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氣候變遷對生態系光合作用的影響

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The Influence of Future Climate Perturbations on Ecosystem Photosynthesis

計畫編號：NSC 92-2111-M-002-011

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Abstract

Increases in atmospheric CO₂ concentration not only affects climate variables such as precipitation, water vapor concentration, and air temperature, but also affects intrinsic ecosystem physiological properties such as the maximum carboxylation capacity and stomatal conductance. De-convolving these two effects remains uncertain in biosphere-atmosphere water and carbon cycling. Using a simplified analytical net ecosystem CO₂ exchange (NEE) model, tested with recently collected flux measurements in a humid grassland ecosystem in Ireland, we assess how much projected climate shifts affect net canopy photosynthesis (A) without physiological adjustments and contrast those findings with physiological adjustments already reported for several grassland ecosystems. Our analysis suggests that the intrinsic grassland ecosystem physiological adjustment of A is about forty five times more important than the resulting climatic forcing shifts from the IS92a scenario (and a double of atmospheric CO₂ concentration). Implications to afforestation policy and future experimental efforts to quantify the carbon sink from humid grassland ecosystems are also discussed.

Keywords: photosynthesis, climate perturbation, net ecosystem exchange

1. Introduction

Grasslands cover about 40% of the ice-free global terrestrial surface, but their contribution to water and carbon fluxes and sensitivity to climatic perturbations remains uncertain. Increases in atmospheric CO₂ concentration (C_a) have two impacts on grassland ecosystems – they modify climate-forcing variables such as precipitation (P) and air temperature (T_a), and they modify intrinsic ecosystem physiological properties such as maximum carboxylation capacity and stomatal conductance. Using a general

circulation model (GCM) coupled with a vegetation (biosphere) model, both Sellers et al. (1996) and Betts et al. (1997) found that increases in C_a could result in a reduced stomatal conductance and transpiration and an increased air temperature. The relative importance of shifts in climate forcing and ecophysiological adjustments on net canopy photosynthesis (A), both arising from increasing C_a , continues to be an active research area for grassland ecosystems (e.g., Jackson et al., 2002; Gill et al., 2002; Shaw et al., 2002). Many studies conducted thus far focus on one of these two aspects. For example, model simulation experiments on photosynthesis typically adjust for climate shifts yet retain “static” ecophysiological properties (e.g., Luo et al., 2001; Medlyn et al., 1999), while most ecological experiments (e.g., chamber based or free air CO₂ enrichment experiments) investigate the effects of elevated C_a on A while retaining similar climatic and hydrologic forcing for ambient and enriched pairs (e.g., Jongen and Jones, 1998; Gill et al., 2002). De-convolving the relative importance of these two effects on A remains an unresolved yet important problem for advancing our understanding on the potential sink for CO₂ in grassland ecosystems.

Using a combination of published data, recently collected flux measurements in a humid grassland ecosystem at Cork, Ireland, and a simplified analytical model developed here, we assess how much projected climate shifts affect net photosynthesis in humid grasslands without physiological adjustments and contrast those findings with physiological adjustments already published for several grassland ecosystems. The humid grassland ecosystems are ideal for our investigation as they are primarily “energy” limited and plant and soil hydraulics exert minor control on A .

Our climate projections are based on the standard Hadley Center model output of the IS92a scenario for Ireland in which C_a doubles over the course of the 21st century. The scenario is based on a 'business as usual' emission rate and assuming a mid-range economic growth but no measures to reduce greenhouse gas emissions. The general circulation model used is HadCM3, which is a new generation of high-resolution coupled atmosphere-ocean general circulation model described by Gordon et al (2000) and Pope et al (2000).

The main novelty in our analysis is an explicit treatment of the interplay between changes in P (which is the key variable forecasted by GCM's), net radiation (R_n), and vapor pressure deficit. That is, for photosynthetic responses, decreases in P may well be accompanied by increases in R_n due to reduction in cloud cover, which increases both transpiration and carbon uptake.

We compare the effects of climate shifts on modeled A with two experiments that explicitly considered how elevated C_a alters the intrinsic physiological properties of grasslands. Our objective is to assess how much the effects of elevated C_a are realized in climate forcing shifts or intrinsic eco-physiological adjustments.

2. Theory

For humid regions characterized by uniformly distributed precipitation across seasons, the latent heat flux, LE (W m^{-2}), can be calculated by the Penman-Monteith equation

$$LE = \frac{\Delta Q_n + \rho c_p D / r_{av}}{\Delta + \gamma (1 + r_{st} / r_{av})}, \quad (1)$$

where Δ is the slope of the saturation vapor pressure-temperature curve calculated at the air temperature T_a , γ ($= \frac{\rho C_p}{0.622 L_v}$) is the psychrometric constant, ρ ($\approx 1.2 \text{ kg m}^{-3}$) is the mean air density, c_p ($= 1005 \text{ J kg}^{-1} \text{ K}^{-1}$) is the specific heat for air, L_v ($= 2.46 \times 10^6 \text{ J kg}^{-1}$) is the latent heat of vaporization, $Q_n = R_n - G_s$, G_s is the soil heat flux (W m^{-2}), D is the vapor pressure deficit, r_{av} is the aerodynamic resistance of water vapor (s m^{-1}), and r_{st} is the stomatal resistance of water vapor ($\approx 100 \text{ s m}^{-1}$ for current grass site). In (1), r_{av} can be estimated by

$$r_{av} = \frac{k u_*}{\ln(z / z_o) - \psi_m(z / L)}, \quad (2)$$

where k ($= 0.4$) is the von Karman constant, u_* is the friction velocity (m s^{-1}), z is the measurement height, z_o is the surface roughness, and $\psi_m(z/L)$ is the stability correction function for momentum and L is the Obukhov length (see Brutsaert, 1984). Equations (1) and (2) can be solved iteratively to incorporate the influence of thermal stability on r_{av} .

The bulk canopy conductance (boundary layer conductance plus stomatal conductance) for CO_2 can be calculated by (Campbell and Norman, 1998)

$$g_{CO_2} = \frac{P_a LE}{1.6 D L_v M_w}, \quad (3)$$

where g_{CO_2} is the bulk canopy conductance ($\text{mol m}^{-2} \text{ s}^{-1}$), M_w ($= 0.018 \text{ kg mol}^{-1}$) is the molecular weight of water, P_a is the atmospheric pressure, and the factor 1.6 is due to the difference in molecular diffusivity between water vapor and CO_2 . The net canopy photosynthesis, A , can be expressed as

$$A = g_{CO_2} \times C_a \times \left(1 - \frac{C_i}{C_a}\right), \quad (4)$$

where C_i is the canopy-averaged intercellular CO_2 concentration (ppm), C_a in ppm, and A in $\mu\text{mol m}^{-2} \text{ s}^{-1}$. By replacing (1) and (3) in (4), we have

$$A = \left(\frac{P_a}{1.6 L_v M_w}\right) \left(\frac{\Delta Q_n + \rho c_p D / r_{av}}{\Delta + \gamma (1 + r_{st} / r_{av})}\right) \left(\frac{C_a}{D}\right) \left(1 - \frac{C_i}{C_a}\right). \quad (5)$$

Based on (5), the projected shift in photosynthesis (dA) can be related analytically to shifts in Q_n , C_a , D , C_i/C_a , and r_{st} by

$$\frac{dA}{A} = \frac{dC_a}{C_a} - \left(\frac{\Delta Q_n dD}{(\Delta Q_n + \rho c_p D / r_{av}) D} - \frac{\Delta dQ_n}{\Delta Q_n + \rho c_p D / r_{av}} \right) - \left(\frac{(\gamma / r_{av}) dr_{st}}{\Delta + \gamma (1 + r_{st} / r_{av})} + \frac{d(C_i / C_a)}{1 - (C_i / C_a)} \right) \quad (6)$$

$$I = II - (III - IV) - (V + VI)$$

In (6), the second term (II) is the shift by increases in C_a , the third and fourth terms (III and IV) represent the shifts by climate changes (i.e., changes in D and Q_n), and the fifth and sixth terms (V and VI) can be interpreted as the physiological shifts. Equation (6) describes that the shift in photosynthesis is simply a linear summation of shifts in atmospheric CO_2 concentration, climate-forcing variables, and eco-physiological properties. If the ratio C_i/C_a is approximately constant for current and elevated C_a (Ehleringer and Cerling, 1995; Liu and Teskey, 1995; Katul et al., 2000), then the physiological shifts are mainly from changes in the stomatal resistance. In (6), if Q_n is not available (or measured), in a first order analysis, it is reasonable to assume that $dQ_n/Q_n \approx dR_n/R_n$. Both dQ_n and dD can be related to shifts in P using existing meteorological measurements at a site. That is

$$dQ_n \approx \frac{\partial Q_n}{\partial P} dP; \quad dD \approx \frac{\partial D}{\partial P} dP,$$

where $\partial Q_n/\partial P$ and $\partial D/\partial P$ are evaluated from time series of Q_n , P , and D . The collection of these time series as well as the experimental setup used to test the model and its assumption is described next.

3. Experiment

The experimental site is a grass covered flat catchment located in North Cork, Ireland (51.90 N, 8.47 W, 195 m above mean sea level). The grassland type is mainly C3 pasture and meadow, varying in height between 5 – 50 cm, and the soil profile consists of a top layer of humus (10-15 cm thick) and a subsoil layer of sandy loam (45 cm thick). The surface roughness for momentum of this site is around 0.03 m. An eddy-covariance system which consists of a sonic anemometer (RM Young 8100) and an open-path $\text{CO}_2/\text{H}_2\text{O}$ gas analyzer (Licor 7500) was used to measure CO_2 and water vapor fluxes at 10 m above the soil surface. The sampling frequency and duration were 10 Hz and 30 minutes, respectively. The R_n and G_s were measured at 10 m above the surface and 5 cm below the surface, respectively. Mean meteorological parameters, including P , measured at 0.5 m above the soil surface, and T_a and D were measured at 3 m above the soil surface. Soil temperature (T_s) and soil moisture were also measured at both 2.5 cm and 5.0 cm below the surface. With the exception of the eddy-covariance system, all measurements were sampled at 1 minute and averaged (or summed) every 30 minutes. Data collection commenced on July 1, 2001 and is continuously running as part of a long-term CELTICFLUX monitoring initiative. The data set used here is the 2002 subset.

4. Results and Discussion

In this section, we assess the model performance and then proceed to quantify the effects of climate shifts on A . The primary assumption in (5) is that the transpiration rate is approximated by the Penman-Monteith formula. We tested this formula in Figure 1, which compares modeled latent heat flux (LE_M) with eddy-covariance measured (LE_{EC}) water vapor flux. The coefficient of determination (R^2) and the root-mean squared error (RMSE) for Figure 1 are 0.81 and 25 ($W m^{-2}$), respectively, and suggest that the agreement between measured and modeled LE is sufficiently accurate for photosynthesis calculations.

Eddy-covariance systems can measure NEE but do not explicitly measure A ; hence, the model performance cannot be directly tested for A . An indirect test of modeled A by (5) can be conducted if measured nighttime CO_2 fluxes are used to calibrate a respiration model that is then used to compute daytime ecosystem respiration (R_E). By combining modeled A with modeled R_E , a comparison between measured and modeled NEE can be conducted and then serves as an indirect test for modeled A . One can also subtract modeled R_E from measured NEE to get a “measured” A and use this value to test the model performance by (5). Both methods are analogous.

To obtain the respiration model, measured night-time NEE were regressed upon T_s using the standard Q_{10} model

$$R_E = R_{E,10} (Q_{10})^{\frac{T_s-10}{10}}, \quad (7)$$

where Q_{10} and $R_{E,10}$ ($\mu mol m^{-2} s^{-1}$) are respiration temperature sensitivity and base respiration at 10 °C, respectively. Figure 2 shows the dependence of R_E on T_s along with the regression fit to (7). The scatter in Figure 2 is large ($R^2 = 0.12$, RMSE = 0.72 $\mu mol m^{-2} s^{-1}$) but typical of such ecosystem R_E models (Novick et al., 2004). We also noticed that the residuals (i.e., the difference between measured and modeled R_E) do not depend on soil moisture. Using measured night-time NEE for a friction velocity (u_*) > 0.2 $m s^{-1}$, we compute a $Q_{10} = 2.02$ and a $R_{E,10} = 3.57$ which are also consistent with reported values for grasslands (Novick et al., 2004). Our choice of the threshold u_* is to ensure that the footprint of the nighttime respiration (and hence the derived Q_{10} and $R_{E,10}$) is not much larger than its near-neutral daytime value (i.e. the source area contributing to nighttime measurements is comparable to the source area contributing to the daytime measurements for scalability of the respiration function). Modeled NEE is then given by $-A+R_E$, where A is computed from (5) with $C_a = 355$ ppm and $C_i/C_a = 0.84$ (for C_3 type grasses), and R_E is computed from (7). The comparison between predicted and measured NEE is shown in Figure 3. Given the scatter in R_E , the agreement between measured and modeled NEE is reasonable ($R^2 = 0.42$, RMSE = 6.13 $\mu mol m^{-2} s^{-1}$).

To compute dA and the climate shift terms (i.e., dQ_n , dD), we determine $\partial Q_n / \partial P$ and $\partial D / \partial P$ from the time series measurements. These quantities are calculated by ensemble-averaging Q_n and D (denoted by angle brackets $\langle \cdot \rangle$) during daylight hours for

different daily precipitation intensity bins, and applying a power-law relation to derive the expected decrease in $\langle Q_n \rangle$ and $\langle D \rangle$ with increasing $\langle P \rangle$ (mm day^{-1}). Kumagai et al. (2004) successfully used such an approach to assess how precipitation shifts affect water cycling in a Bornean tropical rain forest under current and projected precipitation scenarios. Figure 4 shows these measured relationships along with the best-fit power-law curves. We found that $\langle Q_n \rangle = 195 \langle P \rangle^{-0.65}$ and $\langle D \rangle = 0.3 \langle P \rangle^{-0.31}$.

Using these relations and noting that the annual average precipitation intensity is about 4.89 mm day^{-1} at the site, we estimate: $\partial Q_n / \partial P = -9.24 \text{ W m}^{-2} (\text{mm day}^{-1})^{-1}$; $\partial D / \partial P = -0.012 \text{ kpa} (\text{mm day}^{-1})^{-1}$. For December, January, and February (DJF), the mean Q_n , D , Δ , and r_{av} are $16.0 (\text{W m}^{-2})$, $0.14 (\text{kpa})$, $0.067 (\text{kpa/K})$, and $28.6 (\text{s m}^{-1})$ respectively, and the HadCM3 predicts a P increase of 0.55 mm day^{-1} for Ireland. Hence, with these estimates and assuming $dC_a/C_a = 1$ (i.e., a doubling of CO_2 concentration) and no physiological shift (i.e., $V + VI = 0$), we got $dA/A = 0.96$. For March, April, and May (MAM) and for September, October, and November (SON), the reported $dP = 0$ resulting in $dA/A = 1$. For June, July, and August (JJA), the mean Q_n , D , Δ , and r_{av} are $121.0 (\text{W m}^{-2})$, $0.32 (\text{kpa})$, $0.1 (\text{kpa/K})$, and $28.1 (\text{s m}^{-1})$ respectively, and the HadCM3 predicts a decrease in P of 0.66 mm day^{-1} , which leads to $dA/A = 1.01$. When integrating these four seasonal outcomes over the entire year, we found $dA/A = 0.99$. This small departure from unity (i.e., dC_a/C_a) is primarily due to the interplay between shifts in precipitation and the asymmetric expected shifts in D and Q_n for DJF and JJA. Also, notice that, from (6), a positive shift in dD results in a decrease in dA , but a positive change in dQ_n results in an increase in dA . Hence, some influence of dD on dA is canceled, as expected, by dQ_n .

To address our primary objective, we compare our computed $dA/A = 0.99$ derived from climate shifts with other experimental studies that only evaluated physiological adjustments (i.e., assuming $III = IV = 0$) to elevated CO_2 in Table 1. The two grassland ecosystem experiments primarily considered in Table 1 were conducted on markedly different climate and soils (Texas, U.S.A. and Dublin, Ireland); yet the relationship between dA/A and dC_a/C_a is surprisingly similar perhaps suggesting a consistent adjustment in ecosystem physiology (i.e., $V + VI$) with elevated CO_2 . From Table 1, it is clear that these two studies suggest that, for dA/A , the physiological adjustment ($V + VI \approx 0.45$) is about 45 times more important than the expected shifts in climate-forcing terms ($III - IV \approx 0.01$) derived from the IS92a projected climate scenario for Ireland.

5. Implications

Based on our model calculations in conjunction with reported elevated CO_2 experiments for grasslands, two broad implications emerge from our analysis:

- 1) A recent study by Cox et al. (2000) demonstrated that climate models with “dynamic” vegetation predict a drastically different climate and terrestrial carbon sink when compared with their “static” land cover counterparts. For these models, the need to account for a

realistic reduction in $g_{co_2}(1 - C_i / C_a)$ (or down-regulation) with elevated atmospheric CO₂ is equally critical to resolving correct climate forcing terms for future climate scenarios.

2) The Kyoto Protocol allows countries to obtain carbon credits (or get carbon debits) for forest activities to help meet commitments in reducing greenhouse gas emissions. Such allowance is now promoting aggressive afforestation policy in several European countries, most notably in Ireland, in which afforestation aims at increasing forested lands from 9% (in 2000) to 17% (in 2030) as described by Anon (2000). Given that a large portion of land cover (~ 45%) in Ireland will remain predominantly pasture and farmed grasslands, a logical first step is to quantify the magnitude of the carbon sink in such grasslands but for a future climate scenario. By (6), for a 100% increase in elevated CO₂, the increase in photosynthesis after reductions by physiological adjustment (~ 45%) and climate shifts (~ 1%) is still 54%. This study also points out that future research efforts should focus on the magnitude of the physiological adjustments of grassland ecosystems under elevated atmospheric CO₂ as it can be much larger than expected climate forcing shifts.

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Table 1: The relative importance of internal ecophysiological adjustments and external climate forcing on dA/A for grasslands using $dC_a/C_a = 1$.

Study	dA/A	Remarks
Reference State	1.0	No climate or physiological adjustment occurs (i.e., canopy conductance and C_i/C_a are unaltered by elevated CO_2).
Gill et al. (2002)	0.55	External climate is similar for ambient and elevated CO_2 . The dA/A is estimated by us from their data in Figure 1 which shows a linear increase of A with increasing C_a .
Jongen and Jones (1998)	0.58	External climate is similar for ambient and elevated CO_2 . The dA/A is estimated by us from their reported mean values of net primary productivity (NPP) for C3 species under ambient and elevated conditions. Note, if photosynthesis linearly relates to gross primary productivity (GPP), and GPP linearly relates to NPP, then $dA/A \approx dGPP/GPP \approx dNPP/NPP$.
Current Model Results	0.99	No changes in C_i/C_a occur and changes in conductance are strictly due to “external” climatic differences predicted for the IS92a scenario.

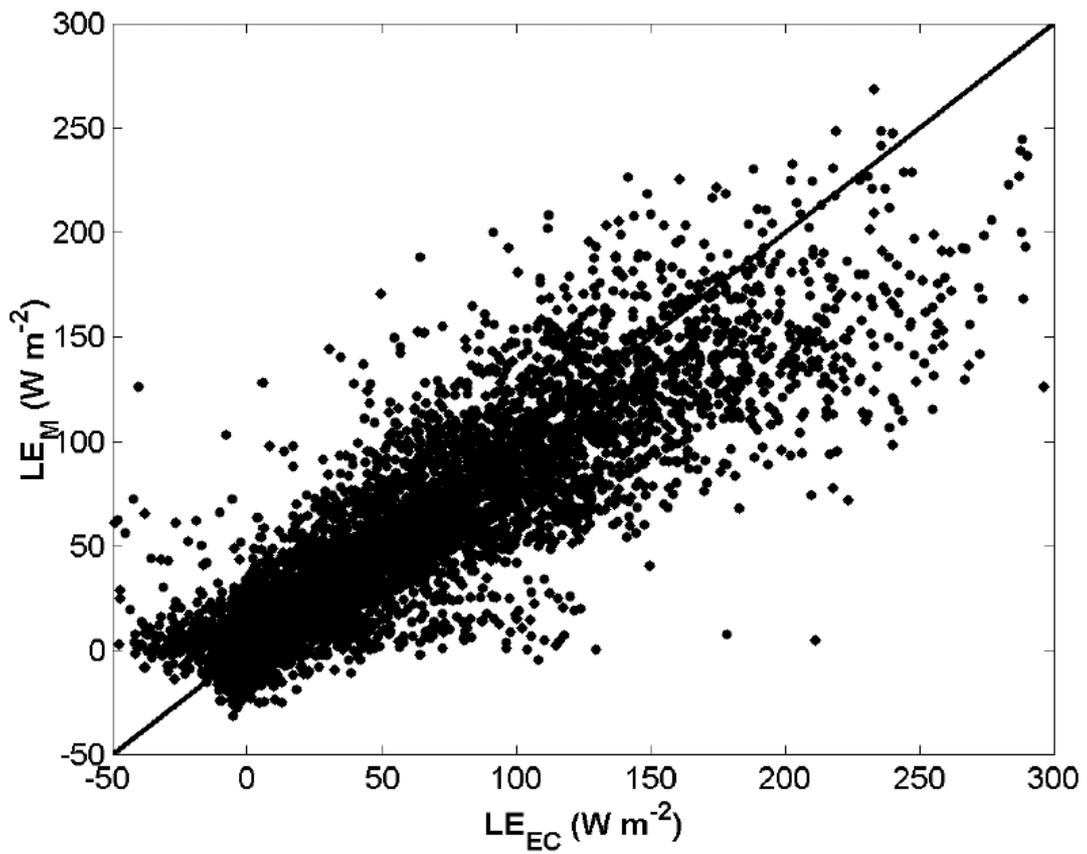


Figure 1: Comparison between modeled latent heat flux (LE_M) by the Penman-Monteith equation and eddy-covariance measured (LE_{EC}) water vapor flux. The 1:1 line is also shown.

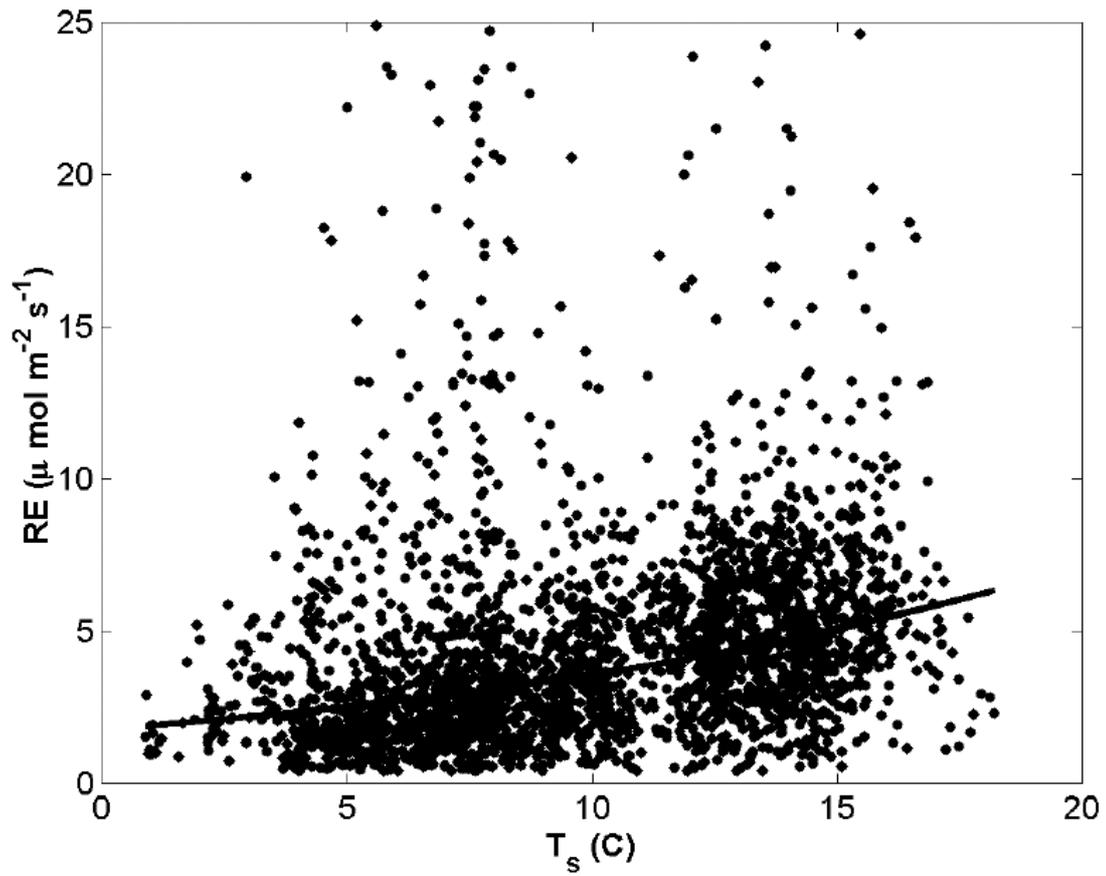


Figure 2: Variation of measured respiration (R_E) with soil temperature T_s for friction velocity (u_*) $> 0.2 \text{ m s}^{-1}$. The solid line represents equation (7).

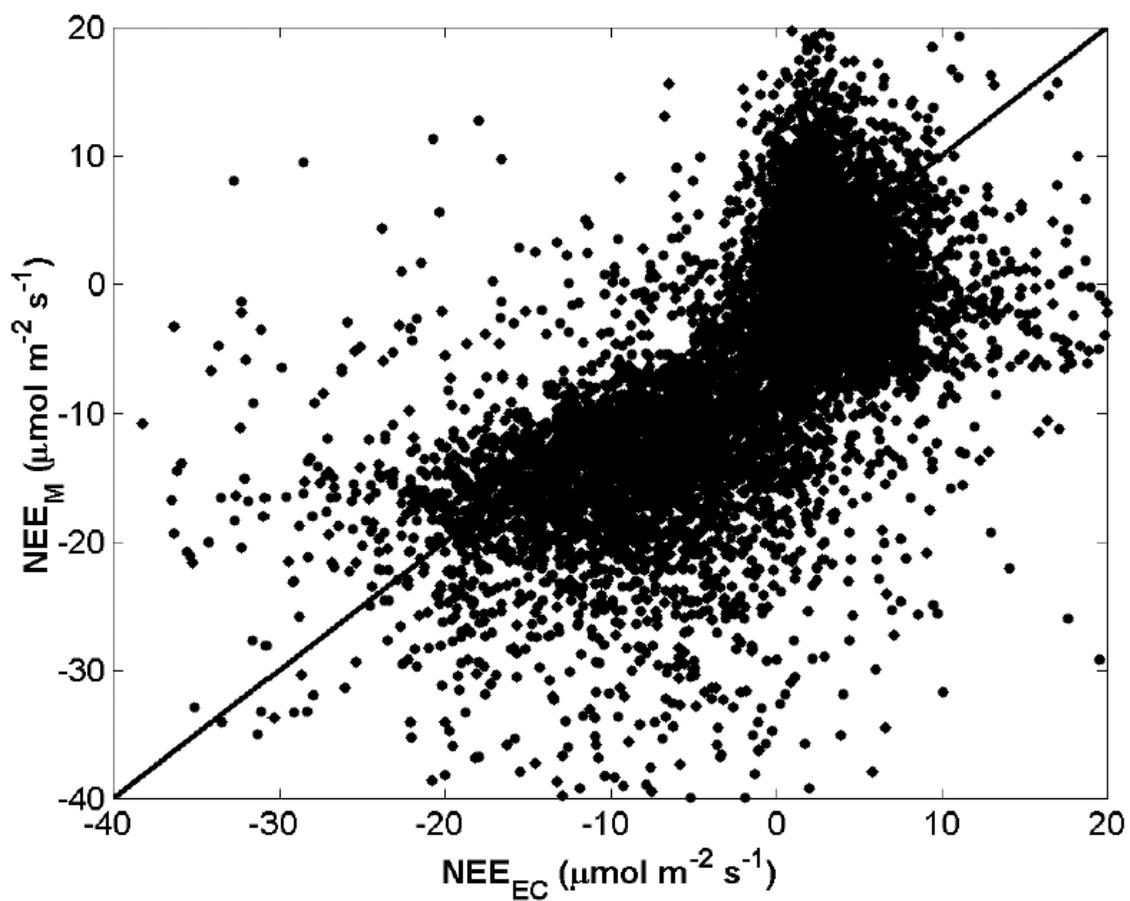


Figure 3: Comparison between predicted (NEE_M) and measured (NEE_{EC}) net ecosystem exchange. The 1:1 line is also shown.

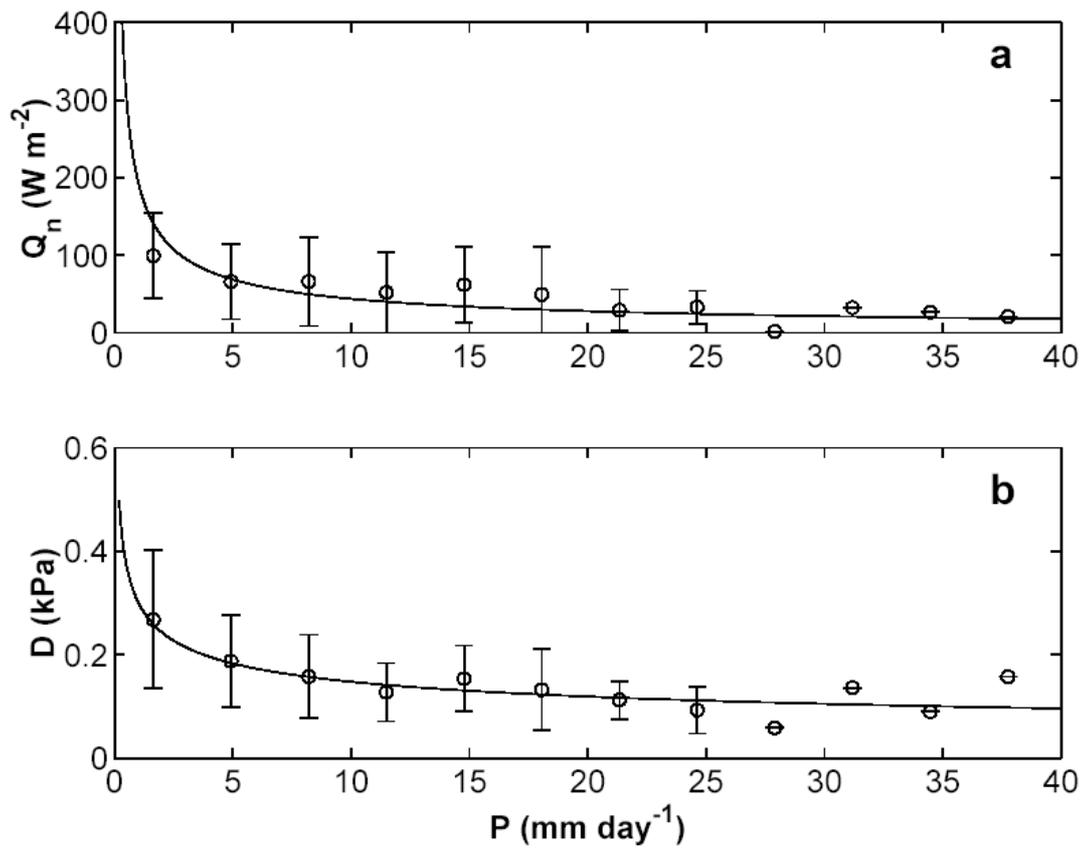


Figure 4: (a) Mean (open circles) and standard deviation (vertical bar) of measured daytime radiation (Q_n) versus daily precipitation (P). The solid line is regression curve. (b) Same as Figure 4a but for vapor pressure deficit (D).

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