | 0.028 |

^aVariables that correlated significantly with NEP are ordered by descending explained residual variance (ERV). Variables that do not significantly correlate with the model residual include: potential radiation Jul–Sep (mm), length of carbon uptake period during midday (days), friction velocity (m/s), precipitation (both annual or by season or month) (mm), VPD (annual or by season or month) (hPa), Growing degree days by season or month (°C day), climatic or actual water balance (mm), Global radiation (annual or by season with exception above) (MJ m^{-2}), soil water content in the upper layer (%).

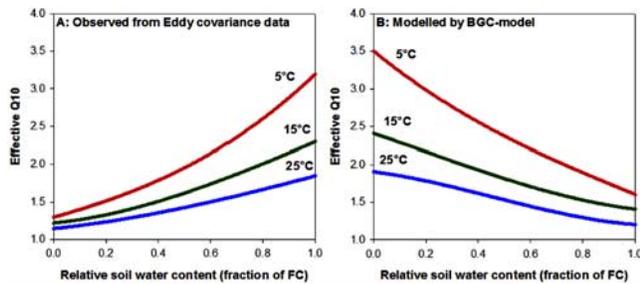


Figure 3. The response of the apparent temperature sensitivity of ecosystem respiration (Q_{10}) to soil water availability and temperature (5, 15, 25°C), according to (a) observed ecosystem respiration and (b) Biome-BGC model output. Both Figures 3a and 3b result from an analysis of daily data with the same regression model equation (2). The Q_{10} value indicates by which factor a process accelerates with an increase of temperature by 10°C.

for temperature driven enhancement of extra-tropical carbon sequestration may be questionable; our results suggest that factors related to the water balance may override temperature effects on ecosystem carbon balances.

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