

# 行政院國家科學委員會專題研究計畫 成果報告

## 氣候變遷對生態系光合作用的影響

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氣候變遷對生態系光合作用的影響

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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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,  $LE$  ( $\text{W m}^{-2}$ ), 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  $\Delta$  is the slope of the saturation vapor pressure-temperature curve calculated at the air temperature  $T_a$ ,  $\gamma$  ( $= \frac{\rho C_p}{0.622 L_v}$ ) is the psychrometric constant,  $\rho$  ( $\approx 1.2 \text{ kg m}^{-3}$ ) 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 ( $\text{W m}^{-2}$ ),  $D$  is the vapor pressure deficit,  $r_{av}$  is the aerodynamic resistance of water vapor ( $\text{s m}^{-1}$ ), 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 ( $\text{m s}^{-1}$ ),  $z$  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  $\text{CO}_2$  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  $\text{CO}_2$ . 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  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  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  $\langle P \rangle$  ( $\text{mm day}^{-1}$ ). 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  $4.89 \text{ mm day}^{-1}$  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  $Q_n$ ,  $D$ ,  $\Delta$ , 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  $0.55 \text{ mm day}^{-1}$  for Ireland. Hence, with these estimates and assuming  $dC_a/C_a = 1$  (i.e., a doubling of  $\text{CO}_2$  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  $Q_n$ ,  $D$ ,  $\Delta$ , 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  $0.66 \text{ mm day}^{-1}$ , 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  $\text{CO}_2$  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  $\text{CO}_2$ . 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  $\text{CO}_2$  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  $CO_2$  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 ( $\sim 45\%$ ) 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  $CO_2$ , the increase in photosynthesis after reductions by physiological adjustment ( $\sim 45\%$ ) and climate shifts ( $\sim 1\%$ ) 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  $CO_2$  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 $\text{CO}_2$ ).
Gill et al. (2002)	0.55	External climate is similar for ambient and elevated $\text{CO}_2$ . 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 $\text{CO}_2$ . 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.

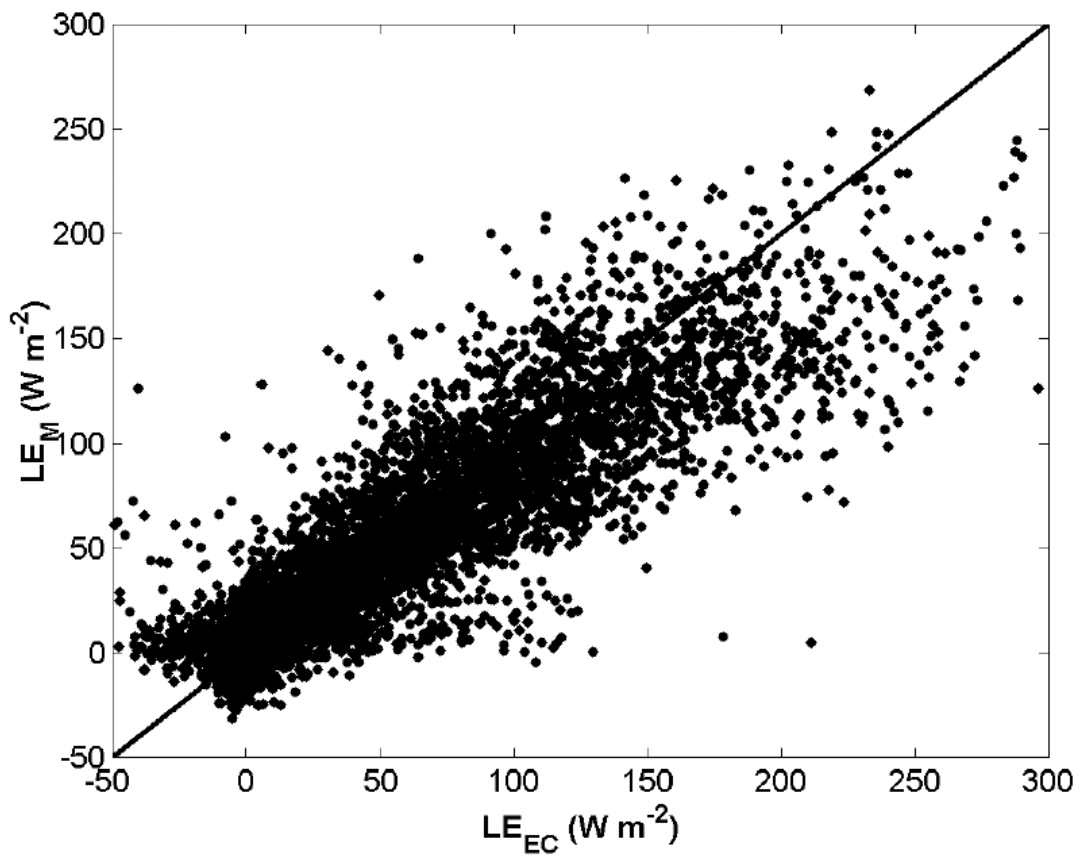


Figure 1: Comparison between modeled latent heat flux ( $LE_M$ ) by the Penman-Monteith equation and eddy-covariance measured ( $LE_{EC}$ ) water vapor flux. The 1:1 line is also shown.

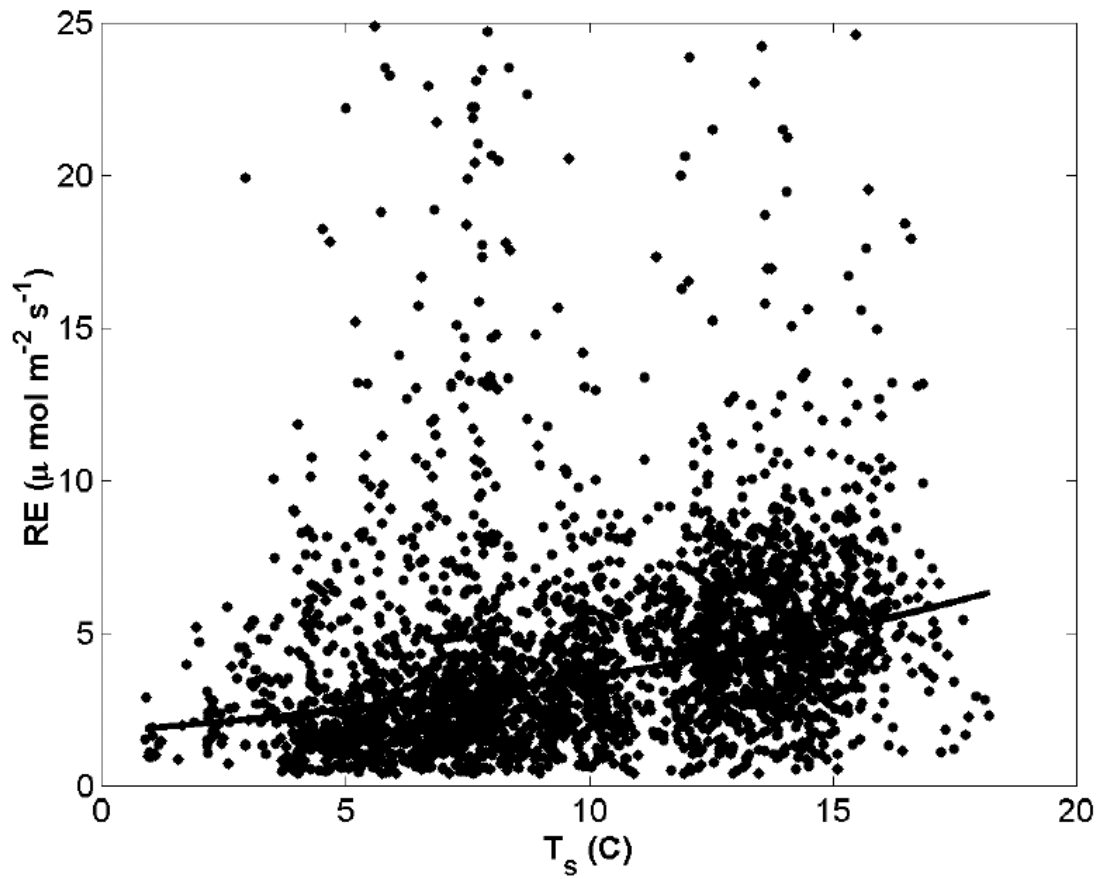


Figure 2: Variation of measured respiration ( $R_E$ ) with soil temperature  $T_s$  for friction velocity ( $u_*$ )  $> 0.2 \text{ m s}^{-1}$ . The solid line represents equation (7).

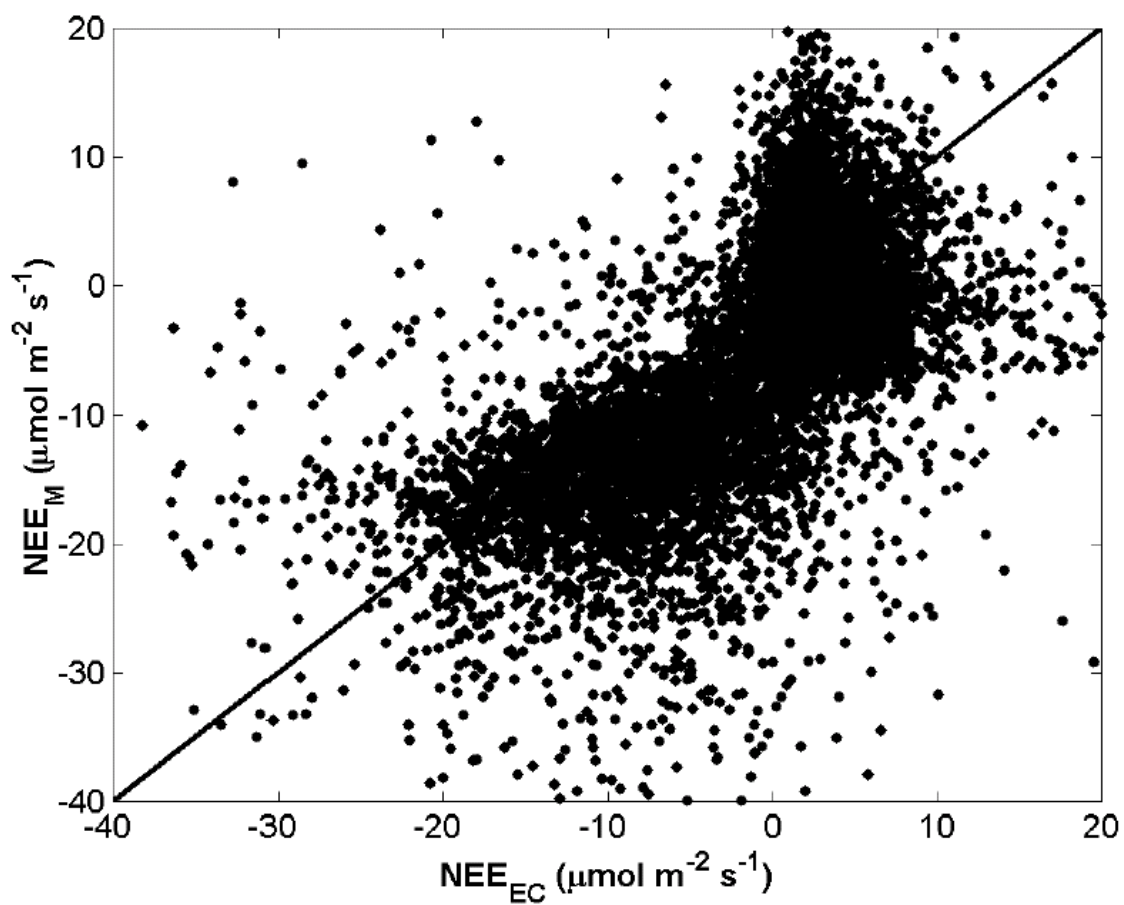


Figure 3: Comparison between predicted ( $NEE_M$ ) and measured ( $NEE_{EC}$ ) net ecosystem exchange. The 1:1 line is also shown.

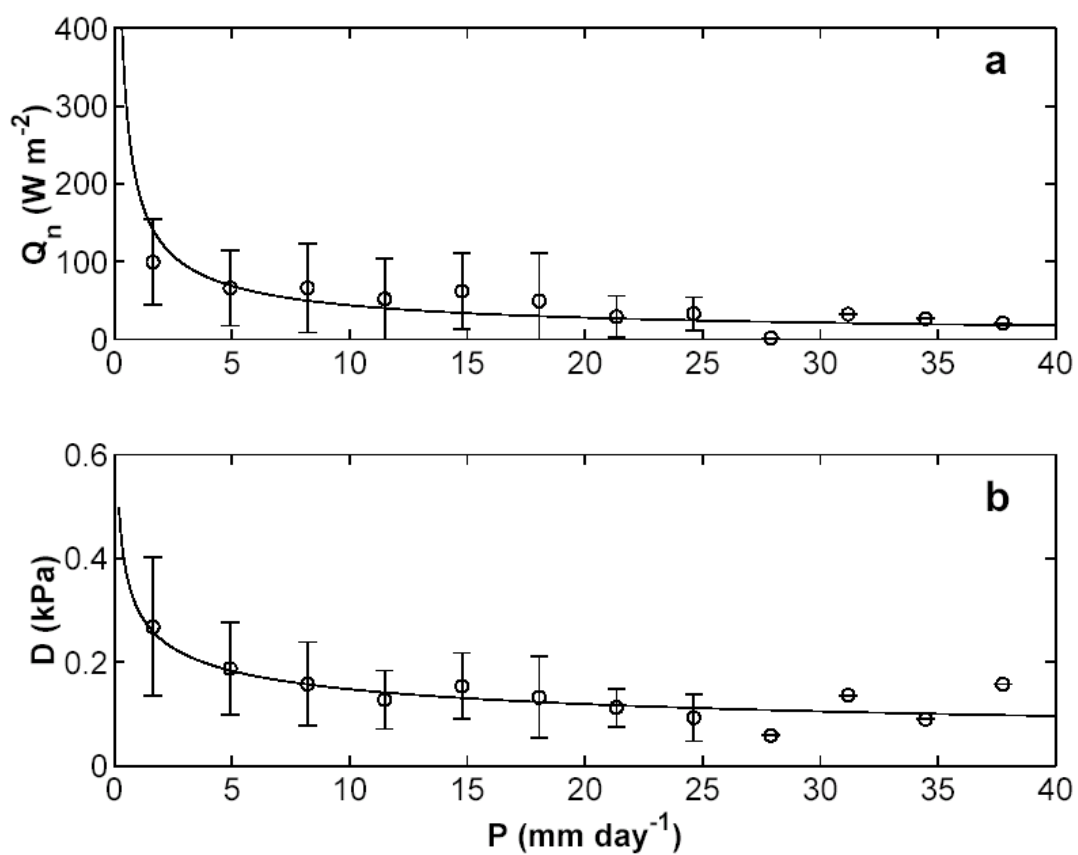


Figure 4: (a) Mean (open circles) and standard deviation (vertical bar) of measured daytime radiation ( $Q_n$ ) versus daily precipitation ( $P$ ). The solid line is regression curve. (b) Same as Figure 4a but for vapor pressure deficit ( $D$ ).

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