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TOPICAL REVIEW

Coupling between the terrestrial carbon and water cycles—a review

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Abstract

The terrestrial carbon and water cycles are strongly coupled. As atmospheric carbon dioxide concentration increases, climate and the coupled hydrologic cycle are modified, thus altering the terrestrial water cycle and the availability of soil moisture necessary for plants' carbon dioxide uptake. Concomitantly, rising surface carbon dioxide concentrations also modify stomatal (small pores at the leaf surface) regulation as well as biomass, thus altering ecosystem photosynthesis and transpiration rates. Those coupled changes have profound implications for the predictions of the carbon and water cycles. This paper reviews the main mechanisms behind the coupling of the terrestrial water and carbon cycles. We especially focus on the key role of dryness (atmospheric dryness and terrestrial water availability) on carbon uptake, as well as the predicted impact of rising carbon dioxide on the water cycle. Challenges related to this coupling and the necessity to constrain it based on observations are finally discussed.

1. Introduction

This review aims at describing recent findings on the coupling between the terrestrial carbon (dioxide) and water cycles. The targeted readers include hydrologists interested in the role of rising CO_2 and in the role of the biosphere on the water cycle, ecologists interested in the role of water on the carbon cycle or climate scientists who want to dig further into the role of the biosphere. By definition, this short review is by no means exhaustive and is meant to provide a simplified context aimed at informing readers outside the field of carbon–water coupling. We nonetheless discuss some potentially relevant diagnostics of this coupling, primarily at the global scale, both in global Earth system models (ESMs) and with remote sensing observations.

1.1. Atmospheric versus surface coupling

The exchange of carbon dioxide and water between the terrestrial biosphere and the atmosphere plays a key role in the Earth's past and future climate. Over the last century, anthropogenic emissions of carbon dioxide, which is the greenhouse gas (GHG) contributing the most to warming, have modified the Earth's climate and the coupled hydrologic cycle (Gregory *et al* 2004, Bony *et al* 2015, Knutti and Rugenstein 2015, Armour 2016, 2017, Knutti *et al* 2017). Changes in climate and the hydrologic cycle include changes in temperature and clouds as well as changes in precipitation distribution, intensity and variability (Friedlingstein *et al* 2006, Gregory *et al* 2009, Friedlingstein *et al* 2014, Friedlingstein 2015, Green *et al* 2019) with important consequences for ecosystems. A changing and warmer climate impacts continental atmospheric dryness (Byrne and O'Gorman 2016), soil moisture (Berg *et al* 2017), as well vegetation function and structure (Zhu *et al* 2016).

In addition to its strong GHG effect, (surface) atmospheric CO_2 is the main source for plant carbohydrates generation through photosynthesis (Sage *et al* 1989, Harley *et al* 1992a, 1992b, Sage 1994, Ainsworth and Long 2005, Ainsworth and Rogers 2007). Plant stomata (small pores at the leaf surface) open or close in order to regulate plant water losses, known as transpiration (Tr), while taking up carbon dioxide CO_2, i.e. gross primary productivity (GPP) (Ball *et al* 1987, Collatz *et al* 1991, 1992, Farquhar 2001, 2002, Medlyn *et al* 2011). As a result, the continental CO_2 and water cycles are intimately coupled at the surface through plant stomata (physiological effect), in addition to the coupling induced by the GHG forcing of CO_2 on climate, and on the coupled water cycle (GHG effect) (Friedlingstein *et al* 2006, Friedlingstein 2015). Those two effects (physiological and GHG) simultaneously affect the terrestrial energy, water and carbon cycles with increasing GHG concentrations and exert profound changes on the biosphere.

1.2. Surface CO_2 effects on vegetation

Increased surface $[CO_2]$ (concentration) modifies photosynthesis directly, as (1) it changes the gradient between intercellular and leaf surface $[CO_2]$ and because (2) it modifies stomatal conductance, instantaneously (through stomatal partial closure). Over long time periods (years to hundreds of years), rising $[CO_2]$ also changes stomatal conductance through modification of stomata density, number and shape (de Boer *et al* 2011, De Boer *et al* 2012, de Boer *et al* 2016). As a result, elevated $[CO_2]$ typically decreases stomatal conductance, yet it increases photosynthesis because of the increased gradient between intercellular and leaf surface CO_2 and increased carboxylation rate of the carboxylase enzyme RuBisCO (in C3 plants).

Over periods from months to years, elevated $[CO_2]$ can lead to increased vegetation biomass, as a result of increased GPP. This increased biomass can be allocated to belowground or aboveground biomass and to the leaves in particular. This increased leaf biomass has been detected by remote sensing observations and is referred to as a 'greening' (Keenan 2015, Lu *et al* 2016, Zhu *et al* 2016, Forzieri *et al* 2017).

The free-air CO2 enrichment (FACE) was a series of experiments which aimed at evaluating this impact of rising surface $[CO_2]$ on ecosystems. In this experiment, CO_2 was near-continuously injected over a studied area (spanning 10–100 m) to artificially increase $[CO_2]$ and to evaluate the impact on ecosystems, in particular in terms of changes in biomass, carbon allocation and water use efficiency: $WUE = GPP/Tr$, with Tr the transpiration flux. Field experiments with enriched $[CO_2]$ such as FACE have confirmed that growth generally increased in elevated $[CO_2]$ conditions and that it had a large impact on belowground biomass, especially on fine roots (Warwick *et al* 1998, Allen *et al* 2000, Calfapietra *et al* 2003, Jackson *et al* 2009). We note though that measuring belowground biomass changes is technically more challenging than aboveground changes (Allen *et al* 2000, Suter *et al* 2002, Pritchard *et al* 2008, Yang *et al* 2008). The biomass growth response varied across species and climate, with some species showing limited biomass growth, especially above ground (Ainsworth and Long 2005). Elevated $[CO_2]$ typically resulted in taller plants with larger stem diameter, increased branching and leaf number. Leaf Area Index (LAI) increase varied widely across species, with a relatively large increase in trees (∼20%) but with minimal changes in grasses. C3 species are expected to be more sensitive to increased $[CO_2]$ than C4 species (Ehleringer and Bjorkman 1977, Morison and Gifford 1983, Ehleringer *et al* 1997). C3 plants use RuBisCO to fix CO_2 and lose a portion of their fixed CO_2 to photorespiration because RuBisCO is also an oxygenase. C3 plants should therefore increase net photosynthesis under elevated $[CO_2]$. C4 plants add another carbon fixing enzyme in addition to RuBisCO (PEP carboxylase), which has high affinity with CO_2 and is able to fix carbon at very low concentration of hydrogen carbonate. When CO_2 is released in the bundle sheath cells it creates a higher concentration of CO_2 than that found in photosynthetic cells of C3 plants. As a result, changes in atmospheric $[CO_2]$ have much less impact on C4 photosynthesis and therefore also on the coupled transpiration flux. Some of the FACE observations have further shown a potential temporal reversal of this response to $[CO_2]$ in C3 versus C4 plants (in grassland species) over long time periods with C3 plants showing reduced response over decadal time scales (Reich *et al* 2018).

Recently, observations of carbonyl sulfide, a proxy for plant photosynthesis, based on aircrafts or point measurements have also confirmed the large increase in growing season GPP over vast regions, such as the US Midwest, confirming the key role of increased $[CO_2]$ (and temperature in cold regions) on the carbon cycle (Campbell *et al* 2008, Berry *et al* 2013, Campbell *et al* 2017a, 2017b), and therefore on the coupled transpiration fluxes. Yet, importantly, most of the observed greening across the globe appears to be located in regions of strong land management (agriculture, reforestation, forest management) (Chen *et al* 2019). This long-term impact of land management, if not carefully accounted for, could lead to incorrect attribution of the observed greening to elevated $[CO_2]$ only, whereas land management likely explains a large portion of the observed global changes.

1.3. Soil moisture effects on water–carbon coupling

While a variety of variables can be relevant for photosynthetic activity and plant development (e.g. nutrients), one important abiotic factor controlling both carbon and water fluxes is soil moisture (Seneviratne *et al* 2010, Zhu *et al* 2016, Humphrey *et al* 2018, Green *et al* 2019). Soil moisture content determines how much water can be extracted by plant roots and regulates stomatal conductance, which in turn determines plant water status, as well as the rate of GPP and Tr (Sperry 2000, Sperry and Love 2015, Anderegg *et al* 2015b, Wolf *et al* 2016, Sperry *et al* 2016, 2017, Anderegg *et al*, 2017, Stocker *et al* 2018). Soil moisture also regulates plant growth through changes in carbon allocation (Korner *et al* 2003, Palacio *et al* 2014). Drought stress increases water tension in the xylem (which conducts sap water from the roots to the leaves), and therefore increases the risk of embolism (due to air bubble formation in the xylem blocking the liquid flow from roots to leaves) and to potential dysfunction of a plant's hydraulic system (Sperry 2003, 2008, McDowell 2011, McDowell and Allen 2015, Sperry and Love 2015).

Water limitation also alters the growth of new cells, especially in the xylem and phloem. The xylem is a transport tissue bringing water and soluble nutrients to the shoot though the trunk and branches (Tyree and Sperry 1989, Hacke and Sperry 2001, Cochard 2002, Sperry *et al* 2003, Franks and Brodribb 2005, Bittencourt *et al* 2016, Gleason *et al* 2016). Xylem water (sap) transport is also used to replace lost water from transpiration and thus is strongly connected to the photosynthesis process. The phloem is the other transport tissue which brings carbohydrates downward in the plant from the leaf source to its sinks (Sala *et al* 2010, Nikinmaa *et al* 2013, Rathgeber *et al* 2016, Castagneri *et al* 2017, Ziaco *et al* 2018). Both xylem and phloem interact through changes in osmotic pressure and water potential, regulating the water and carbohydrate transports in the plant (Botha 2005, Cochard *et al* 2009, Holtta *et al* 2009, Rosner *et al* 2018, Sevanto *et al* 2018), as well as turgor. They therefore interact to modify Tr and GPP (Nikinmaa *et al* 2013, Konrad *et al* 2018). Soil moisture in the root zone strongly regulates both of those xylem (Kennedy *et al* 2018) and phloem processes.

Periods of prolonged soil droughts can trigger extensive hydraulic damage (cavitation) (Sperry and Tyree 1988, Tyree and Sperry 1989, Cochard 2002, Cochard *et al* 2009, Meinzer and McCulloh 2013, Gentine *et al* 2016b, Giardina *et al* 2018), lowering their defense against pathogens (McDowell *et al* 2008). These combined effects can result in plant mortality (McDowell 2011, McDowell and Allen 2015), further reducing transpiration, Tr, and carbon uptake at the ecosystem scale (Anderegg *et al* 2012, Williams *et al* 2013, Matheny *et al* 2014, Morillas *et al* 2017) and releasing carbon through heterotrophic respiration (i.e. decomposition of dead organic matter).

Because droughts reduce evapotranspiration, the partitioning towards the less efficient sensible heat flux cooling mechanism (Bateni and Entekhabi 2012) can markedly increase surface and air temperature as well as vapor pressure deficit (VPD), the difference between saturated and actual water vapor pressure, which represents the atmospheric dryness (Seneviratne *et al* 2010, Gentine *et al* 2016a, Zhou *et al* 2018). Those land–atmosphere feedbacks can further impact the vegetation because of the increased temperature and VPD, which can stress the plant and reduce stomatal opening (see next section). Droughts can also change the intra- and interannual transport efficiency of new xylem (i.e. sap conductivity) at the expense of safety (i.e. resistance to drought) (Eilmann et al 2011, Petrucco *et al* 2017, Guerin *et al* 2018, Prendin *et al* 2018).

Soil moisture is also an important regulator of heterotrophic respiration (Manzoni *et al* 2012, Suseela *et al* 2012, Ryan *et al* 2015, Yan *et al* 2016, 2018, Zhang *et al* 2018a), which represents about half of the total CO_2 emissions from soils. Low soil moisture conditions limit heterotrophic respiration rates through the reduction of solute transport and can trigger microbial dormancy in extreme drought conditions (Manzoni *et al* 2012, Suseela *et al* 2012, Ryan *et al* 2015, Yan *et al* 2016, 2018, Zhang *et al* 2018a). On the other end of the soil moisture spectrum, saturated soil moisture conditions also strongly limit respiration as they suppress oxygen supply so that respiration rates are only maximal at intermediate soil moisture values (Manzoni *et al* 2012, Suseela *et al* 2012, Ryan *et al* 2015, Yan *et al* 2016, 2018, Zhang *et al* 2018a). Soil moisture conditions also regulate surface temperature as evaporation is a more effective cooling mechanism than sensible heating (Bateni and Entekhabi 2012). As such these changes in surface temperature also modifies respiration in addition to biological effects: lower soil moisture conditions increasing respiration because of the increased surface temperature (Green *et al* 2019).

1.4. VPD effects on vegetation

Plant stomata, and therefore GPP and Tr, are regulated by atmospheric dryness, i.e. VPD. Our understanding of the role of VPD and carbon uptake at the leaf level has substantially progressed in recent years and is now relatively well understood (Lin *et al* 2015), compared to the ecosystem scale response. It is believed that plants tend to reduce their stomatal conductance in response to high VPD in order to minimize water losses, Tr, for a given carbon gain, GPP (Farquhar and Sharkey 1982, Katul *et al* 2009, Medlyn *et al* 2011), while maintaining a near steady underlying WUE (uWUE), defined as $\mathrm{WUE.VPD}^{1/2}$ (Zhou *et al* 2015, 2016).

Yet, this regulation varies according to the coordination between xylem and stomatal conductances (Klein 2014, Martínez-Vilalta *et al* 2014, Konings and Gentine 2016), and in particular with soil moisture. In many biomes, VPD appears to be an important regulator of carbon and water fluxes, and ecosystem conductance, sometimes having an effect even stronger than soil moisture (Novick *et al* 2016, Konings *et al* 2017, Giardina *et al* 2018, Lin *et al* 2018). However, a major observational challenge is that VPD is tightly coupled to soil moisture through land–atmosphere interactions so that correct attribution is difficult (Zhou *et al* 2018). Indeed, low soil moisture conditions lead to a lower evaporative fraction, the ratio of latent heat flux (LE) to available energy (Gentine *et al* 2011, 2007), which warms and dries the boundary layer (Gentine *et al* 2016a), together increasing VPD. Low soil moisture generally therefore co-occurs with high VPD due to reduced latent heat and enhanced sensible heat, so that droughts (conditions of low soil moisture and high aridity—VPD) should really be considered as compound events, i.e. as co-occurring (Zscheischler and Seneviratne 2017, Zhou et al 2018, Zscheischler et al 2018). The combination of extremely low soil moisture and high VPD strongly limits carbon uptake and can potentially trigger vegetation mortality (Choat et al 2018, Zhou et al 2018).

High VPD conditions are also key determinants of fire occurrence (Williams and Abatzoglou 2016, Williams et al 2014, 2018), further regulating CO_2 fluxes to the atmosphere. Therefore, year-to-year changes in soil moisture and VPD have profound impacts on the net flux of carbon from the atmosphere to the land (net biome production (NBP)) (Green et al 2019) and are negatively correlated with atmospheric CO_2 growth (Humphrey et al 2018). Finally, VPD also has important impacts on WUE (Zhou et al 2014, 2015), thus directly modifying the coupling between photosynthesis and Tr.

1.5. Water use efficiency = GPP/Tr

A key indicator of ecosystem CO_2–water coupling is the ecosystem WUE. At the leaf level, increased atmospheric $[CO_2]$ facilitates photosynthesis while reducing stomatal opening and conductance, which tends to increases WUE, at least in the short term. Observations support such increase in both leaf-level- and ecosystem-scale WUE across time scales, even though the WUE dependence on ambient CO_2 concentration also exhibits some species and climate dependence (Frank et al 2015, Dekker et al 2016). Other factors can modify WUE such as variations in anatomical stomatal conductance (e.g. stomatal density or stomatal shape) (de Boer et al 2011, De Boer et al 2012, de Boer et al 2016), variations in mesophyll conductance with changing environmental conditions (Bernacchi 2002, Flexas et al 2008, 2012, Niinemets et al 2009, Campany et al 2016), as well as the degree of coupling of the biosphere with the overlying atmosphere as influenced by changes in ecosystem conductance and ecosystem aerodynamic roughness (increasing with aboveground biomass) (Jarvis 1986, Jarvis and Mcnaughton 1986, De Kauwe et al 2017). Ecosystem WUE is also significantly impacted by VPD at hourly and daily scales, as demonstrated with eddy-covariance flux tower observations (Zhou et al 2015, Dekker et al 2016). Interestingly, to our knowledge, the influence of soil moisture on long-term (years to decades) WUE has rarely been assessed, likely because of the challenges in continuously measuring and disentangling the effects of confounding factors such as VPD.

1.6. Extremes

Extremes, especially droughts and heat waves, have now clearly been identified as key components of the terrestrial water and carbon cycles (Knapp et al 2008, Jaeger and Seneviratne 2010, Reichstein et al 2013, Zscheischler et al 2014, Sippel et al 2017, Vogel et al 2017, von Buttlar et al 2018, Yin et al 2018, Green et al 2019). The interannual variability in the carbon cycle is in particular dominated by the occurrence of extremes, especially in transitional climates (monsoonal or semi-arid) (Seneviratne et al 2010), where soil moisture and temperature regulation exert key control on carbon uptake (Poulter et al 2014, Zscheischler et al 2014). The impact of droughts and heat waves can be directly observed over short periods of times (weeks) but extend to multiple years (legacy effects), if there has been major impact on ecosystems, such as large-scale die-off (Anderegg et al 2013, 2015c). Similarly those extremes are important for the water cycle such as the rate of transpiration (Teuling et al 2010, Teuling et al 2013, Miralles et al 2019) or runoff (Yin et al 2018).

2. Global soil moisture impact on carbon cycle

As discussed earlier, soil moisture has a large impact on biosphere-atmosphere gas exchanges, especially on photosynthesis. Plant physiological studies at the level of individual plants have suggested that the soil moisture effect mostly affects the stomatal sensitivity to VPD, and enzyme activity that related to photosynthesis and respiration. However, the soil moisture effect on carbon cycle, especially on ecosystem to global scales, is still less understood mostly due to lack of direct observations.

The effect of soil moisture is usually represented in land–surface models through an empirical regulation of stomata conductance as a function of soil moisture content between a wilting point and unstressed value (Dai et al 2002, De Kauwe et al 2015, Fu et al 2016). These stomata models omit the connection with the xylem and phloem except for a few exceptions (Xu et al 2016, Kennedy et al 2018). These stomatal models also have an atmospheric dryness dependence either in terms of relative humidity (Ball et al 1987), or in terms of VPD: with either a VPD^{-1} dependence (Leuning 1995), or more recently a $VPD^{-0.5}$ dependence. as implemented in a few land–surface models such as the Community Atmosphere Land Exchange or the Community Land Model v5.0 (Medlyn et al 2011, De Kauwe et al 2015, Kennedy et al 2018). This latter VPD exponent is based on a stomatal optimality principle, which assumes that stomata try to maximize GPP while minimizing water losses (Tr). Observations tend to suggest that, at the ecosystem scale, the dependence on VPD might be suboptimal, with an ecosystem conductance exponent ranging between -1 and -0.5 depending on the plant functional type (Lin et al 2018). Importantly, as discussed earlier, we note that because of land–atmosphere interactions, soil moisture and VPD are strongly negatively correlated so that disentangling their effects can be challenging (Zhou *et al* 2018).

In situ data, especially from eddy-covariance flux towers measuring turbulent carbon and water fluxes, have demonstrated that droughts and extremes play a disproportional role on both annual GPP and net ecosystem exchange (Reichstein *et al* 2013, Zscheischler *et al* 2014, Yi *et al* 2015). Therefore, not just the mean but also the (subseasonal and interannual) variability of soil moisture and its extremes are critical for carbon uptake (Zscheischler *et al* 2014).

In recent years, advances in satellite observations have provided new tools helping us understand the coupling between soil moisture and the carbon cycle at the global scale. A global remote sensing of solar-induced chlorophyll fluorescence (SIF) has become widely available from satellites such as GOSAT, GOME-2, SCIAMACHY and OCO-2 (Frankenberg *et al* 2011a, 2011b, Joiner *et al* 2011a, 2012, 2013, Guanter *et al* 2012). SIF corresponds to a small fraction of sunlight absorbed by the chlorophyll which is radiated back at longer wavelengths (660–800 nm) (Agati *et al* 1995, 1996) and is a by-product of photosynthesis. SIF, as measured by satellites, therefore places key constraints on global GPP (Lee *et al* 2015, Ryu *et al* 2019) and has helped us gain a more mechanistic understanding of ecosystem CO_2 exchange, especially in locations where *in situ* measurements are rarely available such as in tropical or high latitude regions. SIF observations from remote sensing platforms have shown great potential to assess vegetation productivity as well as phenology from space (Frankenberg *et al* 2011, Joiner *et al* 2011, 2013, 2014, Frankenberg *et al* 2014, Alemohammad *et al* 2017, Jeong *et al* 2017, Luus *et al* 2017, Sun *et al* 2017, 2018, Gentine and Alemohammad 2018, Zhang *et al* 2018a), as satellite SIF is closely related to ecosystem GPP.

Surface soil moisture has been retrieved from satellite microwave sensors since 1979 with both passive and active sensors (Entekhabi *et al* 2010, Kerr *et al* 2010, Dorigo *et al* 2017), and model estimates of soil moisture down to 2 m are also available from a wide range of land–surface models, global hydrological models and atmospheric reanalyses (Rodell *et al* 2004, Dee *et al* 2011, Beck *et al* 2017, Gelaro *et al* 2017). Soil moisture drought is generally associated with negative impacts on the vegetation, especially in semi-arid regions (Nicolai-Shaw *et al* 2017). However, in cold and temperate climates, increases in solar radiation and air temperature commonly associated with droughts can sometimes have a positive impact on vegetation activity (Zscheischler *et al* 2015). A recent study confirmed this dual behavior with SIF observations, and also concluded that forested ecosystems were more resilient to droughts than nonwoody vegetation (Walther *et al* 2019). Microwave missions are also starting to be used to understand ecosystem-scale water usage strategy using the temporal variations of vegetation water content (vegetation optical depth) in response to dryness (Konings and Gentine 2016, Konings *et al* 2017, Brandt *et al* 2018, Feldman *et al* 2018, Giardina *et al* 2018).

In addition to soil moisture estimates, the NASA-DLR Gravity Recovery and Climate Experiment satellite missions (GRACE and GRACE-FO), also measure changes in terrestrial water storage (TWS), which includes groundwater, soil moisture, surface waters, snow ice and biosphere moisture (Scanlon *et al* 2016). So far, GRACE observations have been largely used in water resources research (Rodell *et al* 2009, Scanlon *et al* 2018) and global hydrological modeling, but rarely in carbon cycle research, except in a few instances (Bloom *et al* 2010, Velicogna *et al* 2015, Andrew *et al* 2017). Global GRACE TWS changes were recently found to be strongly correlated to anomalies in global land carbon uptake (Humphrey *et al* 2018), highlighting the potential of GRACE TWS observations for understanding water–carbon cycles' coupling.

In ESMs, soil moisture variability (on monthly to interannual time scales) and soil moisture trends, have been recently shown to have a major impact on global NBP (i.e. net ecosystem production minus the carbon losses from fire and land cover change) (Green *et al* 2019). Soil moisture variability (beside the natural seasonal cycle) reduces the land carbon sink by a magnitude similar to the total land carbon sink itself, both currently and in the future (Green *et al* 2019). This occurs because of the strong nonlinear response of photosynthesis (figure 1) (Green *et al* 2019), ecosystem respiration (Yan *et al* 2016, 2018) and disturbances (Williams and Abatzoglou 2016) to soil moisture. Because of the nonlinearity of these responses, the occurrence of droughts cannot be compensated by positive soil moisture anomalies (wet periods) of similar magnitude. In other words, the response of carbon uptake to soil water availability is not a zero-sum game. Remote sensing observations based on SIF in lieu of GPP and GRACE TWS in lieu of total soil moisture support the fact that photosynthesis exhibits a strong nonlinear response to total soil moisture availability (including groundwater). Figure 1 indicates that this response is overall similar in observations and in models, even though the exact shape would be critical for a correct response to water stress and is not perfectly captured by models (figure 1).

(Poulter *et al* 2014, Ahlström *et al* 2015, Zhang *et al* 2016)

Current ESMs display a quite strong degree of correlation between photosynthesis and soil moisture (figure 2 and figure S1, available online at stacks.iop.org/ERL/14/083003/mmedia) as assessed using the monthly correlation between GPP and total soil moisture in the growing season. Most models exhibit strong positive correlations in transitional and dry regions, consistently across models (stippling represents where nine out of 11 models agree on the sign of the correlation), especially in the midlatitudes and the tropics, except for several models displaying negative

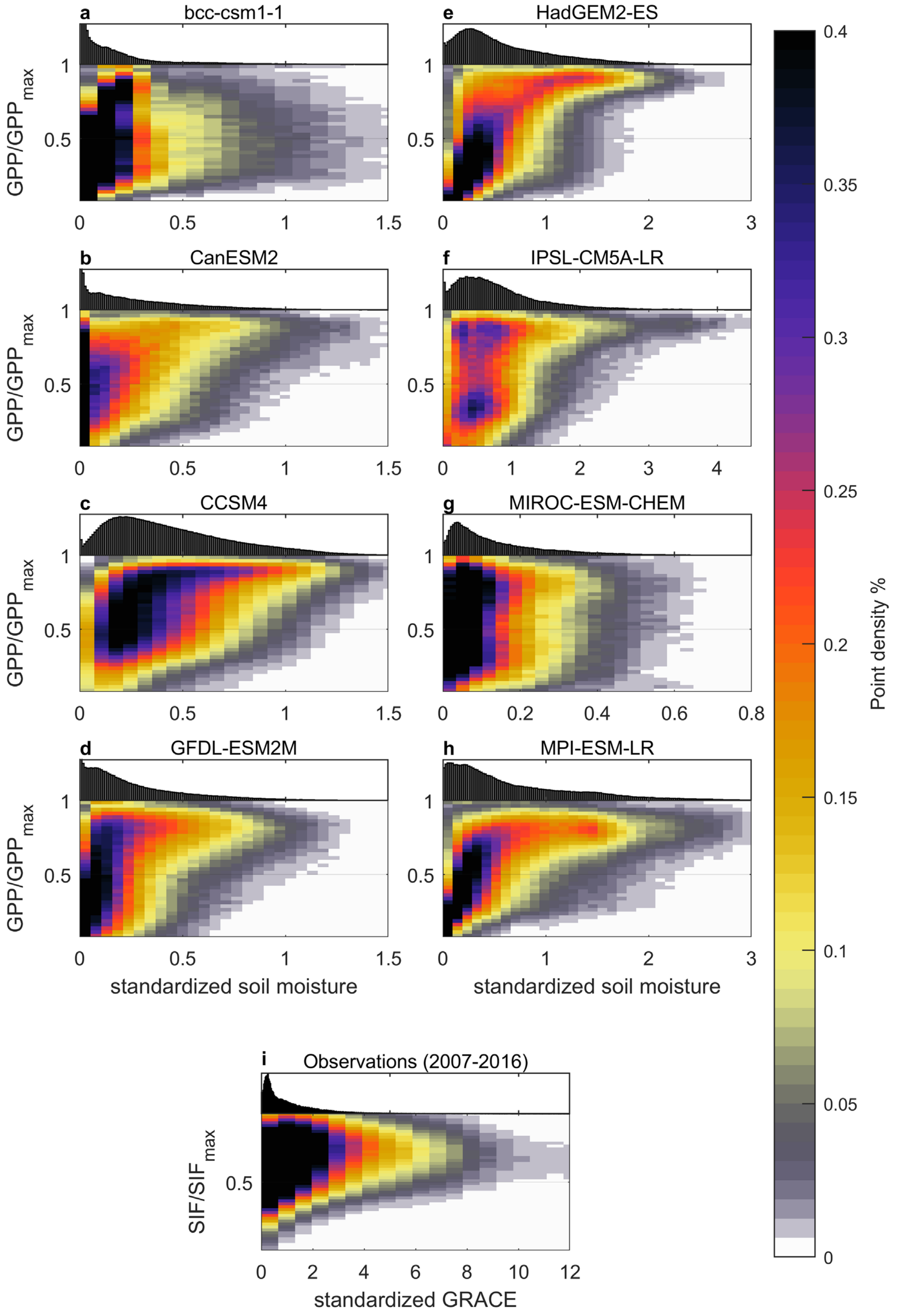

Figure 1. Biosphere photosynthetic activity response curves. Plots of normalized gross primary productivity (GPP) versus standardized soil moisture from CMIP5 models from the historical runs (1971–2000) (a)–(h). Plot of normalized and detrended solar-induced fluorescence (SIF) observations, a proxy for photosynthesis, versus standardized terrestrial water storage (TWS) based on the Gravity Recovery and Climate Experiment (GRACE) (2007–2016) (i). Probability density functions of the soil moisture and TWS data are plotted at the top of the *x*-axes. For soil moisture, owing to large differences in magnitude between models and within the same model between regions, each pixel is standardized by its minimum value in time and its standard deviation in space for easier comparison. The *y*-axis data is divided by the maximum value (SIF_{max} or GPP_{max}) of all points. We emphasize that ESMs do not generally include the full TWS changes and instead only represent soil moisture and some limited groundwater components, with the exception of several ESMs that include some simple representation of the water table and unconfined aquifers (i.e. connected to the surface), and of open water bodies (Swenson and Lawrence 2015).

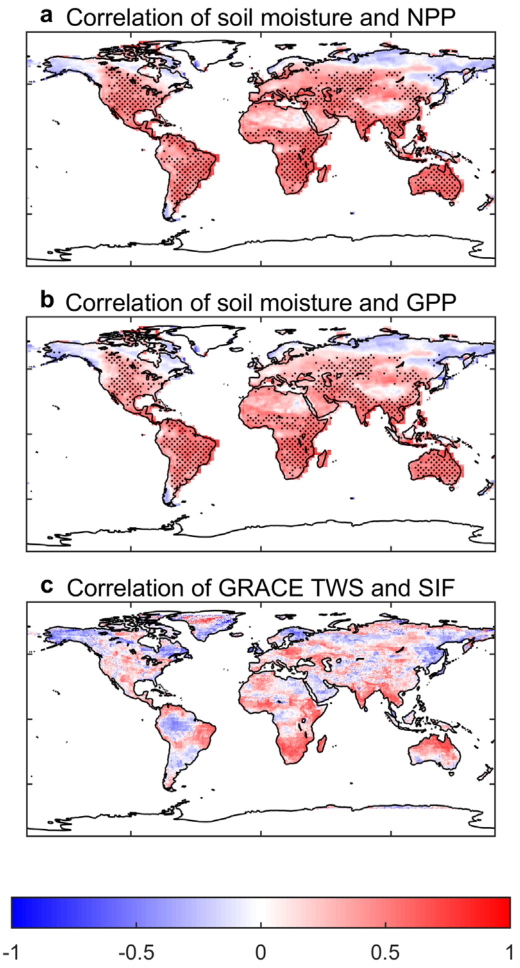

Figure 2. Growing season correlations. Correlations between NPP (a) or GPP (b) and total soil moisture across Earth System models (ESMs) during the growing season (using monthly data from 1971 to 2000). (c) Same figure in the observations, using GOME-2 SIF data instead of GPP and TWS data instead of total soil moisture estimate using GRACE satellites (2007–2016). All data are deseasonalized, and the growing season is defined as the months when SIF/GPP is higher than 30% of the climatology maximum. Stippling represents regions where at least nine of the 11 models used agree on the sign of the correlation as depicted.

correlation in Western/Northern Europe. At high latitudes there are substantial variations in the sign of the correlation between GPP and soil moisture with models either representing a positive or negative value. These differences may be related to uncertainties in the effects of temperature and snow effects on GPP, especially on its phenological cycle.

On the other hand, observations based on SIF (as a proxy for GPP) and GRACE TWS (as a proxy for total soil moisture) clearly emphasize the strong coupling between carbon and water, but mostly in the transitional dry–wet (semi-arid and monsoonal) regions (figure 2(c)). This coupling has also been highlighted in previous studies (Poulter *et al* 2014, Ahlström *et al* 2015, Zhang *et al* 2016). By contrast, there is a clear overestimation of the models' stress especially in wet regions (e.g. the Amazon rainforest). Model-derived correlations are very strong (correlations close to 1) over most regions except in northern latitudes, which is not supported by observations, except for transitional regions. Observations have their own issues, in particular related to the low signal to noise ratio and possible sensor degradation of the remotely sensed SIF data (Zhang *et al* 2018c) and to the fact that GRACE senses all TWS including groundwater and open water bodies, yet the latter is usually strongly correlated with total soil moisture on monthly time scales. Nonetheless, the correlation between GOME-2 SIF and GRACE TWS is strong and positive only in water-limited regions, namely in regions dominated by seasonal dryness such as the Mediterranean or monsoonal regions, the savanna region of Brazil, parts of central America, the Sahel and horn of Africa, southern Africa, eastern Europe, India and southeast Asia as well as the monsoonal part of Australia. Positive correlations are also observed at Northern latitudes, where a decrease in TWS due to low precipitation might also correspond with warm conditions and reduced cloud cover beneficial for photosynthesis. Importantly, the Amazon does not appear to be water stressed—rather a decrease in water storage in the wet season appears beneficial as it is associated with reduced cloud cover and increased light and therefore higher rates of photosynthesis and evapotranspiration (Anber *et al* 2015, Guan *et al* 2015).

Different factors might explain why the response of models to water stress appears to be overestimated at the local scale (figure 2). Land–surface models are known to exhibit a dry bias, because soil moisture decays too fast and this decay stresses ecosystems too much, with little resilience based on deep rooted water (Powell *et al* 2013, Green *et al* 2017, Kennedy *et al* 2018). Inclusions of more physically-based water stress response, i.e. based on plant hydraulics and better representing stomatal response to water stress and xylem interaction, however, does seem to improve this water stress response (De Kauwe *et al* 2015, Xu *et al* 2016, Kennedy *et al* 2018). Better inclusion of groundwater processes might also be important, as they are connected to Tr rates (Maxwell and Condon 2016). Global observations such as the ones presented here could represent an important tool to constrain ESMs and their land–surface model response to water stress and TWS in particular.

Memory and legacy effects further induce multiscale and long-term response of ecosystems and continental carbon fluxes to dryness and are mainly absent from ESMs (Anderegg *et al* 2013, 2015c, Kaisermann *et al* 2017, Sippel *et al* 2018). Soil moisture also regulates plant growth, and especially sap area and tree ring size on interannual time scales, with wet years leading to larger tree rings (Gao *et al* 2018). Indeed, tree rings are commonly used to reconstruct long-term interannual variability in moisture conditions (Cook *et al* 2014b). These moisture-induced interannual variations in xylem structure and functions can also impact sap flow regulation and thus transpiration and photosynthesis. These processes are not represented in models which tend to be too static on interannual time scales. Moisture availability can also affect the allocation to different carbon pools, as well as the leaf to sap area ratio (Guérin *et al* 2018), also modifying the water stress response. These long-term feedbacks between the carbon and water cycles are not properly represented in current models, which also have a too short a soil moisture memory (typically less than a year) (Anderegg *et al* 2015c).

We note that at the global scale there has been a debate on whether temperature or water availability plays the preponderant role on biosphere carbon cycling. Several studies suggested that temperature was a dominant factor compared to precipitation at the global scale (Piao *et al* 2008, Wang *et al* 2013, Anderegg *et al* 2015a). This apparent global domination of temperature was explained by compensating water effects across different regions (with some exhibiting positive and others negative anomalies) (Jung *et al* 2017). This supposed weak global effect of water stress on NBP (Jung *et al* 2017) has been recently debated, considering bulk global measures such as the weaker global CO_2 growth rate response to water storage in models compared to observations (Humphrey *et al* 2018). This apparent contradiction needs to be further resolved. After all, an increasing sensitivity to temperature has been found, which may be related to the decreasing soil moisture (Wang *et al* 2014). This suggests a strong interaction between temperature and soil moisture and their compound effect on regulating the carbon cycle. We also note that Humphrey *et al* (2018) suggested that a lack of long-term memory in soil moisture would explain why global effects of water stress on interannual carbon cycle variability seem to be underestimated. This would be entirely consistent with the hypothesis that models overestimate the response to soil moisture stress at the local to regional scale (figure 2) because of too short soil moisture memory.

3. Global CO_2 impact on water cycle

Changes in the continental carbon cycle also have important implications for the water cycle. As $[CO_2]$ increases, stomatal conductance, biomass and GPP are modified (see section 1), so is Tr. In addition, increase in aboveground biomass also increases the roughness of the canopy, and therefore impacts the turbulent exchange between the atmosphere and the surface. Those various changes modify Tr and thus evapotranspiration (Lemordant *et al* 2016, Swann *et al* 2016, Lemordant *et al* 2018), modulate soil moisture availability (Ainsworth and Long 2005, Leuzinger and Körner 2007, Lemordant *et al* 2016) and potentially runoff (Betts *et al* 2007, Lemordant *et al* 2018).

Idealized ESM experiments can be used to decompose the effect of increasing surface (physiological effects) and atmospheric CO_2 (GHG effect), which can be studied separately with idealized experiments. Future changes of the water cycle induced by increased $[CO_2]$ can thus be quantified in models, with caveats associated to the idealized setup used as well as to uncertain model representation of the water and carbon processes (Swann *et al* 2016, Lemordant *et al* 2016, 2018), as noted earlier. In the FACE observations, which can be used to constrain the physiological CO_2 effects, surface turbulent fluxes could typically not be evaluated because of the heterogenous and unsteady source of CO_2 due to the variable injection rate, and because the experiment was smaller than the typical footprint of an eddy-covariance system (hundreds of meters). Still, FACE experiments have shown that increased surface CO_2 modifies the water cycle, especially the seasonal cycle of soil moisture (Ainsworth and Long 2005), as well as the sensitivity of ecosystem productivity to extreme drought events (Roy *et al* 2016).

One important difference of ESM modeling studies compared to the FACE experiment (omitting the quality of the process representation) is that ESMs naturally account for land–atmosphere feedbacks (Lemordant *et al* 2016), which are critical to fully understand the coupling between the water and carbon cycles. Indeed, modification of the surface fluxes at a regional scale (few kilometers) impact the lower part of the atmosphere (the boundary layer) and thus modify temperature, VPD and also cloud cover (impacting downwelling solar radiation at the surface) (Pielke 2001, Ek and Holtslag 2004, Seneviratne *et al* 2010, Pielke *et al* 2011, de Arellano *et al* 2012, Gentine *et al* 2016a, 2013). For a given biomass level, increased surface CO_2 and lower soil moisture levels tend to close stomata, leading to reduced evapotranspiration and higher sensible heat flux, and thus higher surface temperature and ecosystem respiration (Green *et al* 2019), an effect that is missed by FACE experiments.

ESMs with prescribed surface $[CO_2]$ (physiological effects) versus prescribed atmospheric concentrations (GHG effects) can be used to disentangle the different effects on total evapotranspiration (or LE in W/m2). For example, a combination of different experiments in Climate Model Intercomparison Project Phase 5 (CMIP5) can help delineate the CO_2 effect on vegetation or on global temperature (Taylor *et al* 2012) (data available at https://esgf-node.llnl.gov/projects/cmip5/). A typical way would be using idealized experiments in which the respective impacts of increased $[CO_2]$ between the atmosphere (as a GHG) and at the surface were split. Specifically, for the combined effect, one can use combined runs (atmosphere + surface increased CO_2 concentrations, 1pctCO_2), in which CO_2 increased by one percent every year for 150 years. A second simulation used prescribed historical CO_2 at the surface, atmospheric CO_2 as a GHG is allowed to increase (esmFdbk1 experiment). A third opposite experiment (esmFixClim1 experiment) in which CO_2 was prescribed in the

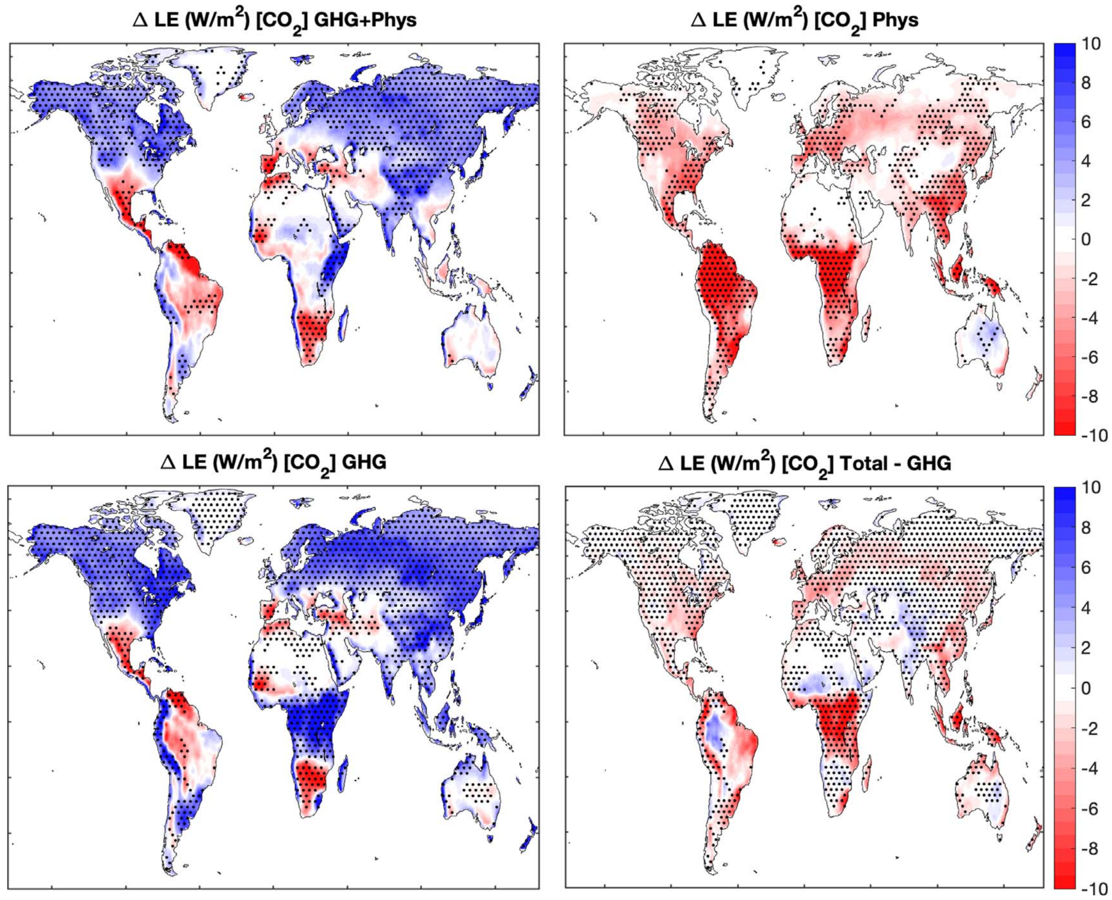

Figure 3. Predicted change due to rising CO$_2$ on surface latent heat flux (evapotranspiration) based on eight Earth system models. 140 year change based on a linear regression. Top left: [CO$_2$] imposed as both a greenhouse gas (GHG) and at the surface (physiology), Top right: [CO$_2$] imposed at the surface (physiology), Bottom left: [CO$_2$] imposed as a GHG. Bottom right: [CO$_2$] imposed as both a greenhouse gas (GHG) and at the surface (physiology)–GHG effects (to test linearity in physiological effects). We used all eight available models not sharing clear lineage (such as different model version or different horizontal resolutions). Models were interpolated to a common 1° × 1° grid, using nearest-neighbor interpolation. Values were averaged over a 20 year time window to minimize the impact of interannual variability. Stippling represents regions where more that five models agree in terms of sign.

atmosphere as the preindustrial value and increased at the surface only so that it should only impact biospheric processes.

Latent heat flux (i.e. evapotranspiration in energy units) increases in many regions, especially at northern latitudes, because of the GHG increased radiation and correlated change in temperature (figure 3(c)). The GHG effect on LE varies spatially, with typically a decrease in dry regions and an increase in wet or cold (snowy) regions where higher temperature increases snowmelt and can extend the growing season. There is a predicted significant decrease (across more than 3/4 of the models) in dry regions, and especially in the Mediterranean, central America, and Southern Africa consistent with previous ESM findings (Seager *et al* 2010, 2014, Cook *et al* 2014a).

The modeled physiological effect of CO$_2$ on latent heat flux is strong in ESMs and mostly negative (because of the higher WUE), figure 3(b), especially over tropical forests. Indeed, in those regions the increase in LAI due to rising CO$_2$ is limited (because biomass is already very high) so that the primary physiological mechanism is a reduction of stomatal conductance, reducing transpiration and ET. However, in several regions the impact of physiological effects is small because of a compensating increase in LAI (Lemordant *et al* 2016, 2018), stimulated by the increase in surface [CO$_2$] (fertilization effect), which can increase evapotranspiration (Williams and Torn 2015) and compensate the reduction in stomatal conductance at higher [CO$_2$]. The GHG effects are more consistent across models (as indicated by the stippling) than the physiological effects, which are more uncertain, yet importantly of the same order of magnitude. In addition, those effects are nonlinear as assessed by the difference between the total (GHG + physiological)—GHG simulation and the direct physiological experiment.

Total soil moisture is predicted to be less impacted by changes in CO$_2$ than evapotranspiration (figure 4). Increased warming effect caused by GHG increases photosynthesis and LE (figure 3), as it increases the duration of the growing season in snow-dominated regions (Hinzman *et al* 2005, Bintanja and Andry 2017, Screen 2017, Jeong *et al* 2018). On the other hand, some currently dry regions are predicted

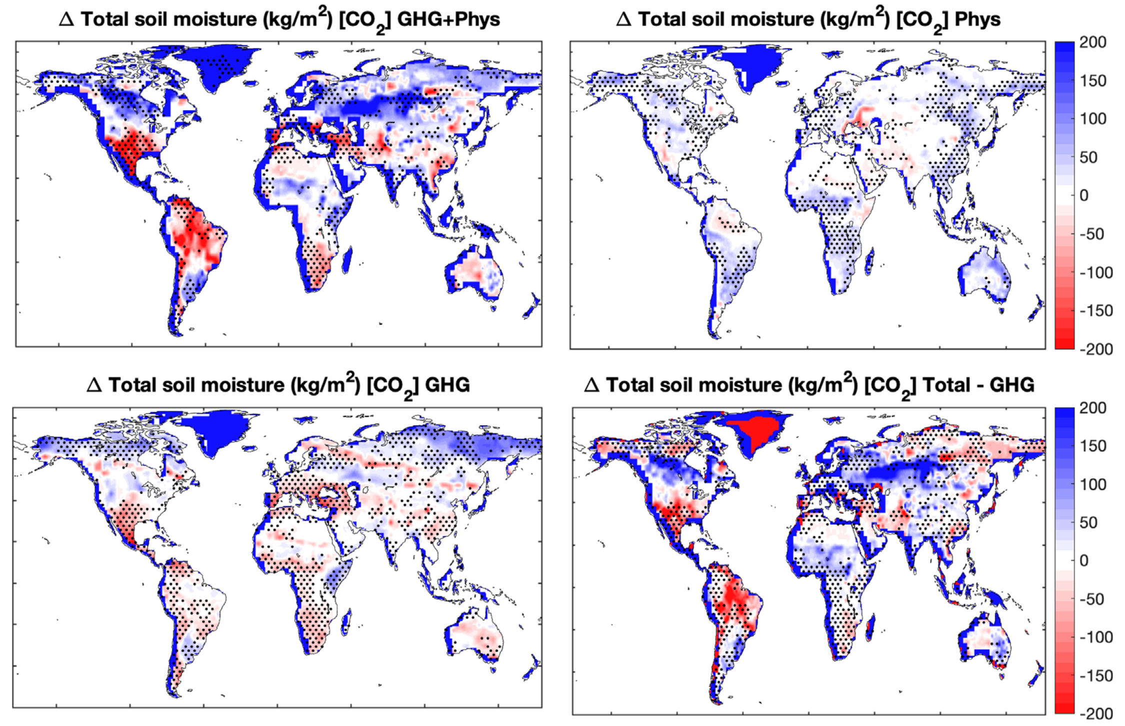

Figure 4. Same as figure 3 but on total soil moisture.

to become even drier (e.g. central America, the Mediterranean), figure 4. This is not only due to increased warming but also related changes in atmospheric circulation and moisture transport to those regions, reducing the moisture convergence over the region (Seager *et al* 2010, 2014, Cook *et al* 2014a). Increased surface physiological [CO$_2$] has an even impact on total soil moisture weaker than the GHG effect and tend to lead to water saving (figure 4(b)), whereas GHG effects tend to reduce soil moisture because of the increased atmospheric demand due to to increased radiation. In many seasonally dry regions, total soil moisture is decreasing because of a reduction in precipitation (Seager *et al* 2010, 2014, Cook *et al* 2014a) but stomatal closure partially compensate that effect (Lemordant *et al* 2016). In wet forested regions, total soil moisture tends to decrease, as a result of increased GHG atmospheric demand. Contrary to ET, most of the uncertainties in total soil moisture originate from the GHG effects rather than from physiological changes. This seemingly contradicting result with the ET impact of physiological effects is due to the compensating effects of increased biomass and decreased canopy conductance with rising [CO$_2$]. Increased biomass decreases soil moisture but decreased conductance tends on the other hand to buffer soil moisture. It is therefore clear that to correctly assess future changes in the water cycle we need better constrained models in terms of WUE (and its change), the (related) impact of [CO$_2$] of stomatal conductance, but also of changes in biomass and phenology, which varies dramatically across models. Runoff changes (figure 5) are in line with the soil moisture tendencies especially in wet regions. In dry regions though there is only limited total runoff change, likely because runoff is already low in those regions. As expected, there is also major increase in runoff in cold and snow-dominated regions because of the increased warming due to GHG. Physiological effects tend to be smaller and are mostly operating in tropical regions, with a typical increase (except in the Amazon) due to the reduction in LE due to stomatal conductance reduction (figure 3).

We thus conclude that ESMs predict a large impact of surface [CO$_2$] (physiological effects) on the water cycle in the future. Yet, the response varies drastically across models so we can only have low confidence in this future ESMs' prediction. The uncertainties are dominated by uncertainties in the physiological impact but uncertainties in the GHG effects (figures 3–5 top right) are non-negligible (figures 3–5 bottom left).

4. Discussion and challenges

This short review aimed at discussing some of what we consider important processes and challenges in observing and simulating the coupling between the water and carbon cycles. Based on this review we argue that the terrestrial water–carbon cycles have to be studied as an interconnected system, given the very large impact they have on each other. Specifically, we emphasized that physiological effects due to increased

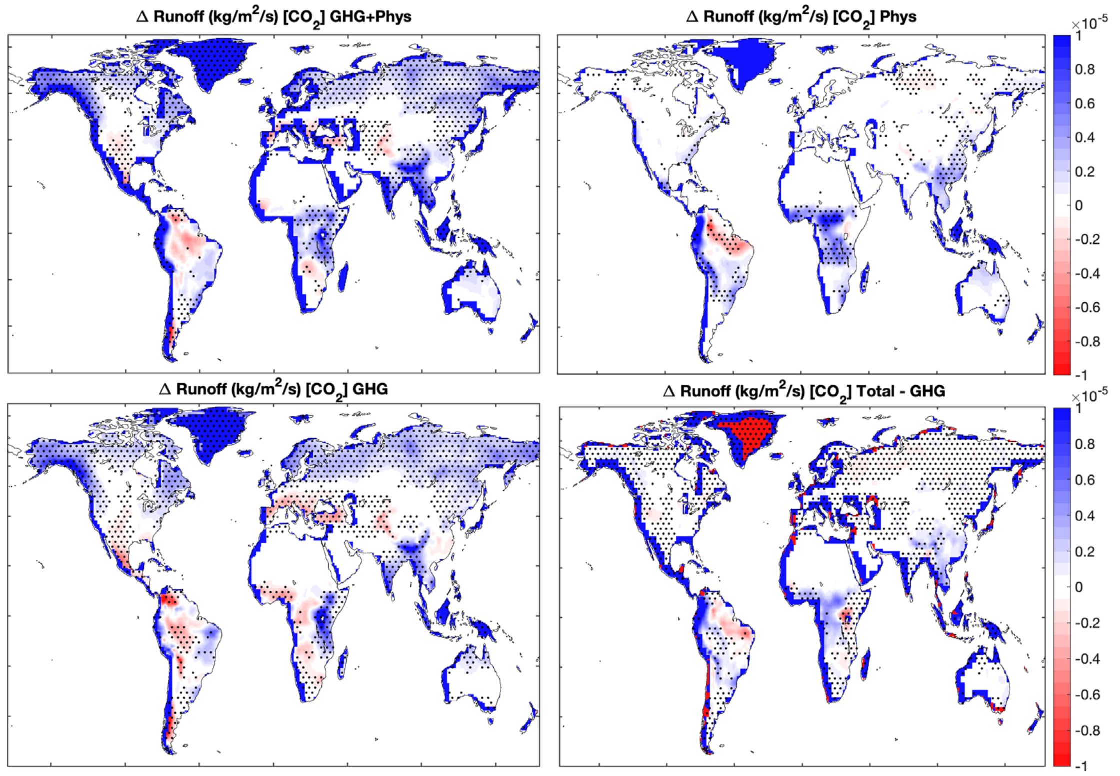

Figure 5. Same as figure 3 but on runoff.

[CO_2] appear in model simulations to be a dominant control of the future water cycle and that the representation of vegetation water stress places key constraints on the capacity of continents to act as a future CO_2 sink. These predictions are however highly uncertain across models, and therefore need to be better constrained to better predict the future carbon and water cycles.

There are however numerous challenges related to these two carbon–water coupling issues. First, most current studies only have limited observational constraints on the effect of increasing [CO_2] at the ecosystem scale and especially on WUE. FACE experiments have helped better understand the impact of rising [CO_2] but omitted land–atmosphere feedbacks, and therefore increased temperature and VPD due to changes in the surface energy partitioning (Lemordant *et al* 2016). This is due to the small footprint of the experiment, as well as the short duration of the experiments (a few years) places limits on our understanding of long-term (multidecadal) time scale response of ecosystem WUE to rising [CO_2] (Mastrotheodoros *et al* 2017, Reich *et al* 2018). Isotopic inferences on WUE might be one of our better constraints on those long-term changes (Frank *et al* 2015) as well as long-term eddy-covariance observations which are now starting to cover a few decades at selected sites (Keenan *et al* 2013). Long-term remote sensing observations of SIF and estimates of ET might help better constrain those changes in WUE (Alemohammad *et al* 2017). There are still challenges on the way though, such as estimating changes in light use efficiency with increased [CO_2] from remote sensing platforms (Gentine and Alemohammad 2018, Zhang *et al* 2018b), as well as partitioning transpiration from total ET, which remains highly uncertain (Jasechko *et al* 2013, Michel *et al* 2016, Miralles *et al* 2016, Wei *et al* 2017, Lian *et al* 2018).

Regarding water stress, it appears critical to correctly and more physically represent it in models, given its very large impact on carbon and water fluxes (Verhoef and Egea 2014). Recent model developments have started to incorporate more realistic plant hydraulics representation of water stress (Eller *et al* 2018, Kennedy *et al* 2018). Yet, one challenge is to constrain those models, especially at the global scale. Recent advances in satellite remote sensing observations are starting to offer unprecedented constraints on those processes, globally. Microwave remote sensing can be used to retrieve surface soil moisture (Barre *et al* 2008, Entekhabi *et al* 2010, Kolassa and Aires 2012, Chan *et al* 2016, Kolassa *et al* 2016, Colliander *et al* 2017, Dorigo *et al* 2017, Kolassa *et al* 2017a, 2017b) as well as to place constraints on vegetation hydraulic strategies (water conservative versus water intensive) (Konings and Gentine 2016, Konings *et al* 2017). In addition, solar-induced fluorescence places key constraints on the rate of photosynthesis at the ecosystem scale (Joiner *et al* 2011b, Frankenberg *et al* 2012, Joiner *et al* 2013, Lee *et al* 2013, Parazoo *et al* 2013, Frankenberg *et al* 2014, Guanter *et al* 2014, Lee *et al* 2015, Guanter *et al* 2015). GRACE and

GRACE follow-on (FO) missions (Andersen *et al* 2005, Humphrey *et al* 2016, Annette Eicker 2018, Humphrey *et al* 2018) allow estimating total TWS and microwave remote sensing missions (SMOS, SMAP, AMSR-2) allow monitoring surface soil moisture and vegetation water storage.

There are still important challenges on the way, though. Understanding changes in ecosystem respiration remains a challenge, especially at the global scale. Indeed, we currently do not have the capacity to monitor it globally, unlike solar-induced fluorescence for photosynthesis, to constrain its response to soil moisture and rising [CO_2]. There has been progress based on *in situ* observations though (Heskel *et al* 2016, Huntingford *et al* 2017, Bond-Lamberty *et al* 2018, Yan *et al* 2018). In addition, CO_2 annual growth rates permit to obtain an integrated view of continental CO_2 exchanges yet do not permit to correctly zoom into regional information (Keenan *et al* 2016, Wang *et al* 2017). Data assimilation with multiple observational constraints on the carbon cycle are still our best constraint on ecosystem exchange and thus on respiration processes at coarse regional scales (Kawa 2004, Baker *et al* 2006, Thum *et al* 2017, MacBean *et al* 2016, 2018).

Another challenge is that VPD and soil moisture are inherently coupled through land–atmosphere interactions (Zhou *et al* 2018). As atmospheric temperature and dryness increases with rising [CO_2], VPD rise will be more disconnected from changes in soil moisture and are likely to have a strong impact on photosynthesis. Therefore, it is critical to correctly disentangle the respective impacts of VPD and soil moisture, especially on fluxes and ecosystem conductance, at the ecosystem scale but so far this has been a challenge because of this strong coupling. New statistical tools to decompose causes and effects might be essential to better understand their respective impacts (Granger 1980, Sugihara *et al* 2012). Dedicated *in situ* experiment with either dry conditions or increased VPD (Grossiord *et al* 2017) might also be critical to better disentangle those effects.

Understanding the impact and response of interannual and decadal time scales variations on ecosystems remains a grand challenge. Indeed, the coupling between the water and carbon cycles is present at multiple time scales from short (leaf–gas exchange), to annual (carbon allocation, changes in xylem, structure…) to interannual (species composition, mortality, legacy…). Again, long-term remote sensing and long-term *in situ* observations could place key constraints on those changes.

Extremes are becoming more extreme with increased GHG concentrations, such as droughts, heat waves, extreme precipitation and runoff. These extreme events will strongly limit the capacity of continental carbon uptake, directly by limiting ecosystem photosynthesis and increasing ecosystem respiration but also through changes in disturbances such as fires (Williams *et al* 2014, Seager *et al* 2015, Williams and Abatzoglou 2016, Williams *et al* 2018), wind damage (Silvério *et al* 2019) or through large-scale mortality (McDowell 2011, Williams *et al* 2013, Adams *et al* 2017). Beside the occurrence of more drought events, systematic high temperature and VPD at levels unprecedented in our recent history will challenge our predictive capacity, which is based mostly on historical, lower temperature and VPD conditions. Dedicated field experiments could be a solution to better understand the impact of high temperature, VPD and the occurrence of intense droughts on ecosystems (Grossiord *et al* 2017).

Finally, a key component of the future carbon and water cycles, omitted or oversimplified in current generation of ESMs is land management. Current models include land-use land cover changes and potential scenarios for their changes (Lawrence *et al* 2016), which are essential for improved terrestrial prediction but the impact of land management still remains an open question. Data availability to constrain it (e.g. water consumption for agriculture, industry) still remains an issue (Ho *et al* 2016, 2017), even if it is improving in many regions of the globe and if remote sensing observations have highlighted that they are the main contributors to overall global greening of the planet (Chen *et al* 2019). Including these processes in ESMs will be important given the pressure on food production due to rising population and increased temperature and VPD pressure on crop production (Ziervogel and Ericksen 2010, Butler and Huybers 2012, Lobell *et al* 2013, Asseng *et al* 2015, Deryng *et al* 2016, Osborne 2016).

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