Low and contrasting impacts of vegetation CO2 fertilization on terrestrial runoff over the past three decades: Accounting for above- and below-ground vegetation-CO2 effects

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Abstract. Elevation in atmospheric carbon dioxide concentration (eCO₂) affects vegetation water use, with consequent impacts on terrestrial runoff (Q). However, the sign and magnitude of the eCO₂ effect on Q is still contentious. This is partly due to the poor understanding of the opposing eCO₂-induced water effects at different scales, being water-saving caused by partial stomatal closure at the leaf-level contrasting with increased water-consumption due to increase foliage cover at the canopy level, leading to highly debated findings among existing studies. None of the existing studies implicitly account for eCO₂-induced changes to below-ground vegetation functioning. Here we develop an analytical eco-hydrological framework that includes the effects of eCO₂ on plant leaf, canopy density, and rooting characteristics to attribute changes in Q and detect the eCO₂ signal on Q over the past three decades. Globally, we detect a very small decrease of Q induced by eCO₂ during 1982-2010 (-1.69%). When assessed locally, along the resource availability (α) gradient, a positive trend (p<0.01) in the Q-eCO₂ response is found ranging from a negative response (i.e., eCO₂ reduces Q) in low α regions (typically dry) to a positive response (i.e., eCO₂ increases Q) in high α areas (typically warm and humid). Our findings suggest a minor role of eCO₂ on changes in global Q over the past three decades, yet highlights the negative Q-eCO₂ response in semi-arid and arid regions which may further reduce the limited water resource there.

1 Introduction

Runoff (Q) is the flow of water over the Earth’s surface, forming streamflow, becoming one of the most important water resources for irrigation, hydropower and other human needs (Oki and Kanae, 2006). Anthropogenic climate change is expected to alter the global hydrological cycle, with greenhouse gas-induced climate warming intensifying the hydrological cycle (Huntington, 2006). Besides climate, terrestrial vegetation also affects the water cycle. It is well-documented that elevated atmospheric CO₂ concentration (eCO₂) reduces stomatal opening, which in turn suppresses leaf-level transpiration (Field et al., 1995; Donohue et al., 2013). If this were the only mechanism that eCO₂ changed vegetation this would increase runoff (Q) (Gedney et al., 2006). However, eCO₂ increases vegetation foliage cover (Donohue et al., 2013; Zhu et al., 2016), leading to enhanced canopy-level transpiration and consequently reductions of Q (Piao et al., 2007). The two opposite responses of vegetation water use to
eCO2 complicate the net effect of eCO2 on $Q$, and existing modeling results are highly debated since they focus on different aspects of how eCO2 affects the plants and thus the water cycle (Gedney et al., 2006; Piao et al., 2007; Huntington, 2008; Cheng et al., 2014; Yang et al., 2016a; Ukkola et al., 2016). Moreover, those previous modelling results have not been thoroughly validated against observations.

In addition to stomatal and above-ground vegetation structure responding to eCO2, the below-ground vegetation structure (i.e., rooting depth) is also affected by eCO2, with eCO2 increases rooting depth overwhelmingly found in observations (Nie et al., 2013) (Supplementary Tables S1 and S2). Deeper rooting depth means larger plant-available water storage capacity by allowing plants to access deeper soil moisture, which potentially increases transpiration water loss and reduces $Q$, especially during dry spells (Trancoso et al., 2017; Yang et al., 2016b). To date, no previous eCO2-$Q$ modeling attempts have explicitly considered the below-ground eCO2-induced feedback (with the above-ground feedbacks): this paper fills that niche.

Here we use a parsimonious, analytical eco-hydrological model based on the Budyko framework (i.e., the Budyko-Choudury-Porporto, BCP model; Donohue et al., 2012), in combination with an analytical rooting depth model based on ecosystem optimality theory (Guswa, 2008), an analytical CO2 fertilization model for steady-state vegetation (Donohue et al., 2017) and observed plant stomatal response to eCO2 (Ainsworth and Rogers, 2007), to detect the impact of eCO2 on $Q$ changes ($dQ$) over the past three decades (i.e., 1982-2010). The Budyko framework describes the steady-state (i.e., mean annual scale) hydrological partitioning as a functional balance between atmospheric water supply (i.e., precipitation, $P$) and demand (i.e., potential evapotranspiration, $E_P$) and a model parameter that modifies the climate-hydrology relationship (Choudhury, 1999; Donohue et al., 2012). In this framework, both $E_P$ and the land surface parameter are affected by the response of vegetation to eCO2 (see Methods). The developed framework allows analytical and transparent attribution of $dQ$ changes, which overcomes the uncertainty raised from non-linear interactions among numerous processes when attributing $dQ$ numerically by using bottom-up earth system models (Yang et al., 2015). To examine the long-term eCO2 impact and to minimize year-to-year “transient” effects (i.e., water storage changes), we performed our analyses using sequential 5-year periods (Yang et al., 2016a; Han et al., 2020), resulting
in six 5-year-means during 1982-2010, with the first period containing 4 years. Additionally, since vegetation response to eCO2 can be greatly mediated by the availability of other resources (e.g., water, light and nutrients) (Donohue et al., 2013; Donohue et al., 2017; Nenami et al., 2003; Yang et al., 2016a; Norby et al., 2010), we examine the impact of eCO2 on Q along a resource availability gradient (Donohue et al., 2017; Friedkubgstein et al., 1999) (see Methods). The resource availability is typically low in dry environments and increases as the climate becomes more humid, which enable us to detect the signal of eCO2 on Q across a dry – wet gradient.

2 Material and methods

2.1 Runoff simulation

The Budyko-Choudhury-Porporato (BCP) model was adopted here to simulate Q and to attribute changes in Q (Yang et al., 2016b; Donohue et al., 2012). Choudhury’s formulation of the Budyko curve is (Choudhury, 1999):

$$E = \frac{PE_p}{(P^n + E_p^n)^{\omega n}}$$

(1)

where E is the actual evapotranspiration (mm yr\(^{-1}\)). P is the precipitation depth (mm yr\(^{-1}\)). \(E_p\) is the potential evapotranspiration (mm yr\(^{-1}\)) and is estimated here using the Shuttleworth-Wallace two-source evapotranspiration model (Shuttleworth and Wallace, 1985) with the assumption of full soil moisture supply (by taking soil surface resistance equal to zero and stomatal resistance equal to its non-water-stressed value) while allowing leaf area and leaf-level conductance to vary with atmospheric CO\(_2\) concentration (\(C_a\)) (Milly and Dunne, 2016). A recent study by Milly and Dunne (2016) showed that the Shuttleworth-Wallace model could most satisfactorily reproduce \(E_p\) estimates from climate models under eCO2. n is a unitless model parameter that encodes all factors other than mean climate conditions and modifies the partitioning of P between E and Q. For steady-state conditions, Q is calculated by subtracting E from P as a result of catchment water balance.

The probabilistic steady state solution of Porporato’s stochastic dynamic soil moisture model shares a similar form with the Budyko curve (Porporato et al., 2004). Porporato’s parameter \(\omega\) is a
dimensionless parameter, which is a function of effective rooting depth \((Z_e, \text{mm})\), mean rainfall intensity \((\beta, \text{mm per event})\) and soil water holding capacity \((\theta, \text{mm}^3 \text{mm}^{-3})\) and exhibits a close relationship with the Choudhury’s parameter \(n\) (Yang et al., 2016b; Porporato et al., 2004). Taking data from Porporato et al. (2004), we deduced the relationship between \(n\) and \(\omega\) as \((R^2=0.96, p<0.001;\) Supplementary Figure S1):

\[
n = 0.82 \ln(\omega) + 0.636 = 0.82 \frac{Z_e \theta}{\beta} + 0.636
\]  

Effective rooting depth \((Z_e)\) was determined using an analytical carbon cost-benefit model based on ecosystem optimality theory proposed by Guswa (2008). The \(Z_e\) model is given as (Guswa, 2008):

\[
Z_e = \frac{\beta}{\theta(1-W)} \ln(X)
\]

\[
X = \begin{cases} 
W \left[1+\frac{\theta}{\beta} \frac{(1-W)^2}{2A} \right] & \text{if } W > 1 \\
W \left[1+\frac{\theta}{\beta} \frac{(1-W)^2}{2A} + \left(\frac{\theta}{\beta} \frac{(1-W)^2}{2A}\right)^2\right] & \text{if } W < 1 
\end{cases}
\]

\[
A = \frac{\gamma_r \times RLD}{SRL \times WUE} \times \frac{1}{E_{P,T} \times f_{GS}}
\]

where \(W\) is the ratio of mean annual \(P\) over potential transpiration, \(E_{P,T}\). \(\gamma_r\) is the root respiration rate (g C g\(^{-1}\) roots day\(^{-1}\)), which is quantified using the \(Q_{10}\) equation (Lloyd and Taylor, 1994). \(RLD\) is the root length density (cm roots cm\(^{-3}\) soil) and \(SRL\) is the specific root length (cm roots g\(^{-1}\) roots). We fixed \(RLD\) to be 0.1 cm roots cm\(^{-3}\) soil and \(SRL\) to be 1500 cm roots g\(^{-1}\), representing the median value of these two parameters reported in the literature, respectively (Caldwell, 1994; Eissenstat, 1997; Fitter and Hay, 2002; Pregitzer et al., 2002). \(f_{GS}\) is the fraction of growing season within a year, with the growing season length quantified according to Zhu et al. (2016). \(WUE\) is the photosynthetic water use efficiency (g C cm\(^{-3}\) H\(_2\)O), which is determined for the first period (i.e., 1982-1985) from the ensemble means from eight Earth system models (described later) of annual gross primary production \((GPP)\) and \(E_T\) estimates (i.e., \(WUE=GPP/E_T\)). For the following periods, \(WUE\) was estimated by considering the
effects of changes in $C_a$ and vapor pressure deficit ($v$) on $WUE$ (Donohue et al., 2013; Wong et al., 1979; Farquhar et al., 1993):

$$WUE_{t+1} = WUE_t + WUE_t \left( \frac{C_{a,t+1} - C_{a,t}}{C_{a,t}} - \frac{1}{2} \frac{v_{t+1} - v_t}{v_t} \right)$$

(6)

where $t$ is time in year. Note that the above equation implicitly assumes the same upscaling factor when converting the leaf-level assimilation and transpiration to the canopy level for a given location (Donohue et al., 2017). The spatial pattern of mean annual $Z_e$ is shown in Supplementary Figure S2.

2.2 Attribution runoff changes

We used the BCP model to attribute changes in $Q$ ($dQ$) due to different influencing factors following the method developed by Roderick and Farquhar (2011). To first order, change in $Q$ ($dQ$) is:

$$dQ = \frac{\partial Q}{\partial P} dP + \frac{\partial Q}{\partial E_p} dE_p + \frac{\partial Q}{\partial n} dn$$

(7)

where $\partial Q/\partial P$, $\partial Q/\partial E_p$ and $\partial Q/\partial n$ represent the sensitivity of $Q$ to changes in $P$, $E_p$ and $n$, respectively, and can be expressed as:

$$\frac{\partial Q}{\partial P} = 1 - \frac{E}{P} \left( \frac{E_p}{E_p + E_p} \right)$$

(8)

$$\frac{\partial Q}{\partial E_p} = -\frac{E}{E_p} \left( \frac{P}{P + E_p} \right)$$

(9)

$$\frac{\partial Q}{\partial n} = -\frac{E}{n} \left[ \frac{\ln(P^n + E_p^n)}{n} - \frac{P^n \ln P + E_p^n \ln E_p}{P^n + E_p^n} \right]$$

(10)

The physiological (stomatal conductance, $C_s$) and structural (Leaf area index, $L$, and effective rooting depth, $Z_e$) impact both $E_p$ and $n$. More specifically, decreases in $C_s$ lower the transpiration rate per leaf area, whereas increases in $L$ and $Z_e$ enhance the canopy level transpiration rate. Additionally, increases in $L$ also reduce soil evaporation by shading the soil surface (Shuttleworth and Wallace, 1985). The impact of eCO$_2$ on parameter $n$ is expressed through its impact on $Z_e$. On one hand, increases in $WUE$ induced by eCO$_2$ permit a larger vegetation carbon uptake per amount of water loss, potentially leading
to more carbon allocated to roots and thus a deeper \( Z_e \). Conversely, increases in plant water demand (as quantified by potential transpiration) would require plants to develop a deeper root to access to soil moisture at deeper depths, and \textit{vice versa} (Guswa, 2008). As a result, we write \( E_P \) and \( Z_e \) as:

\[
E_p = f(C_a, E_{P,M})
\]

\[
Z_e = g(C_a, O)
\]

and changes in \( E_P \) and \( Z_e \) are given by:

\[
dE_p = \frac{\partial E_p}{\partial C_a} dC_a + \frac{\partial E_p}{\partial E_{P,M}} dE_{P,M}
\]

\[
dZ_e = \frac{\partial Z_e}{\partial C_a} dC_a + \frac{\partial Z_e}{\partial O} dO
\]

where \( E_{P,M} \) is the meteorological component of \( E_P \) (without considering \( C_a \)). \( O \) represents factors other than eCO\(_2\) that affects \( Z_e \), which effectively encodes the climate change-induced vegetation change.

Combining Eqs. (2), (7), (13) and (14), we have:

\[
dQ = \frac{\partial Q}{\partial P} dP + \left( \frac{\partial Q}{\partial E_p} \frac{\partial E_p}{\partial C_a} + \frac{0.82 \partial Q}{\partial Z_e} \frac{\partial Z_e}{\partial C_a} \right) dC_a + \frac{\partial Q}{\partial E_p} \frac{\partial E_p}{\partial E_{P,M}} dE_{P,M} + \frac{0.82 \partial Q}{\partial \beta} \frac{\partial \beta}{\partial n} d\beta + \frac{0.82 \partial Q}{\partial Z_e} \frac{\partial Z_e}{\partial O} dO
\]

The first term on the right hand of Eq. (15) represents \( dQ \) caused by \( P \) change, the second term represents \( dQ \) caused by eCO\(_2\) and the third term calculates \( dQ \) induced by changes in \( E_{P,M} \). To maintain simplicity, we calculate \( E_{P,M} \)-induced \( dQ \) by subtracting the effect of eCO\(_2\)-caused changes in \( E_P \) on \( Q \) from \( dQ \) caused by changes in \( E_P \) (i.e., \( \frac{\partial Q}{\partial E_P} dE_P - \frac{\partial Q}{\partial E_P} \frac{\partial C_a}{\partial E_{P,M}} dE_{P,M} \)). The fourth and fifth terms on the right hand of Eq. (15) represent \( dQ \) caused by changes in rainfall intensity and climate change-induced vegetation change, respectively, and we group them as one factor in the attribution of \( dQ \) (i.e., other factors in Fig. 3). Since our primary focus was to examine how eCO\(_2\) affect \( Q \) and its relative
importance to changes in $P$ and $E_P$ the other factors driving $dQ$ change were estimated as the residual of Eq. (15). By introducing Eqs. (9) and (10) into Eq. (15), the sensitivity of $Q$ to eCO$_2$ ($S_{Q_{to\,eCO2}}$) is written as,

$$S_{Q_{to\,eCO2}} = \frac{E}{E_P} \left( \frac{P^*}{P^* + E_p^*} \right) \frac{\partial E_P}{\partial C_a} - E \frac{0.82}{n} Z_e \left[ \frac{\ln(P^n + E_p^n)}{n} - \frac{P^n \ln P + E_p^n \ln E_p}{P^n + E_p^n} \right] \frac{\partial Z_e}{\partial C_a}$$  \hspace{1cm} (16)

The sensitivities of $E_P$ and $Z_e$ to eCO$_2$ (i.e., $\frac{\partial E_P}{\partial C_a}$ and $\frac{\partial Z_e}{\partial C_a}$) are quantified by numerically running the $E_P$ model and $Z_e$ model with and without changes in $C_a$, respectively. The difference between the two simulations under the two $C_a$ scenarios is considered the net effect of eCO$_2$.

### 2.3 Stomatal conductance response to eCO$_2$

The response of leaf-level stomatal conductance ($C_s$) response to eCO$_2$ was determined using 244 field observations across a broad range of bioclimates (Ainsworth and Rogers, 2007). We linearly rescaled the reported change in $C_s$ for the magnitude of eCO$_2$ in each study to obtain the sensitivity of $C_s$ to eCO$_2$: that is, the percentage change in $C_s$ per 1% increase in $C_a$. We then classified the 244 observations based on their biome type to construct a biome type-based look-up table of $C_s$ sensitivity to eCO$_2$.

### 2.4 Resource availability index and leaf area index response to eCO$_2$

The response of $L$ to eCO$_2$ was predicted based on the response of WUE to eCO$_2$ adjusted by the local resource availability. We define the site resource availability index ($\alpha$) based on growing season mean $L$ following Donohue et al. (2017). This is because that observed $L$ at a site is the net response to the local growing conditions and provides an effective proxy of the growing conditions experienced by plants (Donohue et al., 2017). Another advantage of this approach is that $L$ can be readily measured directly or remotely. We calculated $\alpha$ as,

$$\alpha = 1 - e^{-\tau L}$$  \hspace{1cm} (17)
where $\tau$ is an exponential extinction coefficient, which typically varies from 0.3 to 1.2 (Campbell and Norman, 1998) and is set to be 0.7 herein. Broadly across the globe, $\alpha$ also corresponds well with climate aridity. The calculated $\alpha$ increases from 0.0 with low resource availability (typically dry) to 1.0 with high resource availability (typically warm and humid) (Figure 1). This suggests a predominant role of the climate in shaping the global vegetation pattern (Nemani et al., 2003). This also implies that the resource limitations on plant growth are mainly exerted by climate, consistent with the framework of climate limitation on vegetation proposed in previous studies (Nemani et al., 2003; Budyko, 1974; Yang et al., 2015). Then following Norby and Zak (2011), who showed that the observed response of $L$ to eCO$_2$ was a non-linear function of $L$, we estimated the relative change in $L$ induced by eCO$_2$ per Donohue et al., (2017):

$$\frac{dL}{L} = \frac{dWUE}{WUE} (1-\alpha)^2 = \left(\frac{dC_v}{C_v} - \frac{1}{2} \frac{dv}{v}\right)e^{-2\tau L}. \quad (18)$$

2.5 Data

To focus on the impacts of eCO$_2$ on $Q$ via feedbacks through vegetation and to eliminate potential human impacts on $Q$, we limit our analyses to 2,268 strictly selected unimpaired catchments located across the globe (Figure 2). Originally, daily and/or monthly $Q$ observations were collected from more than 22,000 catchments globally (Beck et al., 2019). Three selection criteria were implemented to ensure that only catchments with a continuous $Q$ records that are negligibly affected by human were used. First, catchments with >5% missing data during the entire study period (1982-2010) were removed. A linear interpolation was applied to fill the gaps in the remaining daily $Q$ series. Second, catchments smaller than 100 km$^2$ were excluded. This is to ensure that at least one precipitation pixel (i.e., 0.1° × 0.1°, or ~100 km$^2$) is included for a catchment. Third, we excluded catchments where observed $Q$ is likely to be affected by human interventions, including catchments with: (i) significant forest gain or loss (> 2% of the total catchment area) (Hansen et al., 2013); (ii) irrigated areas larger than 2% (Siebert et al., 2005); (iii) urban areas (http://ionia.esrin.esa.int) larger than 2%; and (iv) the presence of large dams (Lehner et al., 2011) (i.e., where the reservoir capacity in a catchment is larger
than 10% of the catchment mean annual \( Q \). Exactly 2,268 catchments pass the above selection criteria (Figure 2).

Precipitation from 1981 through 2010 was taken from the Multi-Source Weighted-Ensemble Precipitation (MSWEP) version 2 dataset, which has a three-hour temporal resolution and 0.1° spatial resolution (Beck et al., 2019). Other climate variables, including net radiation, air temperature, relative humidity, air pressure and wind speed were generated during MsTMIP (Wei et al., 2014). Monthly \( C_a \) from 1982-2010 was obtained from the Hawaiian Mauna Loa Observatory (http://www.esrl.noaa.gov/gmd/obop/mlo/) and we assume a uniform \( C_a \) concentration across the globe at the mean annual scale (i.e., five years). Monthly \( L \) for 1982-2010 was derived from Zhu et al. (2013) based on AVHRR GIMMS-3g NDVI data (Pinzon and Tucker, 2014). Land cover classification was acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS) land use map (MOD12Q1) available from the NASA data center (Friedl et al., 2010). The global C4 vegetation fraction was obtained from the NASA data center (http://webmap.ornl.gov/ogcdown/dataset.jsp?ds_id=932). Soil texture data at 30’’ spatial resolution was acquired from the Harmonized World Soil Database (HWSD) (Nachtergaele, 2009), which was used to determine the value of \( \theta \) according to the US Department of Agriculture (USDA) soil classification (Saxton and Rawls, 2006). These gridded data were further aggregated for individual catchments at a mean annual scale (i.e., five years).

3 Results and discussion

3.1 Validation of the BCP model in runoff estimation

The validity of the BCP model is tested by comparing the estimated \( Q \) with observed \( Q \), in terms of both spatial and temporal variability, at the 2,268 unimpaired catchments (Figure 3). Spatially, the BCP model well captures the observed spatial variability in \( Q \) at the mean annual scale, with a coefficient of determination \( (R^2) \) of 0.93, root-mean-squared error (RMSE) of 87.9 mm yr\(^{-1}\) and mean bias (estimated \( Q \) minus observed \( Q \)) of -11.4 mm yr\(^{-1}\) (Figure 3a) Temporally, trends in mean annual \( Q \) are also reasonably reproduced by the BCP model, which produces an \( R^2 \) of 0.71, RMSE of 0.71 mm yr\(^{-2}\) and
mean bias of -0.05 mm yr\(^{-2}\) (Figure 3b) In addition, we also perform a sensitivity analysis by comparing the simulated \(Q\) using the BCP model with and without considering eCO\(_2\). Results show that the BCP model, when considering eCO\(_2\), performed differentially better in estimating \(Q\) trends than the BCP model without considering eCO\(_2\), suggesting that the developed analytical framework herein can well capture the eCO\(_2\) signal on the observed \(Q\) changes (Figure 3d).

### 3.2 Plant physiological and structural responses to eCO\(_2\)

The physiological response of plant to eCO\(_2\), that is, the response of stomatal conductance \((C_s)\) to eCO\(_2\) is directly compiled from field experiments and summarized for each plant functional type in Ainsworth and Rogers (2007) (also see Supplementary Figure S3). All those field experiments report a reduction of \(C_s\) in response to eCO\(_2\), with the largest (lowest) \(C_s\) reduction found in C4 crops (shrubs) for the same level of eCO\(_2\). On average, for a 1% increase in atmospheric CO\(_2\) concentration \((C_a)\), \(C_s\) decreases by 0.47\% ± 0.12\% (mean ± one standard deviation), which means that \(C_s\) decreases by 5.67\% ± 1.47\% under a 12.1% increase in \(C_a\) over 1982-2010 (i.e., from ~343.7 ppm in 1982-1985 to 385.2 ppm in 2006-2010; Keeling et al., 2011). This result is consistent with a recent isotope-based study (i.e., ~5% reduction of \(C_s\) during the past three decades, Frank et al. 2015).

For structural response, averaged across global vegetated lands, elevated \(C_a\) has caused an increase of \(L\) by 2.1\% over the past three decades (Figure 4a and b). Despite this relatively small fertilization effect of eCO\(_2\) on \(L\) at the global scale, an evident gradient is found in the \(L\) - eCO\(_2\) response that a larger eCO\(_2\)-induced relative \(L\) increase is found in low resource availability regions (smaller \(\alpha\) value in Figure 1a), and \textit{vice versa} (Figure 4b). This modelled pattern of \(L\) - eCO\(_2\) response agrees very well observations at the Free-Air CO\(_2\) Enrichment (FACE) observations \((R^2=0.96, p<0.01;\) Figure 4c) and is also consistent with large-scale satellite-based observations (Donohue et al., 2013; Zhu et al., 2016; Yang et al., 2016a).

In terms of \(Z_e\), elevated \(C_a\) over the past three decades has resulted in a very minor (~1\%) overall increase of \(Z_e\) averaged across the globe (Figure 4e). Since large-scale observations of \(Z_e\) in response to eCO\(_2\) are not available, we are not able to quantitatively validate the estimated response of \(Z_e\) to eCO\(_2\).
Nevertheless, the modelled result that eCO$_2$ increases $Z_e$ is overwhelmingly found in site- and/or plant-level observations (Nie et al., 2013) (Supplementary Tables S1 and S2). Moreover, similar with $L$, the response of $Z_e$ to eCO$_2$ also exhibits a notable difference along the resource availability gradient (Figure 4d and 4e). The positive response of $Z_e$ to eCO$_2$ is larger in low $\alpha$ regions and gradually decreases as the resource availability becomes higher. In high $\alpha$ regions (e.g., tropical rainforest and southeast Asia), $Z_e$ even shows a slightly decrease in response to eCO$_2$, suggesting a reduced plant water need in a high $C_a$ atmosphere in those regions.

3.3 Attribution of runoff changes over 1982-2010

During the last three decades, atmospheric CO$_2$ concentration ($C_a$) increased by ~12.1%. For the same period, the BCP model detected a very small reduction in $Q$ of ~0.73% (or 2.8 mm yr$^{-1}$) induced by eCO$_2$ across the 2,268 studied catchments (Figure 5). The overall negative effect of eCO$_2$ on $Q$ suggests that the structural forcing of eCO$_2$ on vegetation water consumption (both above- and below-ground) outweighs the physiological effect of eCO$_2$ driving leaf-level water saving. Despite the overall small effect averaged across all catchments, a significant positive trend ($p<0.01$) in the $Q$-eCO$_2$ response is found along the resource availability gradient, from a negative response in low $\alpha$ catchments to a positive response in high $\alpha$ catchments (Figure 5).

We then attribute $dQ$ to different factors between 1982-1985 and 2006-2010 for the study catchments (Figure 6). Compared with the early 1980s, mean observed $Q$ over the 2,268 catchments in the late 2010s decreased by ~5.8 mm yr$^{-1}$, and the observed pattern with comparable magnitude in $dQ$ is well captured by the BCP model (Figure 6). The impact of eCO$_2$ on $dQ$ is estimated to be -2.3 mm yr$^{-1}$ averaged over all 2,268 catchments. Consistent with relative $Q$ changes (in %; Figure 5), the impacts of eCO$_2$ on the absolute $Q$ change (in mm yr$^{-1}$) also exhibit significant upward trend as $\alpha$ increases (~0.97 mm yr$^{-1}$ per 0.1 increase in $\alpha$, $p<0.01$). Compared to that, decreases in $P$ led to a 2.7 mm yr$^{-1}$ decreases in $Q$, and enhanced $E_P$ has resulted in a decreased $Q$ by 1.6 mm yr$^{-1}$ (Figure 6a). The comparable magnitudes of $dQ$ induced by $dP$ and eCO$_2$ only exist when averaged across all 2,268 catchments, while for each resource availability category, the impact of $P$ on $Q$ generally dominates $dQ$ and is often much higher than that of eCO$_2$ (Figure 7). As for the impact $E_P$ on $Q$, it also shows a notable gradient with...
changes in $\alpha$ as detected for the eCO$_2$ effect, with the impact of $E_P$ on $Q$ being increasingly negative as $\alpha$ raises (Figure 6b-f). Other factors include changes in rainfall intensity (Porporato et al., 2004) and climate change-induced vegetation change (e.g., higher $L$) have, in general, exerted a small negative impact on $Q$.

The same conclusions that the impacts of eCO$_2$ on vegetation have limited yet contrasting (between warm-humid, high $\alpha$ regions and dry, low $\alpha$ regions) feedbacks on $Q$ retain beyond the 2,268 catchments (Figure 7a and b). At the global scale, an increase in $C_a$ by 1% only leads to a decrease of $Q$ by $\sim$0.14% (equivalent to $\sim$1.69% for the range of eCO$_2$ experienced over the past three decades). This 1.69% reduction in $Q$, under the context of 12.1% increases in $C_a$, demonstrates a muted response of $Q$ to eCO$_2$. The sensitivity of $Q$ to eCO$_2$ ($S_{Q_{to\,eCO2}}$) is generally more negative in global arid ecosystems where $\alpha$ is low, with an exception in extreme arid zones (i.e., when $\alpha<0.1$; Figures 7a and b). This is because in extremely dry areas, the availability of water defines the outcome and the sensitivity of $Q$ to any changes in land surface properties is very small (Donohue et al., 2013; Roderick et al., 2014). The negative $S_{Q_{to\,eCO2}}$ diminishes quickly as $\alpha$ increases and turns to a positive $S_{Q_{to\,eCO2}}$ in high $\alpha$ regions. The overall small $S_{Q_{to\,eCO2}}$ is further manifested when comparing $S_{Q_{to\,eCO2}}$ with the sensitivities of $Q$ to climate variables (i.e., $P$ and $E_P$). Averaged over the globe, a same relative change in $P$ and $E_P$ would respectively lead to a $\sim$10-times and $\sim$4-times stronger impact on $Q$ than eCO$_2$ does, highlighting a predominant role of climate in shaping the global $Q$ regime (Figure 7c-f and Supplementary Figure S4).

4. Discussion and concluding remarks

Elevation in atmospheric CO$_2$ concentration is regarded as the ultimate driver of anthropogenic climate change, with consequent impacts on terrestrial runoff. Although the impacts of climate change on $Q$ has been extensively documented in previous studies, the response of $Q$ to eCO$_2$ through vegetation feedbacks is less understood and remains controversial in existing studies (Gedney et al., 2006; Piao et al., 2007; Huntington, 2008; Cheng et al., 2014; Yang et al., 2016a; Ukkola et al., 2016). Here, by developing an analytical attribution framework, we detected a very small response of global $Q$ to eCO$_2$-induced changes in vegetation functioning (Figure 5-7), suggesting that the eCO$_2$ vegetation feedback
only exert a minor impact on water resources for the range of eCO$_2$ that we have experienced over the past three decades.

We also detected a significant positive trend ($p<0.01$) in the $Q$-eCO$_2$ response along the resource availability gradient (Figure 5-7), which is consistent with field experiments (Norby and Zak, 2011; De Kauwe et al., 2013; Körner and Arnone, 1992) (Figure 4c), satellite observations (Donohue et al., 2013; Zhu et al., 2016; Yang et al., 2016a), and model attributions (Cheng et al., 2014; Lian et al., 2018). This $Q$-eCO$_2$ response mechanism suggests that the structural response of vegetation to eCO$_2$ (i.e., increases in $L$ and $Z_c$) is larger in areas with lower resource availability, and gradually decreases as resources become less limiting on plant growth (Figure 4). The positive response of $Q$ to eCO$_2$ in high $\alpha$ catchments (primarily located in tropical rainforests) implies a dominant effect of eCO$_2$-induced partial stomatal closure over increases in $L$ and $Z_c$ on $E$ in these environments. This is reasonable, as both theoretical predictions and in-situ observations have consistently reported a negligible response of $L$ to eCO$_2$ in humid and close-canopy environments (Donohue et al., 2017; Yang et al., 2016a; Norby and Zak, 2011; Körner and Arnone, 1992). In such environments, water is generally abundant with light and/or nutrient availability being the most limiting resources for vegetation growth (Nemani et al., 2003; Yang et al., 2015), and plants have evolved to efficiently capture light by maximizing their above-ground structure (i.e., $L$). As a result, in these tropical rainforests plants have already absorbed most of the incident light and any extra leaves would not materially increase the light absorption (Yang et al., 2016a).

Our findings have important implications for improved understanding of the global hydrological cycle and managing the world’s water resources in a changing climate. Climate models have predicted an increased $Q$ that is primarily driven by an increased $P$ for the 21st century (Milly and Dunne, 2016; Swann et al., 2016; Yang et al., 2018). Here we show that eCO$_2$ would mitigate this positive impact of climate change on $Q$ in relatively dry regions but exaggerate the $Q$ increase in relatively wet regions via its impacts on vegetation water use. In addition, higher $C_a$ and increased $P$ enhance the availability of resource for vegetation growth, which increases vegetation coverage or $L$ (Piao et al., 2020; Zhang et al., 2020a; Zhang et al., 2020b). This suggests that the structural response of vegetation to eCO$_2$ may
eventually decrease and the physiological effect of vegetation to eCO\(_2\) may become increasingly dominant in the overall response of vegetation water use to eCO\(_2\), leading to an increasing water-saving effect of plant in response to eCO\(_2\) under future climate change (Zhang et al., 2020b). In fact, analyses of the state-of-the-art climate model outputs have already consistently shown this water-saving effect of eCO\(_2\) at the global scale and especially in relatively warm and humid environments where \(L\) is high (Yang et al., 2019). Yet, the impacts of eCO\(_2\) on \(Q\) in relatively dry regions are still highly uncertain and show a great diversity between climate models (Zhang et al., 2020b). In this light, our findings based on the well-validated analytical framework provide insightful guidance for climate model development that improves the models’ capability in representing the vegetation and hydrological responses to eCO\(_2\).

350 Data availability

All data for this paper are properly cited and referred to in the reference list.

Author contribution

YY and TRM designed the study. YY performed the calculation and drafted the manuscript. TRM, DY, YZ, SP, SP, and HEB contributed to results discussion and manuscript writing.

355 Competing interests

The authors declare that they have no conflict of interest.

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References


List of Figures

Figure 1 Spatial distributions of (a) resource availability index and (b) climate aridity zones for 1982-2010.

Figure 2 Location of global catchments. The grey dots show the locations of the original 21,856 catchments, and red dots are the 2,268 catchments that pass the selection criteria and are used herein.

Figure 3 Validation of estimated $Q$ at catchments. a. Model performance in predicting mean annual $Q$ in 2,268 catchments. Red dots in global maps show the location of catchments. b. Model performance in predicting $Q$ trend in 2,268 catchments during 1982-2010. c, same as a, but for each resource availability category. d, same as b, but for each resource availability category. The legend from c applies to d. In c and d, the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 5% and 95% percentiles.

Figure 4 Relative changes in $L$ and $Z_e$ caused by eCO$_2$. a, Spatial distribution of relative change in $L$ induced by eCO$_2$ during 1982-2010. b, Same as a, but for each but for each resource availability category. c, Validation of predicted $L$ change against in situ measurement during six Free Air CO$_2$ Enrichment (FACE) Experiments. Note that only FACE sites with undisturbed vegetation are used (see Donohue et al., 2017 for selection of undisturbed FACE sites). d, Spatial distribution of relative change in $Z_e$ induced by eCO$_2$ during 1982-2010. e, Same as d, but for each resource availability category. In b and e, the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 1% and 99% percentiles.

Figure 5 Relative $Q$ change induced by eCO$_2$ during 1982-2010 at catchments. a, Relative change in $Q$ induced by eCO$_2$ as a function of resource availability index for all 2,268 catchments. The red line is the best linear fit. b, Same as a, but for each resource availability category. In b, the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 1% and 99% percentiles.

Figure 6 Attribution of changes in $Q$ between 1982-1985 and 2006-2010 at catchments. a, Attribution of changes in $Q$ between 1982-1985 and 2006-2010 for all 2,268 catchments. b-f, Attribution of changes in $Q$ between 1982-1985 and 2006-2010 for catchments within each resource availability category. Error bars indicate one tenth of standard deviation of each response among catchments. For each subplot the values above the observed $dQ$ and modelled $dQ$ columns represent the mean value and have units of mm yr$^{-1}$. Whereas the values in parenthesis of the four columns to the right of the vertical grey dashed line represent the percent contribution each factor induced in the observed $dQ$ change. The number of catchments in each group is provided on Figure 3(d).
Figure 7 Sensitivity of $Q$ to eCO$_2$ and its relative importance to $P$ and $E_P$ across the globe.  

- **a**, Spatial distribution of $Q$ sensitivity to eCO$_2$ (% change in $Q$ per 1% change in $C_a$).  
- **b**, Boxplot of $Q$ sensitivity to eCO$_2$ for each resource availability category.  
- **c**, Relative importance of eCO$_2$ on $Q$ compared to changes in $P$ on $Q$ (% change in $Q$ per 1% change in $C_a$ compared to % change in $Q$ per 1% change in $P$).  
- **d**, Boxplot of the relative importance of eCO$_2$ on $Q$ compared to changes in $P$ on $Q$ for each resource availability category.  
- **e**, Relative importance of eCO$_2$ on $Q$ compared to changes in $E_P$ on $Q$ (% change in $Q$ per 1% change in $C_a$ compared to % change in $Q$ per 1% change in $E_P$).  
- **f**, Boxplot of the relative importance of eCO$_2$ on $Q$ compared to changes in $E_P$ on $Q$ for each resource availability category.  

In **b**, **d** and **f** the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 1% and 99% percentiles.
Figure 1 Spatial distributions of (a) resource availability index and (b) climate aridity zones for 1982-2010.

Figure 2 Location of global catchments. The grey dots show the locations of the original 21,856 catchments, and red dots are the 2,268 catchments that pass the selection criteria and are used herein.
Figure 3 Validation of estimated $Q$ at catchments. a. Model performance in predicting mean annual $Q$ in 2,268 catchments. Red dots in global maps show the location of catchments. b. Model performance in predicting $Q$ trend in 2,268 catchments during 1982-2010. c, same as a, but for each resource availability category. d, same as b, but for each resource availability category. The legend from c applies to d. In c and d, the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 5% and 95% percentiles.
Figure 4 Relative changes in \( L \) and \( Z_e \) caused by eCO\(_2\). 

\( \textbf{a} \), Spatial distribution of relative change in \( L \) induced by eCO\(_2\) during 1982-2010. 

\( \textbf{b} \), Same as \( \textbf{a} \), but for each but for each resource availability category. 

\( \textbf{c} \), Validation of predicted \( L \) change against \textit{in situ} measurement during six Free Air CO\(_2\) Enrichment (FACE) Experiments. Note that only FACE sites with undisturbed vegetation are used (see Donohue et al., 2017 for selection of undisturbed FACE sites). 

\( \textbf{d} \), Spatial distribution of relative change in \( Z_e \) induced by eCO\(_2\) during 1982-2010. 

\( \textbf{e} \), Same as \( \textbf{d} \), but for each resource availability category. In \( \textbf{b} \) and \( \textbf{e} \), the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 1% and 99% percentiles.
Figure 5 Relative $Q$ change induced by eCO$_2$ during 1982-2010 at catchments. a, Relative change in $Q$ induced by eCO$_2$ as a function of resource availability index for all 2,268 catchments. The red line is the best linear fit. b, Same as a, but for each resource availability category. In b, the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 1% and 99% percentiles.
Figure 6 Attribution of changes in $Q$ between 1982-1985 and 2006-2010 at catchments. a, Attribution of changes in $Q$ between 1982-1985 and 2006-2010 for all 2,268 catchments. b-f, Attribution of changes in $Q$ between 1982-1985 and 2006-2010 for catchments within each resource availability category. Error bars indicate one tenth of standard deviation of each response among catchments. For each subplot the values above the observed $dQ$ and modelled $dQ$ columns represent the mean value and have units of mm yr$^{-1}$. Whereas the values in parenthesis of the four columns to the right of the vertical grey dashed line represent the percent contribution each factor induced in the observed $dQ$ change. The number of catchments in each group is provided on Figure 3(d).
Figure 7 Sensitivity of $Q$ to eCO$_2$ and its relative importance to $P$ and $E_P$ across the globe. 

- **a.** Spatial distribution of $Q$ sensitivity to eCO$_2$ (% change in $Q$ per 1% change in $C_a$). 
- **b.** Boxplot of $Q$ sensitivity to eCO$_2$ for each resource availability category. 
- **c.** Relative importance of eCO$_2$ to $P$ on $Q$ (%) for each resource availability category. 
- **d.** Boxplot of the relative importance of eCO$_2$ on $Q$ compared to changes in $P$ on $Q$ for each resource availability category. 
- **e.** Relative importance of eCO$_2$ to $E_P$ on $Q$ (%) for each resource availability category. 
- **f.** Boxplot of the relative importance of eCO$_2$ on $Q$ compared to changes in $E_P$ on $Q$ for each resource availability category. 

In b, d and f, the upper / lower box edges represent the quantile divisions, the inner horizontal line is the median, the dots indicate the mean value, and the dashed line represent the 1% and 99% percentiles.

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