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Photosynthetic responses of a humid grassland ecosystem to future climate perturbations

Cheng-I Hsieh ^{a,*}, Ger Kiely ^b, Adrian Birkby ^b, Gabriel Katul ^{c,d}

^a Department of Bioenvironmental Systems Engineering, National Taiwan University, 1 Roosevelt Road, Sec. 4, Taipei 10673, Taiwan

^b Department of Civil and Environmental Engineering, University College Cork, Cork, Ireland

^c Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708-0328, USA

^d Department of Civil and Environmental Engineering, Duke University, Durham, NC 27708, USA

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Abstract

Increases in atmospheric CO_2 concentration not only affects climate variables such as precipitation and air temperature, but also affects intrinsic ecosystem physiological properties such as bulk stomatal conductance and intercellular CO_2 concentration. De-convolving these two effects remains uncertain in biosphere–atmosphere water and carbon cycling. Using a simplified analytical net ecosystem CO_2 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 published field data on physiological adjustments for several grassland ecosystems. Our analysis suggests that the intrinsic grassland ecosystem physiological adjustment of A is about 45 times more important than the resulting climatic forcing shifts from the IS92a scenario (and a doubling of atmospheric CO_2 concentration). Also, our analysis shows that increase in precipitation results in concomitant decrease in the two climate variables—net radiation and vapor pressure deficit, and these decreases have opposite (and almost canceling) effects on A. Implications to afforestation policy and future experimental efforts to quantify the carbon sink from humid grassland ecosystems are also discussed. © 2005 Elsevier Ltd. All rights reserved.

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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 [17]. 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 intercellular CO₂ concentration (C_i) and bulk stoma-

E-mail address: hsieh@ntu.edu.tw (C.-I. Hsieh).

tal conductance. Using a general circulation model (GCM) coupled with a vegetation (biosphere) model, both Sellers et al. [19] and Betts et al. [2] 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., [10,8,20]). Many studies conducted thus far focus on one of these two aspects (i.e., the impacts of climate forcing shifts or ecophysiological adjustments on net canopy photosynthesis). For example, model simulation experiments on photosynthesis typically adjust for meteorological shifts yet retain

^{*} Corresponding author. Tel.: +886 2 33665294; fax: +886 2 23635854.

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"static" ecophysiological properties (e.g., [15,16]), 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., [11,8]). 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 in this study, 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 with elevated atmospheric CO₂ being the only altered variable. The humid grassland ecosystems are a logical starting point for our investigation as they are primarily "energy" limited, and plant and soil hydraulics often exert minor control on A. That is, the canopy conductance can be described by two key climatic variables, available energy and vapor pressure deficit (D).

Our climate projections are based on the Hadley Center GCM output for Ireland in which C_a doubles over the course of the 21st century and leads to changes in the seasonal *P* fluctuations. 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 *D*. For example, increases in *P* may well be accompanied by decreases in R_n due to reduction in cloud cover, which decreases both transpiration and carbon uptake. However, increases in *P* are also accompanied by decreases in *D*, which increases canopy conductance and carbon uptake.

We compare the effects of climate shifts predicted by the GCM on modeled A with results from two experiments that explicitly considered how elevated C_a alters the intrinsic physiological properties of grasslands (retaining all other climatic variables unaltered). 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

To achieve the study objective, we first propose a simplified water-carbon model and then conduct an analysis on how perturbations in C_a , climatic (e.g., R_n and D), and physiological factors (e.g., C_i) manifest themselves in A.

2.1. Simplified water-carbon model

For humid regions, the latent heat flux, LE (W m⁻²), can be calculated by the Penman–Monteith equation

$$LE = \frac{\Delta Q_{\rm n} + \rho c_p D/r_{\rm av}}{\Delta + \gamma (1 + r_{\rm st}/r_{\rm av})},\tag{1}$$

where Δ (kPa K⁻¹) is the slope of the saturation vapor pressure-temperature curve calculated at the air temperature $T_{\rm a}$, $\gamma = \frac{\rho c_p}{0.622 L_V}$ is the psychrometric constant, $\rho \approx 1.2 \text{ kg m}^{-3}$ is the mean air density, c_p (=1005 J kg⁻¹ K⁻¹) is the specific heat for air, L_v (=2.46 × 10⁶ J kg⁻¹) is the latent heat of vaporization, $Q_{\rm n} = R_{\rm n} - G_{\rm s}$, $R_{\rm n}$ is, as before, the net radiation, $G_{\rm s}$ is the soil heat flux (W m⁻²), D is, as before, the vapor pressure deficit (kPa), $r_{\rm av}$ is the aerodynamic resistance of water vapor (s m⁻¹), and $r_{\rm st}$ is the minimum bulk stomatal resistance to water vapor ($\approx 100 \text{ s m}^{-1}$ for the current grass site). In (1), $r_{\rm av}$ can be estimated by

$$r_{\rm av} = \frac{ku_*}{\ln(z/z_0) - \psi_{\rm m}(z/L)},$$
(2)

where k (=0.4) is the von Karman constant, u_* is the friction velocity (m s⁻¹), z is the measurement height, z_0 is the surface roughness, and $\psi_m(z/L)$ is the stability correction function for momentum and L is the Obukhov length (see [3]). Eqs. (1) and (2) can be solved iteratively to incorporate the influence of thermal stability on r_{av} .

The canopy conductance (boundary layer conductance plus stomatal conductance) for CO_2 can be calculated by [4]

$$g_{\rm CO_2} = \frac{P_{\rm a} \rm LE}{1.6 D L_{\rm v} M_{\rm w}},\tag{3}$$

where g_{CO_2} is the canopy conductance (mol m⁻² s⁻¹), M_w (=0.018 kg mol⁻¹) is the molecular weight of water, P_a is the atmospheric pressure (kPa), and the factor 1.6 is due to the difference in molecular diffusivity between water vapor and CO₂. The net canopy photosynthesis, A, can be expressed as

$$A = g_{\rm CO_2} \times C_{\rm a} \times \left(1 - \frac{C_{\rm i}}{C_{\rm a}}\right),\tag{4}$$

where C_i is, as before, the "canopy-averaged" intercellular CO₂ concentration in ppm, C_a in ppm, and A in µmol m⁻² s⁻¹. By replacing (1) and (3) in (4), we have

$$A = \left(\frac{P_{\rm a}}{1.6L_{\rm v}M_{\rm w}}\right) \left(\frac{\varDelta Q_{\rm n} + \rho c_p D/r_{\rm av}}{\varDelta + \gamma (1 + r_{\rm st}/r_{\rm av})}\right) \left(\frac{C_{\rm a}}{D}\right) \left(1 - \frac{C_{\rm i}}{C_{\rm a}}\right).$$
(5)

Eq. (5) was derived by assuming that the bulk stomatal conductance is mainly driven by available energy and vapor pressure deficit with no soil moisture controls, as is expected in humid grasslands (and the reason why they serve as a logical starting point for such an analysis).

2.2. Internal physiological shifts versus climatic shifts

Eq. (5) shows how photosynthesis varies with "climatic" factors such as Q_n , C_a , D and "physiological"

parameters such as C_i/C_a and r_{st} . Hence, it is possible to analytically track how shifts in climatic and physiological factors alter photosynthesis using multivariate calculus. Noting that $A = f(Q_n, C_a, D, C_i/C_a, r_{st})$, the total derivative can be expressed as

$$dA = \left(\frac{\partial A}{\partial Q_{n}}\right) dQ_{n} + \left(\frac{\partial A}{\partial C_{a}}\right) dC_{a} + \left(\frac{\partial A}{\partial D}\right) dD + \left(\frac{\partial A}{\partial (C_{i}/C_{a})}\right) d(C_{i}/C_{a}) + \left(\frac{\partial A}{\partial r_{st}}\right) dr_{st}.$$
 (6a)

Upon evaluating all the partial derivative terms using the formulation in (5) and replacing them in (6a), dividing by Eq. (5), and re-arranging, 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

$$\frac{\mathrm{d}A}{A} = \frac{\mathrm{d}C_{\mathrm{a}}}{C_{\mathrm{a}}} - \left(\frac{\varDelta Q_{\mathrm{n}}\,\mathrm{d}D}{(\varDelta Q_{\mathrm{n}} + \rho c_{p}D/r_{\mathrm{av}})D} - \frac{\varDelta \mathrm{d}Q_{\mathrm{n}}}{\varDelta Q_{\mathrm{n}} + \rho c_{p}D/r_{\mathrm{av}}}\right) \\ - \left(\frac{(\gamma/r_{\mathrm{av}})\mathrm{d}r_{\mathrm{st}}}{\varDelta + \gamma(1 + r_{\mathrm{st}}/r_{\mathrm{av}})} + \frac{\mathrm{d}(C_{\mathrm{i}}/C_{\mathrm{a}})}{1 - (C_{\mathrm{i}}/C_{\mathrm{a}})}\right) \\ \mathrm{I} = \mathrm{II} - (\mathrm{III} - \mathrm{IV}) - (\mathrm{V} + \mathrm{VI})$$
(6b)

In (6b), the second term (II) is the relative change in photosynthesis due to increases in C_a , the third and forth terms (III and IV) represent the shifts by climatic variables (i.e., changes in D and Q_n), and the fifth and sixth terms (V and VI) can be interpreted as the physiological shifts. If the ratio C_i/C_a is approximately constant for current and elevated C_a [7,14,12], then the physiological shifts are mainly from changes in the bulk stomatal resistance. In (6b), if Q_n is not available (or measured), it is reasonable to assume that $dQ_n/Q_n \approx dR_n/R_n$ in a first order analysis. The collection of time series as well as the experimental setup used to test the simplified carbon–water model (Eqs. (1) and (5)) and evaluate how GCM precipitation projections can be used to predict dD and dQ_n are discussed 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 and 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 eddycovariance system which consists of a sonic anemometer (RM Young 8100) and an open-path CO₂/H₂O gas analyzer (Licor 7500) was used to measure CO₂ and water vapor fluxes at 10 m above the soil surface. The sampling frequency and duration were 10 Hz and 30 min, 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 min and averaged (or summed) every 30 min. 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 simplified water-carbon model performance and then proceed to quantify the effects of climate shifts on *A*.

4.1. Evaluating the simplified water-carbon model

The primary assumption in (5) is that the transpiration rate is well approximated by the Penman–Monteith formula. We tested this formula in Fig. 1, which compares modeled latent heat flux (LE_M) with eddycovariance measured (LE_{EC}) water vapor flux. The coefficient of determination (R^2) and the root-mean square error (RMSE) for Fig. 1 are 0.81 and 25 (W m⁻²), respectively, and suggest that the agreement between measured and modeled LE is sufficiently accurate for canopy conductance and photosynthesis calculations.

Eddy-covariance systems can measure net ecosystem carbon exchange (NEE) but not A. Notice that NEE = $-A + R_E$; R_E = ecosystem respiration. Hence,

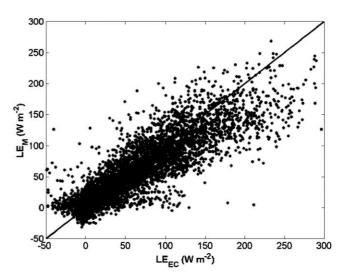


Fig. 1. Comparison between modeled latent heat flux (LE_M) by the Penman–Monteith equation and eddy-covariance measured (LE_{EC}) water vapor flux. The 1:1 line is also shown.

Eq. (5) cannot be explicitly tested with measured NEE. An indirect test of modeled A by (5) can be conducted if measured nighttime CO₂ 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. This comparison serves as an indirect test for modeled A (i.e., Eq. (5)) because all the errors in the R_E model will express themselves in the NEE model. 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 a standard Q_{10} model

$$R_{\rm E} = R_{\rm E,10} (Q_{10})^{\frac{T_{\rm S} - 10}{10}},\tag{7}$$

where Q_{10} and $R_{E,10}$ (µmol m⁻² s⁻¹) are respiration temperature sensitivity and base respiration at 10 °C, respectively. Fig. 2 shows the measured dependence of $R_{\rm E}$ on $T_{\rm s}$ along with the regression fit to (7). The scatter in Fig. 2 is large ($R^2 = 0.12$, RMSE = 0.72 μ mol m⁻² s⁻¹) but typical of such ecosystem $R_{\rm E}$ models [17]. We also noticed that the residuals (i.e., the difference between measured and modeled $R_{\rm E}$) do not depend on soil moisture. Using measured night-time NEE for a friction velocity $(u_*) > 0.2 \text{ m s}^{-1}$, we compute a $Q_{10} = 2.02$ and a $R_{E,10} = 3.57$ which are also consistent with reported values for temperate grassland ecosystems experiencing periodic harvesting [17]. Here the criterion of nocturnal $u_* > 0.2$ is to ensure that the nocturnal flow is fully turbulent (i.e., no canopy waves or other transient non-turbulent phenomena are present) and that the CO₂ storage flux (i.e., CO₂ stored between the sur-

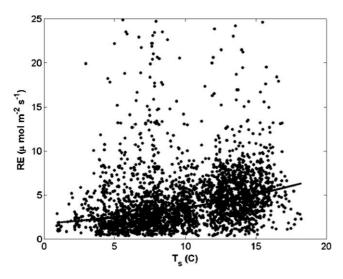


Fig. 2. Variation of measured nighttime ecosystem respiration ($R_{\rm E}$) with soil temperature $T_{\rm s}$ for friction velocity (u_*) > 0.2 m s⁻¹. The solid line represents Eq. (7).

face and the eddy-covariance sensor height) is minimal so that the eddy-covariance technique represents $R_{\rm E}$ (see [5] for detailed discussion). Furthermore, this criterion ensures 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 NEE measurements for spatial scalability of the nighttime derived respiration function to daytime). Modeled NEE is then given by $-A + R_{\rm E}$, where A is computed from (5) with $C_a = 355$ ppm assuming a constant $C_i/C_a = 0.84$ (for C_3 type grasses), and R_E is computed from (7). The comparison between predicted and measured NEE is shown in Fig. 3. Given the scatter in $R_{\rm E}$, the agreement between measured and modeled NEE is reasonable ($R^2 = 0.42$, RMSE = 6.13 µmol m⁻² s⁻¹).

4.2. Relating projected shifts in climatic forcing to photosynthesis

To calculate the projected shift in photosynthesis using (6b), dC_a , dQ_n , dD, $d(C_i/C_a)$, and dr_{st} are all needed. As earlier stated, our climate projections for dC_a (and meteorological variables that permit us to determine dQ_n , dD) are based on the Hadley Center GCM 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 assuming a mid-range economic growth but no measures to reduce greenhouse gas emissions are taken. The GCM output used in this study is based on the HadCM3, which is a new generation of high-resolution coupled atmosphere–ocean general circulation model described by Gordon et al. [9] and Pope et al. [18].

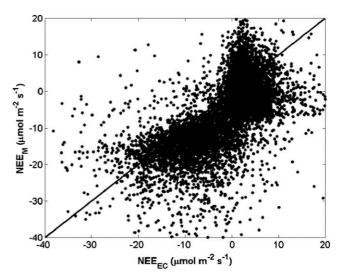


Fig. 3. Comparison between predicted (NEE_M) and measured (NEE_{EC}) net ecosystem exchange. The 1:1 line is also shown.

Under the IS92a scenario, the GCM uses current $C_a = 350$ ppm and a future $C_a = 700$ ppm; hence, $dC_a = 700 - 350 = 350$ ppm (and $dC_a/C_a = 350/350 = 1$). When evaluating how climatic shifts in dQ_n , dD alone effects A in Eq. (6b), we assume static physiological properties (i.e., both $d(C_i/C_a)$ and dr_{st} are zero). The HadCM3 does not provide output data for dQ_n and dD, but provides seasonal variations in dP. Hence, both dQ_n and dD must be related to seasonal shifts in P (i.e., dP) using existing meteorological measurements at the site. Both dQ_n and dD can be related to dP using

$$dQ_n \approx \frac{\partial Q_n}{\partial P} dP; \quad dD \approx \frac{\partial D}{\partial P} dP$$
 (8)

where $\partial Q_n / \partial P$ and $\partial D / \partial P$ are evaluated from time series of Q_n , P, and D collected at the site as follows: (1) first ensemble-average Q_n and D (denoted by angle brackets $\langle \cdot \rangle$) during daylight hours for different daily precipitation intensity bins, (2) apply 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), and (3) compute $\langle \partial Q_n / \partial P \rangle$ and $\langle \partial D / \partial P \rangle$ from the derived relationship in step 2. Kumagai et al. [13] 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. Fig. 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 $\langle D \rangle = 0.3 \langle P \rangle^{-0.31}$ represent the ensemble data at the site reasonably well (Fig. 4).

Using these relations and noting that the annual average precipitation intensity is about 4.89 mm day⁻¹ at the site, we estimate: $\partial Q_n/\partial P = -9.24 \text{ W m}^{-2}$ (mm day⁻¹)⁻¹; $\partial D/\partial P = -0.012 \text{ kPa}$ (mm day⁻¹)⁻¹. Again, the negative sign in the partial derivatives is not a surprise, as increases in precipitation ought to result in

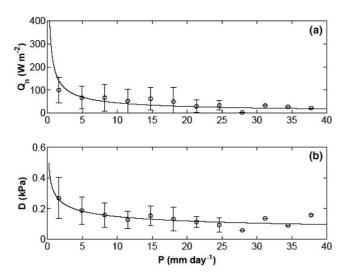


Fig. 4. (a) Mean (open circles) and standard deviation (vertical bar) of measured daytime radiation (Q_n) versus daily precipitation (P). The solid line is regression curve. (b) Same as (a) but for vapor pressure deficit (D).

simultaneous decreases in net radiation and vapor pressure deficit. While a decrease in vapor pressure deficit leads to an increase in A, the decrease in Q_n leads to a decrease in A as evidenced from Eq. (6b) leading to a cancellation effect.

For December, January, and February (DJF), the mean Q_n , D, Δ , and r_{av} are 16.0 (W m⁻²), 0.14 (kPa), 0.067 (kPa K^{-1}), and 28.6 (s m⁻¹) respectively, and the HadCM3 predicts a P increase of 0.55 mm day⁻¹ for Ireland. Hence, with these estimates and with $dC_a/C_a = 1$ (i.e., a doubling of CO₂ concentration) and no physiological shift (i.e., V + VI = 0), we estimate dA/A = 0.96. For March, April, and May (MAM) and for September, October, and November (SON), the GCM 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 (W m⁻²), 0.32 (kPa), 0.1 (kPa K^{-1}), and 28.1 (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. Recall that, from (6b), 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 .

4.3. Discussion

To address our primary objective, we compare our computed dA/A = 0.99 derived from only climate shifts with other experimental studies that only evaluated physiological adjustments (i.e., assuming III = 0 and IV = 0) to elevated CO₂. The two grassland ecosystem experiments [8,11] primarily considered in this study were conducted on markedly different climate and soils (Texas, USA and Dublin, Ireland). Both experiments indicate that incident radiation and microclimate within the CO₂ enriched grass plots were maintained identical to the control (or ambient) (i.e., III = 0 and IV = 0). For the Gill et al. [8] experiment in Texas, USA, we calculated dA/A and dC_a/C_a from their data reported in Fig. 1 directly. Their experimental data showed that dA/A = 0.55 while $dC_a/C_a = 1$. From (6b), we can estimate the physiological adjustments (i.e., V + VI) by

Physiological adjustments (V + VI)

 $= dC_a/C_a - dA/A - (III - IV).$

Hence, the shifts by physiological properties for the experiment are 0.45 (1 - 0.55 - 0 + 0 = 0.45).

For the Jongen and Jones [11] experiment in Dublin, Ireland, we assumed that (1) their reported net primary productivity (NPP) linearly relates to the gross primary productivity (GPP), and (2) GPP $\approx A$; thereby permit-

Table 1

The relative importance of ecophysiological adjustments and climate forcing on dA/A for grasslands while $dC_a/C_a = 1$. (Recall, from (6b), $\frac{dA}{A} = \frac{dC_a}{C_a} - \left(\frac{dQ_n}{(AQ_a + ac}\frac{D}{D}/r_a)}{\frac{dQ_n}{(AQ_a + ac}\frac{D}{D}/r_a)}\right) - \left(\frac{(\gamma/r_a)}{(AQ_a + ac}\frac{dr_a}{D}/r_a)}{\frac{dQ_n}{(AQ_a + ac}\frac{dQ_n}{D}/r_a)}\right) = \frac{dQ_n}{(AQ_a + ac}\frac{dQ_n}{D}/r_a) + \frac{d(C_i/C_a)}{(AQ_a + ac}\frac{dQ_n}{D}/r_a)}$ I = II - (III - IV) - (V + VI))

$C_{\rm a} = \langle (\Delta Q_{\rm n} + \rho c_p D/r_{\rm av}) D \rangle$	$\Delta Q_{\rm n} + \rho c_p D/r_{\rm av}$ $(\Delta + \gamma (1 + r_{\rm st}/r_{\rm av}))$	$1-(C_i/C_a)$
Study	dA/A	Remarks
Reference state	1.0	No climate or physiological adjustment occurs (i.e., III = IV = V = VI = 0; hence, $dA/A = dC_a/C_a - 0 = 1 - 0 = 1$)
Gill et al. [8]	0.55	No climate shift occurs in this experiment (i.e., $III = IV = 0$)
Jongen and Jones [11]	0.58	No climate shift occurs in this experiment (i.e., $III = IV = 0$)
Current model results	0.99	No physiological adjustment occurs (i.e., $V = VI = 0$)

ting us to calculate dA/A from their measured dNPP/NPP for the reported dC_a/C_a . Their measurements showed that dA/A = 0.58 while $dC_a/C_a = 1$. Hence, the physiological adjustments for this experiment are 0.42 (1 - 0.58 - 0 + 0 = 0.42). Surprisingly, these two experiments suggest consistent physiological adjustments (≈ 0.45) with elevated CO₂ despite climate and soil differences across these two experiments. The dA/A values from these two experiments and our study are summarized in Table 1.

Our study shows that dA/A = 0.99 while $dC_a/C_a = 1$ and without physiological adjustments (i.e., V = 0 and VI = 0). Again, from (6b), the climate shifts can be calculated as

Climate shifts (III – IV) = $dC_a/C_a - dA/A - (V + VI)$.

Hence, the adjustments by climatic factors for our study are 0.01 (1 - 0.99 - 0 - 0 = 0.01). It is clear that, for these two studies, 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. Again, an important reason why the shifts in climate forcing on A is small relative to the physiological adjustment is because an increase in P leads to concomitant decreases in dD and dQ_n , and decreases in dD and dQ_n have opposite (and almost canceling) effects on dA. Considering only cloud cover or vapor pressure deficit in isolation would have yielded an erroneous conclusion about the relative importance of climatic forcing shifts on dA.

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. [6] 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 [1]. 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 (6b), for a 100% increase in elevated CO₂, the increase in photosynthesis after reductions by physiological adjustment (~45%) and climate shifts ($\sim1\%$) 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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