



## Review Article

The uncertain role of rising atmospheric CO<sub>2</sub> on global plant transpiration

Sergio M. Vicente-Serrano<sup>a,\*</sup>, Diego G. Miralles<sup>b</sup>, Nate McDowell<sup>c,d</sup>, Tim Brodrigg<sup>e</sup>,  
Fernando Domínguez-Castro<sup>f,g</sup>, Ruby Leung<sup>c</sup>, Akash Koppa<sup>b</sup>

<sup>a</sup> Instituto Pirenaico de Ecología, Spanish National Research Council, Zaragoza, Spain

<sup>b</sup> Hydro-Climate Extremes Lab (H-CEL), Ghent University, Ghent, Belgium

<sup>c</sup> Atmospheric Sciences and Global Change Division, Pacific Northwest National Lab, PO Box 999, Richland, WA 99352, United States of America

<sup>d</sup> School of Biological Sciences, Washington State University, PO Box 644236, Pullman, WA 99164-4236, United States of America

<sup>e</sup> School of Biological Sciences, University of Tasmania, Hobart, Tasmania, Australia

<sup>f</sup> Aragonese Agency for Research and Development Researcher (ARAID), Zaragoza, Spain

<sup>g</sup> Department of Geography, University of Zaragoza, Zaragoza, Spain



## ARTICLE INFO

## Keywords:

Transpiration  
CO<sub>2</sub>  
Atmospheric water demand  
Earth system models  
Climate change  
Projections

## ABSTRACT

As CO<sub>2</sub> concentration in the atmosphere rises, there is a need for improved physical understanding of its impact on global plant transpiration. This knowledge gap poses a major hurdle in robustly projecting changes in the global hydrologic cycle. For this reason, here we review the different processes by which atmospheric CO<sub>2</sub> concentration affects plant transpiration, the several uncertainties related to the complex physiological and radiative processes involved, and the knowledge gaps which need to be filled in order to improve predictions of plant transpiration. Although there is a high degree of certainty that rising CO<sub>2</sub> will impact plant transpiration, the exact nature of this impact remains unclear due to complex interactions between CO<sub>2</sub> and climate, and key aspects of plant morphology and physiology. The interplay between these factors has substantial consequences not only for future climate and global vegetation, but also for water availability needed for sustaining the productivity of terrestrial ecosystems. Future changes in global plant transpiration in response to enhanced CO<sub>2</sub> are expected to be driven by water availability, atmospheric evaporative demand, plant physiological processes, emergent plant disturbances related to increasing temperatures, and the modification of plant physiology and coverage. Considering the universal sensitivity of natural and agricultural systems to terrestrial water availability we argue that reliable future projections of transpiration is an issue of the highest priority, which can only be achieved by integrating monitoring and modeling efforts to improve the representation of CO<sub>2</sub> effects on plant transpiration in the next generation of earth system models.

## 1. Introduction

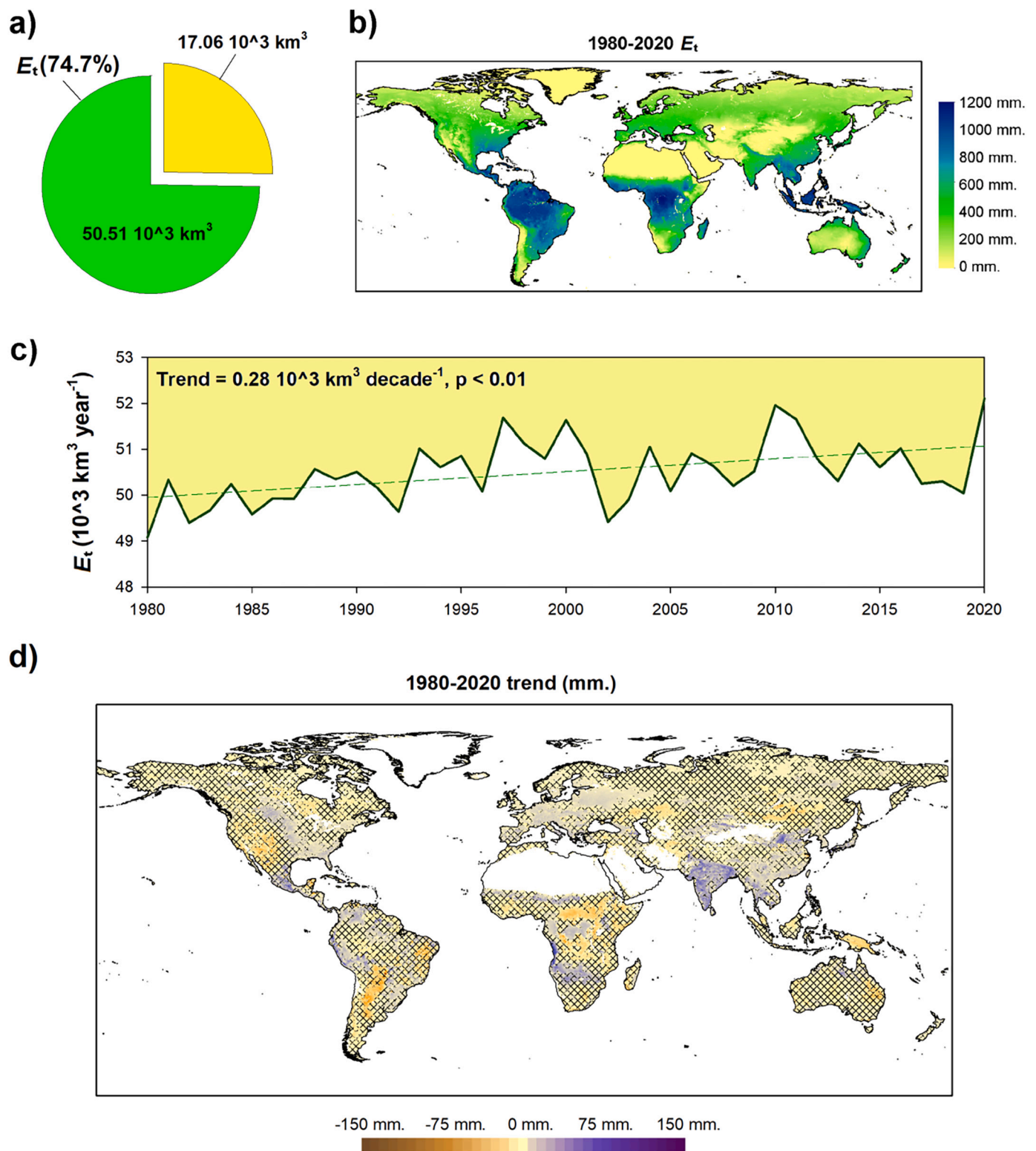
Terrestrial evaporation ( $E$ ), defined as total water flux from land to the atmosphere, is one of the most important elements of the global water cycle (Trenberth et al., 2007). Globally,  $E$  amounts to two-thirds of the total precipitation over land (Oki and Kanae, 2006), strongly affecting soil water availability, runoff, groundwater, plant photosynthesis, and vegetation growth (Wang and Dickinson, 2012). Moreover,  $E$  modulates the atmospheric boundary layer growth during the day, influencing the generation, development, and spatiotemporal propagation of convective storms, heat waves, and droughts (Miralles et al., 2019). Over larger scales, it regulates processes that are paramount for climate behavior, such as the water vapor and cloud feedbacks (Rind

et al., 1991). Different components or sources of  $E$  are usually considered individually due to their disparate nature: plant transpiration ( $E_t$ ), rainfall interception loss ( $E_i$ ), and direct evaporation of water from soils ( $E_s$ ), water bodies, and snow-covered surfaces. According to satellite-, isotope-, and model-based studies,  $E$  is dominated by  $E_t$  at the global scale, with average contributions of  $E_t$  to  $E$  typically ranging between 60–80% (Fig. 1a) (Jasechko et al., 2013; Wei et al., 2017). At the global scale, the  $E_t$  flux is  $\approx 50.5 \cdot 10^3 \text{ km}^3 \text{ year}^{-1}$  (Fig 1a), which is larger than the discharge from all the world's rivers added together (Dorigo et al., 2021). For this reason,  $E_t$  determines global water availability for human and ecological uses.

The different components of  $E$  often diverge in their core environmental drivers.  $E_s$  is essentially determined by soil and surface water

\* Corresponding author.

E-mail address: [svicen@ipe.csic.es](mailto:svicen@ipe.csic.es) (S.M. Vicente-Serrano).



**Fig. 1.** a) 1980-2020 global average of annual magnitude of  $E_t$  and percentage regarding total  $E$ . The data is obtained from a combined remote sensing and modelling-based approach to obtain the GLEAM v3 dataset (<https://www.gleam.eu/>) (Miralles et al., 2011), b) Spatial distribution of 1980-2020 average annual  $E_t$  ( $\text{mm m}^{-2}$ ), c) 1980-2020 trend in annual  $E_t$  ( $\text{km}^3 \text{ decade}^{-1}$ ) obtained by means of a linear regression analysis, d) 1980-2020 trend in the annual  $E_t$  obtained by means of a linear regression analysis ( $\text{mm m}^{-2} \text{ 41 years}^{-1}$ ). Strip represent areas in which trends are not statistically significant (tau Mann-Kendall test considering serial correlation, p-value > 0.05)

availability and by the meteorological conditions that dictate atmospheric evaporative demand (AED) (Vicente-Serrano et al., 2020a), which is the potential of the atmosphere to vaporize water as a function of its radiative (i.e., net solar radiation) and aerodynamic (air temperature, wind speed and air humidity) state.  $E_t$  in turn, is mainly controlled by the characteristics of rainfall and vegetation structural properties such as leaf area and storage capacity (Teklehaimanot and Jarvis, 1991). The spatial variability in  $E_t$  (Fig. 1b) reflects vegetation density, atmospheric physics (i.e., precipitation and AED), soil water availability, atmospheric  $\text{CO}_2$  concentration ( $a\text{CO}_2$ ), and plant physiological mechanisms (Sitch et al., 2003). There is large inter- and intra-specific variation in plant responses to these environmental conditions due to many interacting biochemical and biophysical processes (Flo et al., 2021), resulting in non-linear positive and negative feedbacks among the different drivers and mechanisms involved (Katul et al., 2012; Xu et al., 2016b).

Due to its importance for hydrology and climate, it is crucial to evaluate the response of  $E_t$  to ongoing global changes. Our understanding of the degree that different variables and mechanisms drive  $E_t$  remains incomplete, and these potential mechanisms and their influence on  $E_t$  are expected to change as climate changes. Anthropogenic contributions to radiative forcing through increased  $a\text{CO}_2$  are expected to influence precipitation patterns (Dai et al., 2018; Douville et al., 2021) and increase AED (Brutsaert, 2017; Vicente-Serrano et al., 2020a), and thus affect the frequency and severity of drought events (Cook et al., 2018; Dai et al., 2018). Additionally, enhanced  $a\text{CO}_2$  has complex plant physiological influences, which are interdependent with the radiative effect of  $a\text{CO}_2$ . Thus, it is necessary to conduct an integrated assessment of the influence of  $a\text{CO}_2$  on global  $E_t$  based on both empirical and modeling studies. The mechanisms underlying impacts of increasing  $a\text{CO}_2$  on  $E_t$  involve plant, soil, and atmospheric processes at different scales, i.e. at leaf, plant, and ecosystem scales. Rising  $a\text{CO}_2$  could directly alter leaf stomatal conductance ( $g_s$ ), or change the leaf area and canopy structure, or even influence ecosystems at larger scales as a consequence of changes in water availability and temperature.

The challenge to assess all these complex processes and interactions at different spatial scales is amplified by the difficulties to measure  $E_t$  in the field. Different direct and indirect methods exist to derive  $E_t$ , such as partitioning methods based on eddy-covariance (Baldocchi et al., 2001; Nelson et al., 2020) and sapflow measurements (Poyatos et al., 2016), among others (Stoy et al., 2019). These methods are not always comparable and provide spatially fragmented information (Wei et al., 2017). For this reason, model-based approaches using remote sensing and reanalysis data as inputs have been developed in recent years to estimate  $E_t$ . Global studies using these data often suggest that both  $E$  and  $E_t$  have increased over the past four decades (Fig. 1c) (Miralles et al., 2014; Zhang et al., 2016). This increase is spatially variable (Fig. 1d) (Swann and Koven, 2017; Zeng et al., 2018) but dominant and consistent with the observed global increase in precipitation (Zhang et al., 2007) and AED (Brutsaert, 2017), and physiological regulation by increasing leaf area (Zeng et al., 2018).

Given the large implications for global ecosystems, water resources availability, and the climate system, systematizing the existing uncertainties and the knowledge gaps is an important step to disentangle the complex conundrum related to the influence of enhanced  $a\text{CO}_2$  on global  $E_t$ . Fig. 2 shows a scheme of the main influences of increased  $a\text{CO}_2$  on  $E_t$  by means of different direct and indirect mechanisms and feedbacks, including both positive (red lines) and negative (blue lines) influences. Fatichi et al. (2016) analyzed the partition of direct and indirect effects of  $a\text{CO}_2$  on  $E_t$ , and concluded these effects tend to compensate each other, with small net  $E_t$  changes expected in wet regions and negligible in semiarid ecosystems. In this study, we review the state of knowledge regarding the interactions and feedbacks among the complex physiological and radiative processes induced by  $a\text{CO}_2$  changes, and their potential contribution to global changes in  $E_t$ .

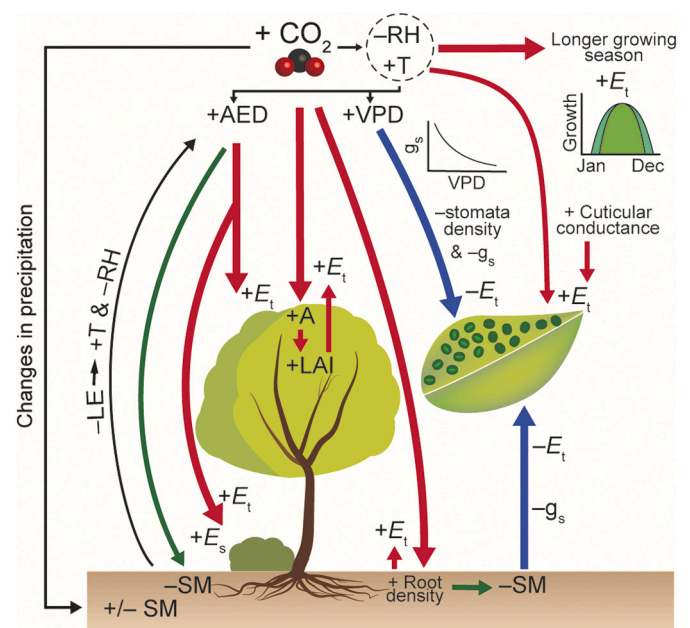


Fig. 2. Scheme including the direct and indirect effects of enhanced  $a\text{CO}_2$  on plant transpiration ( $E_t$ ).  $E_s$ : soil evaporation,  $g_s$ : diffusive conductance of leaves, A: Photosynthesis, LAI: Leaf Area Index, AED: Atmospheric Evaporative Demand, LE: Latent Heat, SM: Soil moisture, VPD: Vapor Pressure Deficit, T: air Temperature, RH: Relative Humidity. Red lines represent positive influence on  $E_t$ . Blue lines represent a negative influence on  $E_t$ . Black lines represent climate fluxes and influences.

## 2. Physiological and morphological effects of $a\text{CO}_2$

### 2.1. Direct influence of $a\text{CO}_2$ on leaf surface conductance

The majority of  $E_t$  occurs through the stomatal pores that cover leaf surfaces and regulate the diffusive conductance to water vapor and  $\text{CO}_2$  (Brodribb and McAdam, 2017). Enhanced  $a\text{CO}_2$  has been shown to reduce  $g_s$  at the leaf scale (Ainsworth and Rogers, 2007; Ceulemans and Mousseau, 1994), resulting in a larger ratio of photosynthesis to transpiration (i.e. water use efficiency (Norby et al., 1999)); this has been supported by a myriad of experimental studies (Drake et al., 1997; Gimeno et al., 2016; Keel et al., 2006; Long et al., 2004). This influence of  $a\text{CO}_2$  on  $g_s$  underlies the predicted reduction of  $E_t$  under enhanced  $a\text{CO}_2$  by the current generation of climate models (Roderick et al., 2015). Projections from Earth System Models (ESMs) have suggested that aridity and drought severity in the future could be ameliorated by the reduction of  $E_t$  caused by the increased water use efficiency by plants (Berg and McColl, 2021; Berg and Sheffield, 2018; Greve et al., 2019; Lemordant et al., 2018; Lian et al., 2021; Scheff, 2018; Swann, 2018; Swann et al., 2016; Yang et al., 2019).

However, the response of  $g_s$  to  $a\text{CO}_2$  – and the degree to which this effect propagates to global  $E_t$  – remains uncertain despite its universal representation in ESMs. According to field studies, the control of  $g_s$  by  $a\text{CO}_2$  is not homogeneous across world biomes and plant species (Batke et al., 2020; Ward et al., 2013). There are noticeable knowledge gaps in equatorial and tropical biomes, where some experimental studies have shown no sensitivity of  $g_s$  to enhanced  $a\text{CO}_2$  (Wesolowski et al., 2020), or even a positive response (Purcell et al., 2018). Studies in mid and high latitudes also suggest that mature forests show a much smaller response of  $g_s$  to  $a\text{CO}_2$  than young trees (Körner et al., 2005; Medlyn et al., 2001). Important differences in the  $g_s$  responses to  $a\text{CO}_2$  have been observed between herbs, shrubs, and trees (Ainsworth and Long, 2005; Ainsworth and Rogers, 2007), and also between angiosperms and gymnosperms (Brodribb et al., 2009; Klein and Ramon, 2019) have been reported. The average percentage reduction of  $g_s$  in response to  $a\text{CO}_2$  varies from 50%



in dense meadows, to 15% in broadleaved forests, and to less than 10% in coniferous forests (Körner et al., 2007). This response is seasonally dependent (Lauriks et al., 2020) and non-linear (Batke et al., 2020; Medlyn et al., 2011), as it tends to saturate for high  $aCO_2$ , just as  $CO_2$  stimulation of photosynthesis saturates (De Kauwe et al., 2021). Moreover, arid vegetation tends to respond in a different manner to  $aCO_2$  (Zhou et al., 2013), and even increases in  $g_s$  have been observed under enhanced  $aCO_2$  in arid plants (Morgan et al., 2004; Pataki et al., 2000).

The extent to which the  $g_s$  response to  $aCO_2$  is translated to changes in  $E_t$  is still a subject of debate. Some studies argue that this mechanism would substantially reduce  $E_t$  (Leakey et al., 2009), particularly in herbaceous crop landscapes (Bernacchi et al., 2007) and closed forests (Warren et al., 2011). These results suggest soil water savings (Franzaring et al., 2010) and the increase of runoff and other hydrologic pools and fluxes in the future (Betts et al., 2007; Roderick et al., 2015). Nevertheless, there are still important uncertainties as some experimental studies also suggest that the expected reduction of  $E_t$  as consequence of the reduction in  $g_s$  in response to enhanced  $aCO_2$  can be as low as 5% for a doubling of  $aCO_2$  from the preindustrial values (Körner et al., 2007; Leuzinger and Körner, 2010). Notably, this reduction in  $E_t$  could be mostly limited to seedlings (Lauriks et al., 2020), which are only responsible for a minor component of global  $E_t$  due to their limitations in number and coverage. Moreover, there is growing evidence that the  $g_s$  response to  $aCO_2$  may already be close to saturation (Batke et al., 2020). Studies in areas that have not experienced changes in vegetation coverage and precipitation do not show changes in streamflow that would support decreased  $E_t$  in response to  $aCO_2$  increases in the past decades, or at least would indicate that if  $aCO_2$  had a negative influence it was overcome by the effect of other drivers such as the increased temperatures (Knauer et al., 2017; Yang et al., 2021).

## 2.2. Influence of $aCO_2$ on plant morphology

The plant morphological changes in response to enhanced  $aCO_2$  occur at different levels, from the leaf structure to the entire plant. Plants can adapt to increased  $aCO_2$  by reducing stomatal density of the leaves, which limits maximum  $g_s$  (Lammertsma et al., 2011). However, the importance of this mechanism under future scenarios of increased  $aCO_2$  is also highly uncertain (Körner, 2017). Recent evidence suggests that it could saturate under elevated  $aCO_2$  (García-Amorena et al., 2006; Tricker et al., 2005), while other studies indicate important differences across species and elevation ranges (Ainsworth and Rogers, 2007), including divergent trends, with a positive correlation between stomatal density and  $aCO_2$  in some species and families (Jordan et al., 2020; Reid et al., 2003). The average reduction in stomatal density in response to elevated  $aCO_2$  at a global scale appears to be below 5% (Xu et al., 2016a). This makes it unlikely that morphological changes at the leaf level, driven by enhanced  $aCO_2$ , would significantly influence global  $E_t$  trends.

Other aspects of plant physiology are likely to be more sensitive to enhanced  $aCO_2$ . In the absence of changes in meteorological drivers or soil moisture content, higher  $aCO_2$  would promote photosynthesis ( $A$ ), and increased leaf area and plant growth (McDowell et al., 2020; Walker et al., 2020), which is supported by multiple free air  $CO_2$  enrichment and chamber experiments (e.g., Ainsworth and Long, 2005; Drake et al., 1997; McCarthy et al., 2007; Pan et al., 2022). This effect is also not homogeneous across ecosystems: mature forests in moderate rainfall regions have shown small changes in leaf and root mass (Jiang et al., 2020) compared with plant communities located in water limited and transitional areas (Lauriks et al., 2020; Zhu et al., 2018).

An increase in vegetation coverage and leaf area in response to  $aCO_2$  is expected to have a direct positive influence on global  $E_t$  (Zeng et al., 2018). Although there are few long-term experiments that combine enriched  $aCO_2$  and changes in plant coverage, current literature suggests that enhanced vegetation growth could offset, at least partially, the direct influence of  $aCO_2$  on  $E_t$  that is mediated by changes in  $g_s$  (Duan

et al., 2014). The degree to which this happens would vary as a function of vegetation type and characteristics (e.g., mature vs. young forests, wet vs. semiarid ecosystems) (Cheng et al., 2017; Duan et al., 2018; Fatichi et al., 2016; Guerrieri et al., 2019; Jiang et al., 2021; Tricker et al., 2005). This assessment is reinforced by several studies in hydrological catchments experiencing increases in plant coverage, which have shown an overall reduction in streamflow as a consequence of enhanced  $E_t$  given more water consumption by vegetation (Filoso et al., 2017; Peña-Angulo et al., 2021; Vicente-Serrano et al., 2021). Thus, although there is evidence of a global increase in plant water use efficiency ( $WUE$ ) – defined as the photosynthesis per unit of water transpired ( $A/E_t$ ) – over recent decades (Mathias and Thomas, 2021; Walker et al., 2020), the enhancement of photosynthesis in response to  $aCO_2$  seems to be the dominant driver of this  $WUE$  increase in comparison to a hypothetical reduction in  $E_t$  in response to  $aCO_2$  (Adams et al., 2020; Guerrieri et al., 2019; Marchand et al., 2020; Mathias and Thomas, 2021). Finally,  $aCO_2$  has a noticeable effect on plant root systems, characterized by higher root length and density of fine roots (Iversen, 2010; Nie et al., 2013; Uddin et al., 2018) as consequence of  $aCO_2$  effects on carbon cycling by means of root respiration and rhizodeposition (Pritarch et al., 2008). This leads to an increase in the capacity of plants to access soil water, which could enhance  $E_t$ , particularly in water limited environments and during periods of surface water stress everywhere. Moreover, higher  $E_t$  as consequence of more developed root systems would manifest above ground through both increased  $g_s$  and increased leaf area.

All these effects of  $aCO_2$  on plant morphology would suggest a positive influence of  $aCO_2$  on  $E_t$  mediated by higher leaf area and deeper root systems that could counteract the influence of  $aCO_2$  on  $E_t$  mediated by  $g_s$  (see Sect. 2.1), adding uncertainty and complexity when attempting to predict how  $aCO_2$  affects  $E_t$  trends. Finally, there can also be impacts of possible limitations related to plant nutrient availability. In particular human-induced reductions in the availability of phosphorus and nitrogen may limit plant  $A$  and have been suggested as a constraint on vegetation growth and  $E_t$  (Peñuelas et al., 2013; Sardans and Peñuelas, 2012), adding a new layer of complexity when assessing the integral influence of  $aCO_2$  on  $E_t$ .

## 3. Radiative effects of $aCO_2$

### 3.1. Impacts of $aCO_2$ driven by changes in temperature, atmospheric demand and water availability

The direct and indirect physiological and plant morphological effects of  $aCO_2$  described above overlap with the influence that enhanced  $aCO_2$  has on  $AED$  and soil water deficit (Xu et al., 2013). Near-surface air temperature will increase in the future globally (IPCC, 2021), while, over land, relative humidity ( $RH$ ) is expected to decrease (Byrne and O’Gorman, 2018). Precipitation is projected to increase on average, although with large spatial variability and projected declines in many subtropical regions (IPCC, 2021); meanwhile, periods of precipitation deficits are expected to be longer worldwide (Pendergrass et al., 2017).

Changes in temperature and vapor pressure deficit ( $VPD$ ), which is the difference between the actual and the saturation vapor pressure of the air, are strongly relevant for  $E_t$ , not only as drivers of  $AED$ , but also as modulators of the direct influence of enhanced  $aCO_2$  on  $g_s$  (Leuzinger and Körner, 2007). Plants respond to increasing  $VPD$  through reductions in  $g_s$  (Grossiord et al., 2020; Medlyn et al., 2001). As for most physiological responses, the effect of  $VPD$  on  $g_s$  is strongly dependent on species (Körner et al., 2007; Sinclair et al., 2017), xylem and leaf characteristics (Klein, 2014; Martins et al., 2016), and plant height (Lansu et al., 2020). Nevertheless, although high  $VPD$  causes a reduction in  $g_s$ , this effect is not generally strong enough to prevent a net increase in  $E_t$ , due to the increased  $AED$ , in most vegetation types (Grossiord et al., 2020; Massmann et al., 2019; Sinclair et al., 2017).  $E_t$  is thought to show a linear response to  $VPD$  in the low  $VPD$  range, but follows a saturation curve at high  $VPD$  values (Beer et al., 2009; Grossiord et al., 2020; Motzer et al.,

2005). It is necessary to consider the joint influences of changes in  $VPD$  and  $aCO_2$  on  $E_t$ . Existing studies based on chamber and free-air  $CO_2$  enrichment experiments in forests and grasslands suggest that the potential enhanced  $E_t$  caused by increases in  $VPD$  could counteract potential  $E_t$  reductions linked to stomatal response to  $aCO_2$  and  $VPD$  itself (Hasper et al., 2016; Morgan et al., 2011), and that  $aCO_2$ -driven effects in  $g_s$  and  $E_t$  could be only relevant at conditions of low  $AED$  (Leuzinger and Körner, 2007), basically during periods in which a low  $E_t$  is recorded and when the net effects of  $aCO_2$  would be less relevant. This suggests a dominance of the potential effects of  $VPD$  on  $E_t$  over the direct influence of  $aCO_2$  on  $E_t$  via  $g_s$  (Duan et al., 2014; Hasper et al., 2016; Jiao et al., 2019).

There are large uncertainties in the response of vegetation to  $VPD$  in tropical regions, which are strongly relevant for global  $E_t$ . In these areas, although  $g_s$  also shows high sensitivity to  $VPD$  variations (Ghimire et al., 2018; Kosugi et al., 2012; Mendes and Marengo, 2017; Slot and Winter, 2017), the vast majority of experimental studies show a net positive response of  $E_t$  to  $VPD$  (Granier et al., 1996; Igarashi et al., 2015; McJannet et al., 2007; Siddiq et al., 2017; Siddiq and Cao, 2016; Vourlitis et al., 2008; Wallace and McJannet, 2010; Yoshifuji et al., 2020), and although there are important differences among the different forest types of these regions (Gotsch et al., 2016; Grossiord et al., 2019; McJannet et al., 2007), only a few studies suggest a near neutral response (Fang et al., 2021; Marengo et al., 2014). Thus, it is suggested that in wet equatorial forests  $E_t$  is mainly driven by variations of climate, but tropical forests characterised by a dry season, would show a more dominant role of  $g_s$  on  $E_t$  (Costa et al., 2010).

Although several uncertainties remain, most studies based on controlled experiments support the hypothesis that under a strong increase in  $VPD$  – such as observed in recent decades and projected in the future due to the radiative forcing induced by  $aCO_2$  – global  $E_t$  would primarily be controlled by elevated  $AED$ . This conclusion is consistent with observational studies, since the changes in precipitation (Liu et al., 2021) and the increase in  $AED$  (Brutsaert, 2017; Miralles et al., 2014) have been suggested as the dominant drivers of the estimated  $E_t$  increase over the last two decades.

Moreover, the effect of  $aCO_2$  on  $E_t$  is also dependent of soil water availability. Some studies in mid and high latitudes have suggested that soil water availability has a stronger influence on  $E_t$  than the physiological effects of  $aCO_2$  (Hasper et al., 2016; Leuzinger and Körner, 2010). Under low soil moisture, the effect of enhanced  $aCO_2$  on  $g_s$  is small (Naumburg et al., 2003; Pataki et al., 2000), since water deficits exert a larger control on  $g_s$  and on whole-plant hydraulic conductance (Bourbia et al., 2021; Grossiord et al., 2020; Xu et al., 2016b). Moreover, the relative impact of rising  $aCO_2$  and water availability on  $E_t$  differ among species depending on plant water use strategy (Martínez-Vilalta et al., 2014). Decreasing diffusive and hydraulic conductance in response to drying soils and increased  $AED$  has significant implications for  $A$  and plant mortality (see Section 3.2). Under such water stress, enhanced  $aCO_2$  is less likely to increase water use efficiency and influence  $E_t$  (Duan et al., 2014; Menezes-Silva et al., 2019; Xu et al., 2016a).

There are other relevant plant processes associated with the radiative effects of  $aCO_2$ . First is the increase in the length of plant vegetative periods as a consequence of temperature rise, a phenomenon already observed in recent decades (Parmesan and Yohe, 2003) and that may contribute to enhancing  $E_t$  (Zhang et al., 2020). In water-limited regions, this phenomenon would have limited implications on total  $E_t$  as it is mostly controlled by water availability driven by precipitation, but it can affect its seasonality (Lemordant et al., 2016). On the other hand, in humid regions, in which  $E_t$  is usually not constrained by water availability, longer vegetative periods can increase  $E_t$  (Frank et al., 2015; Lian et al., 2020). This issue must be fully considered to assess  $E_t$  scenarios as mechanistic models suggest a dominant role of this factor to explain the net increase of  $E_t$  under climate change in cold humid regions (Kirschbaum and Mcmillan, 2018).

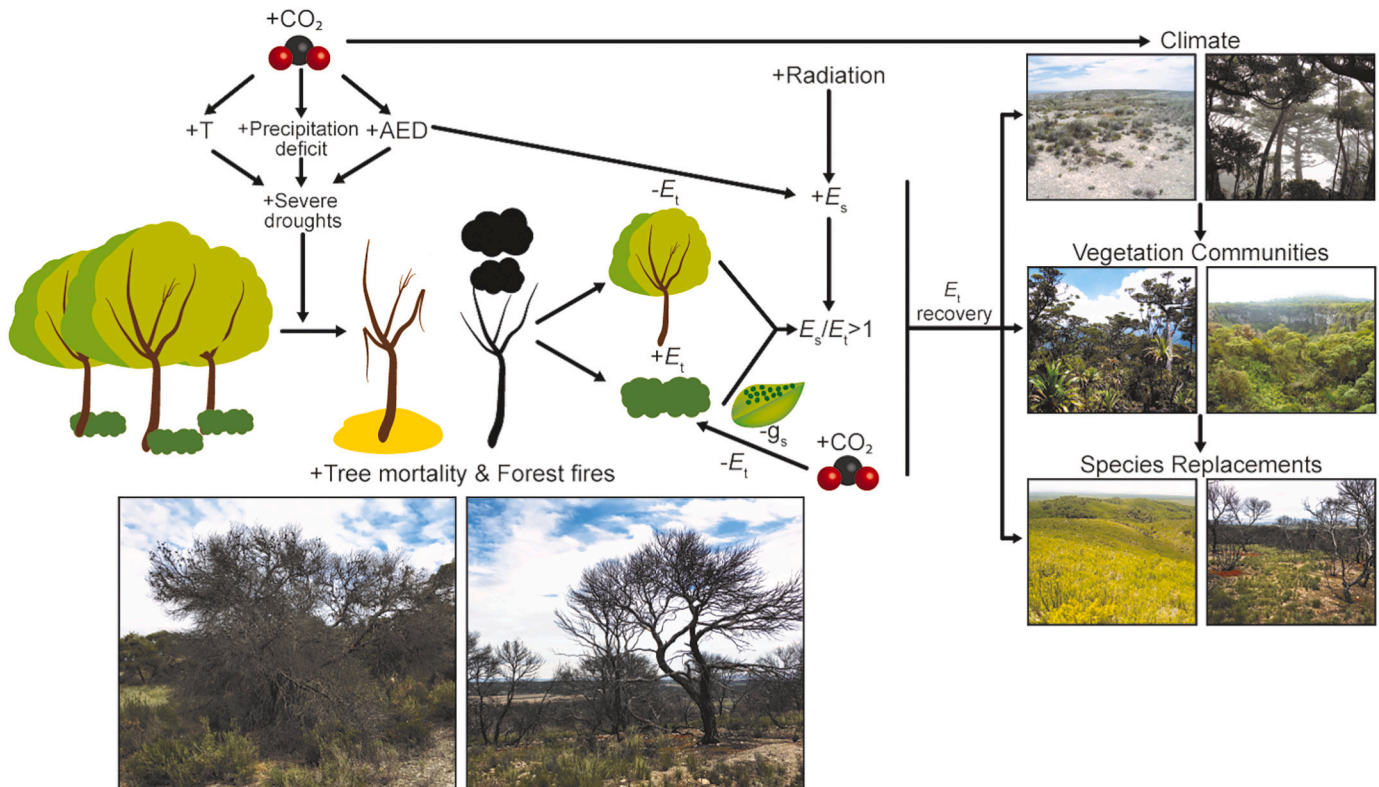
Finally, a potentially relevant influence of  $aCO_2$  radiative effects on

$E_t$  is that they increase the frequency and magnitude of extreme heat episodes (Seneviratne et al., 2014). Extreme temperatures have been reported to cause heat stress and stomatal closure, leading to a decline in both  $A$  and  $E_t$  (Grossiord et al., 2020). However, there is evidence that high temperature causes stomata to depart from their normal water-conserving behaviour, increasing  $g_s$  apparently to provide evaporative cooling to the leaf (Drake et al., 2018; Urban et al., 2017). This would explain that during periods of extreme heat and if water is available, rates of  $E_t$  far exceeding typical values have also been recently reported, and suggested as a last resort against overheating (Chaves et al., 2016; Drake et al., 2018; Krich et al., 2022). Moreover, during periods of low  $g_s$  such as in dry and hot conditions, an increase in leaf cuticular conductance with temperature causes an increase of  $E_t$  from leaf tissues (Schreiber, 2001). Although cuticular conductance is typically an order of magnitude lower than  $g_s$  (Riederer, 2006), it increases exponentially with temperature (Schreiber, 2001; Slot et al., 2021), even in plants that are well adapted to temperature extremes (Bueno et al., 2019). The impact of higher cuticular and stomatal water loss under anomalously high temperature are not considered in contemporary ESMs, but have the potential to largely affect  $E_t$  at high temperature and threaten plant survival during extreme heat (Brodrribb et al., 2020). These processes involving extreme heat will gain importance in a warmer world, and should be fully considered when assessing global  $E_t$  projections.

### 3.2. Effects of $aCO_2$ on $E_t$ caused by increased forest mortality and wildfires

Periods of precipitation deficits, soil dryness, and enhanced  $AED$  render the role of  $aCO_2$  in  $g_s$  as secondary in importance (Menezes-Silva et al., 2019; Xu et al., 2016b). In both dry and energy-limited regions, vegetation tends to be negatively affected by water deficits (Vicente-Serrano et al., 2013). Thus, an increase in forest mortality due to drought, insect outbreaks (Anderegg et al., 2013; Brodrribb et al., 2020), and forest fires (Holden et al., 2018) have been recorded in response to enhanced heat,  $AED$  and more severe droughts associated to increased  $aCO_2$ . Under future climate projections, more frequent plant mortality episodes in both dry and humid regions are projected (McDowell et al., 2016; Menezes-Silva et al., 2019). In this regard, the benefits of  $aCO_2$  on plant productivity could be offset, or even lead to a negative net effect, if enhanced  $aCO_2$  promoted plant phenotypes that are less resilient to water stress (Bobich et al., 2010), thereby increasing the vulnerability to drought (Anderegg et al., 2019). Moreover, in response to increased  $CO_2$  forcing and the associated drying and warming, wildfire events are expected to be more frequent and affect larger areas (Schoennagel et al., 2017; Scholten et al., 2021). The consequences of changes in vegetation coverage associated with enhanced tree mortality and more frequent and severe forest fires for future  $E_t$  is uncertain, and observational studies strongly differ as a function of site characteristics, vegetation type and age, and climate (Goeking and Tarboton, 2020; Zhang and Wei, 2021).

After large-scale tree mortality, not only  $E_t$ , but also  $E_i$ ,  $E_s$ , ground-water recharge, and runoff generation are affected (Adams et al., 2012; Stephens et al., 2021) (Fig. 3).  $E_t$  is usually reduced immediately after tree mortality and forest fires given the disappearance of the dominant vegetation (Anderegg et al., 2016), although the effects of both phenomena may differ, as forest fires usually affect understory vegetation and soil characteristics (Certini, 2005), leading to more intense and persistent effects on  $E_t$  (Dore et al., 2012; Ma et al., 2020). After such a disturbance, the partitioning between  $E_t$  and  $E_s$  is strongly altered;  $E_s$  can be dominant, increasing by more than 50% in comparison to previous vegetation stages (Biederman et al., 2014; Raz-Yaseef et al., 2010). Thus, in some particular cases an overall increase of total evaporation ( $E$ ) in response to plant mortality has been documented (Biederman et al., 2015; Morillas et al., 2017) and this has been attributed not only to the increase of  $E_t$  by the understory vegetation after tree mortality (Bennett et al., 2018), but also to the increase of  $E_s$  as a consequence of higher



**Fig. 3.** Effects of tree mortality and forest fires associated to the influence of enhanced  $aCO_2$ . After disturbance the period of  $E_t$  recovery will depend on different factors, which are also connected with direct and indirect atmospheric  $CO_2$  effects.

available energy, since the ground is not shaded by canopies (Biederman et al., 2014) and trees do not consume this extra energy as they transpire. Forest fires also change the albedo and aerodynamic conductance, which could dramatically alter  $E$  (Liu et al., 2019). It is necessary to stress that any given ecosystem operates within the continuum of energy to water limited circumstances, leading to energy budget balancing  $E_s$  for  $E_t$  in more semi-arid systems, that causes less than expected increases in post-disturbance runoff (Adams et al., 2012; Biederman et al., 2015; Goeking and Tarboton, 2020).

Abrupt plant changes as consequence of forest mortality and wildfires impose additional uncertainties on the future  $E_t$  trends. On the one hand, herbs usually colonize first the areas affected by disturbances, and although they have lower leaf area and shallower roots than forests, they show a stronger sensitivity of  $g_s$  to  $aCO_2$  in comparison to forests (see Section 2.1), and they tend to have a higher  $E_t$  per leaf area than tress species under well-watered conditions (Wang et al., 2019). This suggests that  $E_t$  in the new vegetation coverage could be more affected by the direct physiological influence of increased  $aCO_2$ . On the other hand, increased radiative effects associated with enhanced  $aCO_2$  are likely to be more relevant resulting in more  $E$  in the colonizing vegetation in comparison to the pre-disturbance conditions. Specifically, in semiarid forests,  $E$  does not usually change in response to tree mortality and forest fires (Adams et al., 2012; Bennett et al., 2018; Huxman et al., 2005) since the generation of runoff and groundwater is low, and the role of the changes in vegetation coverage in the partition between  $E_t$  and  $E_s$  is of less relevance for the total  $E$  (Tsamir et al., 2019). For this reason, if semiarid areas expanded globally (Huang et al., 2016a), total  $E$  would decrease as a consequence of reduced water availability, but the ratio  $E_s/E_t$  would certainly increase, making total  $E$  less sensitive to the direct and indirect physiological effects of  $aCO_2$  that affect  $E_t$ .

A final important source of uncertainty is related to how vegetation recovers after a disturbance. Most observational studies have shown that  $E_t$  recovers gradually after tree mortality and forest fires, due to the

regeneration and growth of the remaining vegetation (Adams et al., 2012; Anderegg et al., 2016; Bearup et al., 2014; Dore et al., 2012). In fact, there are studies that suggest a temporary increase of  $E_t$  in relation to pre-disturbance conditions (Anderegg et al., 2016). Plant recovery depends on different factors, including plant communities, soil quality, average climate, etc. (Morris et al., 2011; Mou et al., 1993) (Fig. 3), so while regeneration may be quick and  $E_t$  may recover rapidly under mesic and warm conditions (Kelly et al., 2020), in colder or arid climates, in which the regeneration is slow, the effects of the disturbance on  $E_t$  can prolong for decades (Adams et al., 2012). The effect of the interactions between the different species that colonize the forests can be also relevant, as the overall response of ecosystem  $E_t$  is controlled by the diversity of hydraulic functional traits and the response of distinct plant functional groups (Anderegg et al., 2018, 2019; Werner et al., 2021), as well as competition and facilitation among different species for water (Grossiord, 2020; Grossiord et al., 2014). Moreover, after the disturbance, dominant species may be replaced by others with different hydraulic strategies (Batllori et al., 2020). The most extreme cases are related to the occurrence of landscape degradation after a disturbance, as a consequence of soil or climate limitations for plant recovery (Vicente-Serrano et al., 2020b). In these cases, the change in the magnitude of  $E$  and in the partition between  $E_t$  and  $E_s$  in relation to the pre-disturbance conditions can be dramatic as soils become more exposed to radiation (Raz-Yaseef et al., 2010). A representative example of this phenomenon is the case of shrub encroachment, where  $E_t$  is restricted to plant patches that are islands of soil humidity (Reynolds et al., 1999) surrounded by soils where surface moisture is depleted by  $E_s$  (Huxman et al., 2005).

#### 4. $E_t$ simulation in Earth Surface Models

$E_t$  is represented in the ESMs by modeling complex biophysical and biochemical processes including multiple feedbacks (Flato et al., 2013).



The Monin–Obukhov Similarity Theory provided the original equations to calculate  $E$  in ESMs, as the sum of  $E_s$ ,  $E_t$ , and  $E_i$ , calculating each component independently relative to the specific humidity gradient between surface and near-surface atmosphere based on resistances to evaporation due to turbulent transfer, moisture limitations, and additionally for  $E_t$ , stomatal physiology (Monin and Obukhov, 1954). These basic equations have evolved in current ESMs and the modelling of  $E_s$ ,  $E_t$  and  $E_i$  is now more complex and requires a number of resistances, which are connected in serial and/or parallel. How many resistances are used and how they are parameterized in the solution of the energy budget depends on the specific ESM, but current schemes incorporate biogeochemical and ecological processes when estimating these water, energy and carbon fluxes (Christoffersen et al., 2016; Sellers et al., 1997; Wullschlegel et al., 2014).

#### 4.1. Influence of $aCO_2$ on $E_t$ according to Earth Surface Models

The Intergovernmental Panel on Climate Change (IPCC) Coupled Model Intercomparison Projects Phase 5 and Phase 6 (CMIP5 and CMIP6) simulations by ESMs forced with future scenarios of greenhouse gas concentrations suggest that global changes in  $E_t$  could be limited because the modelled physiological effect of  $aCO_2$  on  $g_s$  offsets other factors (Fowler et al., 2019; Milly and Dunne, 2016; Roderick et al., 2015; Scheff, 2018; Swann et al., 2016; Yang et al., 2019), particularly under high  $CO_2$  scenarios. This assessment could have strong implications for future hydrology (Lemordant et al., 2018; Scheff, 2018; Yang et al., 2019), and limit the increase in aridity (Berg and McColl, 2021; Lian et al., 2021) and drought severity (Berg and Sheffield, 2018; Scheff, 2018).

Other modeling suggest that  $E_t$  has increased in the last few decades, particularly as a consequence of the dominant increase of the leaf area and global warming, and show just a small influence of the effects of  $aCO_2$  on  $g_s$  (Cernusak et al., 2019; Liu et al., 2021). There are also model studies that predict an increase of  $E_t$  in future scenarios as a consequence of the increases in  $A$  and leaf area and longer growing seasons, suggesting that runoff would decline in large areas of North America, Europe and the Amazon as consequence of enhanced plant water consumption (Mankin et al., 2018, 2019).

Nonetheless, future projections of leaf area and vegetation coverage are affected by strong uncertainties (De Kauwe et al., 2021; Park and Jeong, 2021; Song et al., 2021; Zhao et al., 2020). Based on 16 CMIP5 models for the RCP8.5 scenario, Mankin et al. (2019) suggested that reduced  $E_t$  by the direct physiological effects of  $aCO_2$  on  $g_s$  could have only a small effect on runoff, since it would affect areas that are already humid (as equatorial biomes) (Franks et al., 2017; Park et al., 2020), while in the vast majority of mid-latitude semi-arid and sub-humid regions,  $E_t$  would increase in response to higher leaf area and AED.

Fig. 4 compares the  $E_t$  estimates of CMIP6 models based on three different experiments: (a) 1pctCO<sub>2</sub>, which represents the effects of CO<sub>2</sub> increases at a rate of 1% per year until quadrupling of the preindustrial concentrations considering coupled CO<sub>2</sub> effects in both carbon cycle and radiation; (b) 1pctCO<sub>2</sub>-bgc, which represents 1% per year increasing CO<sub>2</sub> coupled to the carbon-cycle while radiative forcing is kept at the preindustrial CO<sub>2</sub> and (c) 1pctCO<sub>2</sub>-rad, which represents 1% per year increasing CO<sub>2</sub> coupled to the radiation forcing while the carbon cycle responds to the preindustrial CO<sub>2</sub>. We analyzed the simulated  $E_t$  s considering  $aCO_2$  from 285 to 1136 ppm, which correspond to the  $aCO_2$  for preindustrial (1850) and SSP5-85 emissions scenario for 2100, respectively. The models used are BCC-CSM2-MR, CanESM5, CanESM5-CanOE, CESM2, CMCC-ESM2, CNRM-ESM2-1, GFDL-ESM4, GISS-E2-1-G, IPSL-CM6A-LR, MIROC-ES2L, MRI-ESM2-0 and UKESM1-0-LL.

The analysis of the  $E_t$  projections in the recent CMIP6 models show a general agreement in the spatial patterns of annual  $E_t$  (Fig. 4a) with the  $E_t$  estimated from the remote sensing-based approach showed in Fig. 1b, although the average values obtained from the models tend to be lower.

There are important differences between the experiments 1pctCO<sub>2</sub>-

bgc and 1pctCO<sub>2</sub>-rad in the projections of  $E_t$  for 2050 and 2100 (Fig. 4b). The 1pctCO<sub>2</sub>-bgc experiment isolates the effect of enhanced  $aCO_2$  in the carbon cycle and it shows a general decrease of the annual  $E_t$  (Figs. 4c and d) for  $aCO_2$  corresponding to the SSP5-85 scenario by 2050 and 2100. The main decrease of  $E_t$  is recorded in humid tropical and equatorial regions. These regions show an increase of the leaf area in CMIP6 projections (Zhao et al., 2020) and they are characterised by sufficient availability of water to supply the needs of the vegetation canopy, so the results of the 1pctCO<sub>2</sub>-bgc experiment in these areas suggest clear dominance of the role of  $aCO_2$  on  $g_s$  in explaining the  $E_t$  projections in comparison to the enhancement of  $E_t$  as consequence of higher leaf area. In mid-latitude areas of Europe and North America, leaf area is also projected to increase, but the dominant  $E_t$  decrease in the 1pctCO<sub>2</sub>-bgc experiment in these areas suggests a dominance of the  $g_s$  decline in ESMs.

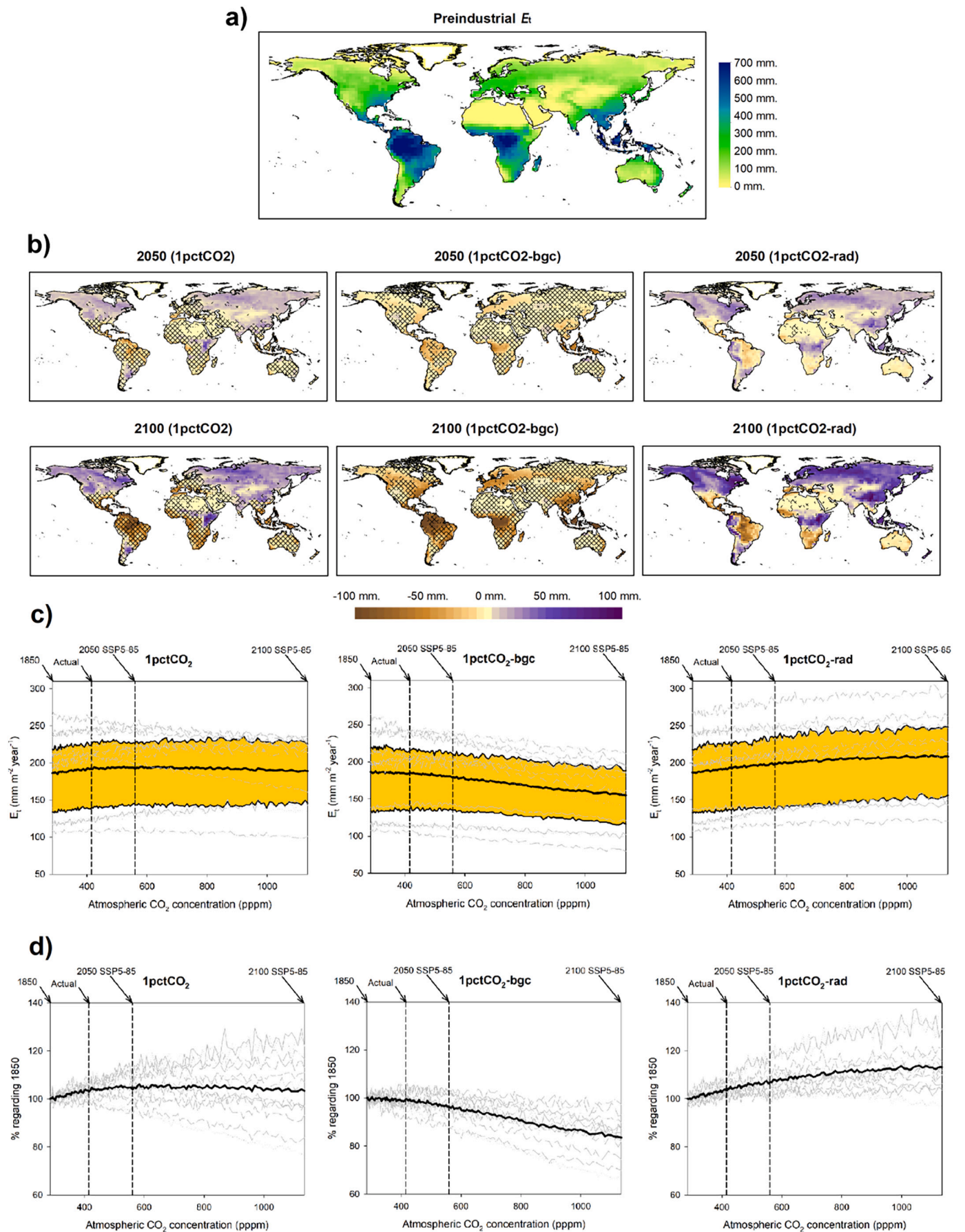
The projections of the 1pctCO<sub>2</sub>-rad experiment, which isolates the effect of enhanced  $aCO_2$  on the radiative forcing, show dominant global increase of  $E_t$ , which would affect mid-latitudes of the Northern and Southern Hemispheres, central Africa and southeast Asia. Exceptions are the Mediterranean, southern North America, southern Africa, Australia and Amazonia, in which CMIP6 models project a decrease of precipitation (Douville et al., 2021; Li et al., 2021), which would limit the available water for transpiration. In the rest of the regions, characterized by sufficient soil moisture content, the strong projected increase of AED would enhance  $E_t$  (Vicente-Serrano et al., 2020a).

The coupled influences of enhanced  $aCO_2$  in both carbon cycle and radiative forcing (1pctCO<sub>2</sub> experiment) show small global changes in average  $E_t$ . Nevertheless, there are important spatial differences with a dominant  $E_t$  increase over most of Eurasia and North America, Southern South Africa, and East Asia that suggest the dominance of radiative influences, and dominant decrease in Amazonia, central and southern Africa, southern Europe and southeast Asia, which would be related to the effects of  $aCO_2$  on  $g_s$ , and the projected reduction of precipitation in some areas (Douville et al., 2021; Li et al., 2021).

It is difficult to assess the accuracy of these projections, although the general increase observed in the experiment 1pctCO<sub>2</sub>-rad qualitatively agrees with observational studies based on recent decades, which have reported positive  $E_t$  trends following global warming (Brutsaert, 2017; Miralles et al., 2014). In any case, it is worth mentioning that the agreement between models in the projections of carbon cycle influences on  $E_t$  is weaker than agreement in the influence of radiative forcing. The projections of the 1pctCO<sub>2</sub>-bgc experiment show larger spread among the models and notably this problem propagates to the coupled experiment 1pctCO<sub>2</sub>, adding more uncertainty to the projections. This problem is not new: radiative effects associated with enhanced  $aCO_2$  were also more consistent than the physiological effects across CMIP5 ESMs (Gentine et al., 2019). These results suggest that the difficulties of establishing a robust assessment of future  $E_t$  mostly relate to the inherent uncertainties in the modeling of plant processes by ESMs. This reflects our limited process understanding and model representation of the direct and indirect physiological and morphological effects of  $aCO_2$  and their connection with the radiative effects of  $aCO_2$  reviewed above, and other relevant physical processes (such as atmospheric turbulence or root access to secondary water resources).

#### 4.2. Uncertainty in $g_s$ formulations in Earth System Models

Of particular concern is the fact that the direct physiological mechanisms linking  $aCO_2$  and dynamic responses of the stomata (and hence  $g_s$ ) are poorly understood, yet very influential in current climate model projections of  $E_t$  (Franks et al., 2017). This applies both to the response of stomatal aperture (Saxe et al., 1998) as well as stomatal density to  $aCO_2$  (Konrad et al., 2008). A key source of uncertainty relates to how ESMs determine  $g_s$  based on semi-empirical approaches that combine  $A$ ,  $CO_2$  and  $RH$  or  $VPD$  (Ball et al., 1987; Medlyn et al., 2017) and use parameters related to the vegetation type that are often poorly



(caption on next page)



**Fig. 4.** a) Spatial distribution of the preindustrial (1850–1880) annual average  $E_t$  ( $\text{mm m}^{-2}$ ). b) Mean spatial distribution of the difference in the annual  $E_t$  simulated with the three experiments in the 30 year in which the  $a\text{CO}_2$  correspond to the concentrations of the years 2050 (2035–2065) and 2100 (2070–2100) in the SSP5-85 emissions scenario regarding to preindustrial  $E_t$ . Striped correspond to areas in which less than of the 70% of the models agree with the sign of the average change. c) Evolution of the global average  $E_t$  from 285 to 1136 ppm of  $\text{CO}_2$  in the three simulation experiments. Black lines represent the global average and in color the 25<sup>th</sup> and 75<sup>th</sup> centiles of the different models. Gray lines correspond to the evolution of the global average  $E_t$  obtained with the independent models. d) same as c) but the evolution showed in percentages regarding  $E_t$  in 1850.

constrained (Medlyn et al., 2011). These parameters exhibit a significant spread in the measurements from different methods (e.g. using leaf gas exchange, leaf isotopes, eddy covariance towers) (Medlyn et al., 2017). Stomatal physiology and soil-to-leaf water transport properties (e.g., xylem hydraulic conductance) vary widely among species (Brodribb and Feild, 2010; Xu et al., 2016a). Moreover, the structure of the model used to calculate  $g_s$  adds another source of uncertainty. All these semi-empirical models provide a similar sensitivity of  $g_s$  to  $a\text{CO}_2$ , which often does not capture the range of variability in observations (Medlyn et al., 2017). Moreover, still several ESMS use  $g_s$  models based on RH instead of  $VPD$  (Knauer et al., 2015) despite strong evidence that stomata respond to  $VPD$  (Aphalo and Jarvis, 1991; Oren et al., 1999). This is not a trivial choice and it has important implications in the projections of plant  $E_t$  since in the nature  $g_s$  is linked to  $VPD$  through hydraulic conductance (Brodribb and McAdam, 2017). Thus,  $VPD$ -based models may lead to up to 10% higher  $WUE$  than models using RH (Sato et al., 2015), with the latter yielding a poorer performance when comparing  $g_s$  estimates with observations (Raczka et al., 2016). In addition, parameterizations used by these models noticeably alter the relationship between  $g_s$  and  $a\text{CO}_2$  (Franks et al., 2017). Using satellite-based estimates, Forzieri et al. (2020) suggested that  $E_t$  in ESMS could be oversensitive to the effects of  $a\text{CO}_2$  on  $g_s$  (see Section 2.1). More mechanistic models of  $g_s$  (e.g., Buckley, 2019) would be needed to capture different sensitivities to  $a\text{CO}_2$ , but current models have not been tested for this aspect. In the 42 different CMIP6 models listed by Zhou et al. (2022), 7 of them do not use a  $g_s$  model, 24 use the Ball-Berry (Ball et al., 1987), 5 the Leuning (Leuning, 1995), 3 the JULES (Clark et al., 2011) semi-empirical models, and only 3 models use a semi-mechanistic  $g_s$  model (Knauer et al., 2015); this means that the vast majority of ESMS still use uncertain semi-empirical  $g_s$  models for this purpose.

This model uncertainty in the effect of  $a\text{CO}_2$  on  $g_s$  can be relevant to determine  $E_t$  trends in some regions. The reduction of  $E_t$  in dense mature equatorial and tropical forest areas seen in CMIP5 models (Fig. 4b) (Lemordant et al., 2018; Park et al., 2020), which suggests substantial direct physiological influences of  $a\text{CO}_2$  on  $g_s$ , could contradict experimental studies that have exhibited low sensitivity of  $g_s$  to elevated  $a\text{CO}_2$  in dense mature humid forests (Körner et al., 2005; Medlyn et al., 2001; Saxe et al., 1998) and dry tropical forests (Purcell et al., 2018; Wesolowski et al., 2020). Although these results may not be fully representative of the behavior in tropical and equatorial forests in which there are very few experiments, a recent meta-analysis on the drivers of  $WUE$  change in dense mature forests in different world regions, including some tropical forests, suggested that  $g_s$  did not change substantially between 1901 and 2015 in response to  $a\text{CO}_2$  increase (Mathias and Thomas, 2021). These observations suggest that the reduction of  $E_t$  projected by the ESMS associated to a reduced  $g_s$  in these areas may be affected by uncertainties, even more considering the high sensitivity of  $E_t$  to  $VPD$  increase observed experimentally there (Granier et al., 1996; Igarashi et al., 2015; McJannet et al., 2007; Siddiq et al., 2017; Siddiq and Cao, 2016; Vourlitis et al., 2008; Wallace and McJannet, 2010; Yoshifuji et al., 2020). In semiarid and sub-humid regions in which  $E_t$  is limited by water availability, and in cold regions in which  $E_t$  is limited by energy, there is more consensus that any potential control of  $g_s$  by  $a\text{CO}_2$  would have a limited influence on  $E_t$  (Lemordant et al., 2018; Park et al., 2020; Skinner et al., 2018).

#### 4.3. Other physiological uncertainties in Earth System Models

The uncertainty in the modeling of the relevant plant–water processes is not restricted to the estimation of  $g_s$ . Most ESMS do not explicitly consider the entire water transport across the soil–plant–atmosphere continuum. Plant hydraulics is one of the most relevant mechanisms that regulate the whole-plant physiology (McDowell et al., 2019) and only recently have some models included it in their formulations (Kennedy et al., 2019; Wu et al., 2020). This is a substantial limitation, since water transport determines plant hydration and is thus a core driver of plant performance and plant–atmosphere responses (Brodribb et al., 2020; Choat et al., 2018; McDowell et al., 2019). Liu et al. (2020) showed that in comparison to the use of a plant hydraulic model, the estimates of  $g_s$  currently included in most ESMS produce a low sensitivity of  $E_t$  to  $VPD$ , which is compensated by the overestimation of the sensitivity of  $E_t$  to soil moisture (Liu et al., 2020; Powell et al., 2013). This aspect could limit the assessment of the relationships between these three variables in the ESMS projections for future climate scenarios under chronically increasing  $VPD$ . Moreover, the relationships used by ESMS to relate plant gas exchange and soil water availability do not consider the complex differences in the response to drought among different plant types (De Kauwe et al., 2021; Medlyn et al., 2016). This is still an issue that is poorly investigated, and in which allometric adjustment between roots and leaves in response to  $a\text{CO}_2$  seems to play an important role (Hao et al., 2018). Thus, root density and depth, which are strongly affected by  $a\text{CO}_2$  (See section 2.2), and the access to groundwater, are also important sources of uncertainty for a correct assessment of plant–water interactions in the climate models. ESMS do not include other relevant plant–water mechanisms such as the increase of the leaf cuticular conductance associated with warming conditions and the possible decoupling between  $A$  and  $E_t$  in response to extreme heat (See section 3.1).

The limitations of ESMS to estimate  $E_t$  are not only related to how they represent plant–water interactions. The interaction between plant growth and mortality and  $a\text{CO}_2$  in ESMS is also very relevant, and the magnitude and projected changes in  $A$ , plant coverage, and leaf area are important to interpret  $E_t$  projections. ESMS projections of  $E_t$  portray a dominant increase of leaf area (Mahowald et al., 2016), which would support also a net increase in  $E_t$  in response to greening (Cernusak et al., 2019; Filoso et al., 2017; Mankin et al., 2019). Nevertheless, leaf area projections by ESMS are affected by strong uncertainties (De Kauwe et al., 2021; Park and Jeong, 2021; Song et al., 2021; Zhao et al., 2020), and  $E_t$  modeling in ESMS is less sensitive to changes in the leaf area index than in  $g_s$  (Cernusak et al., 2019; Forzieri et al., 2020). These two factors are also introducing important uncertainties in the ESMS projections of  $E_t$  since ESMS would tend to underestimate a possible effect of a hypothetical and uncertain greening on  $E_t$ . Thus, the low sensitivity of  $E_t$  to changes in leaf area in ESMS could explain some  $E_t$  underestimation by ESMS (Dong et al., 2022; Mankin et al., 2019), which could be primarily attributed to the inaccurate representation of light distribution in the canopy (Lian et al., 2018), and to problems modeling water uptake by roots (Lawrence et al., 2007; Lian et al., 2018), both issues being strongly related to  $a\text{CO}_2$  (See section 2.2). In any case, how resistances are parameterized in models may be relevant, since the ratio of  $E_t$  to  $E$  is simulated much more realistically in models based on mechanistic principles (Decker et al., 2017; Paschalis et al., 2018).

Current ESMS do not factor in the likelihood of plant mortality episodes in response to climate extremes induced by  $\text{CO}_2$  radiative forcing

(See section 3.2), and as not all the models include a dynamic change of vegetation coverage with plant competition (Huang et al., 2016b), they cannot account for the role of relevant plant processes as secondary succession, replacement of species, drought-induced tree mortality, land degradation, etc., which are expected to be strongly affected by radiative effects of  $aCO_2$  (See section 3.2). Also, possible changes in plant functional traits in response to climate change can be essential to evaluate how  $E_t$  is affected by  $aCO_2$  (Anderegg et al., 2019; Anderegg et al., 2016), but they are also not accurately considered in the current generation of ESMs (Fisher et al., 2018; Wullschlegler et al., 2014).

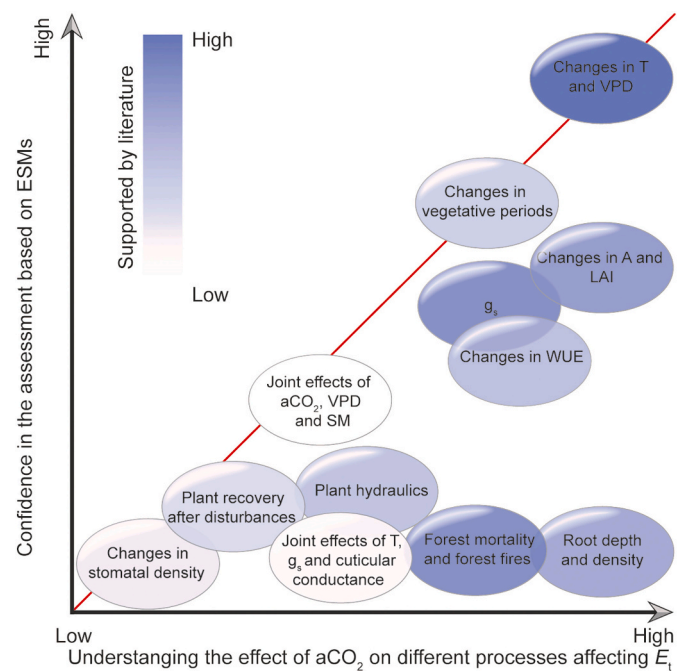
In summary, the coupled physiological and radiative mechanisms involved in  $E_t$  under enhanced  $aCO_2$  are poorly understood, which limits their accurate representation in ESMs. Likewise, physiological processes in ESMs are also subject to important simplifications (De Kauwe et al., 2021; Forkel et al., 2019; Green et al., 2020; Manusch et al., 2012). These limitations cause not only uncertainties in the magnitude of  $E_t$  (De Kauwe et al., 2013) but even in the sign of  $E_t$  trends (Knauer et al., 2017). ESMs still need improvement in representing complex interacting processes including changes in climate, plant coverage and physiology and human land and water management to confidently simulate future  $E_t$  trends in response to  $aCO_2$  changes, but gaps in understanding many of the complex processes limit progress in modeling.

## 5. Conclusions and future research perspectives

$E_t$  is one of the most relevant variables determining water budget over continental areas, and affecting temperature and precipitation, while modulating critical climate processes such as the cloud, lapse rate and water vapour feedback. Nevertheless, there are strong uncertainties in understanding its complex dynamics. There is a large debate on how  $E_t$  may change in future scenarios with strong implications for soil moisture, runoff availability, aridity, drought severity, etc. The role of  $aCO_2$  on  $E_t$  is a key source of uncertainty. In this review, we have addressed the direct and indirect mechanisms and feedbacks that mediate the complex interaction between  $aCO_2$  and global  $E_t$  changes.  $E_t$  is determined by different physiological and radiative effects of  $aCO_2$ , including feedbacks with water availability, climate, and vegetation dynamics, which are often coupled. Our literature review shows that frequently  $CO_2$ -induced changes (decreased  $g_s$ , increased LAI, higher AED, altered soil moisture, etc.) influence  $E_t$  in opposite directions, which makes the overall sensitivity highly uncertain. Plant behavior is particularly divergent across vegetation types and environmental conditions, and these differences may not be well represented in our models due to uncertainty in our understanding of these processes (Fig. 5).

Different research priorities are necessary to improve empirical measurements and modelling to improve our knowledge of  $E_t$  dynamics and its possible response to rising  $CO_2$ . To advance our knowledge of the global  $E_t$  response to enhanced  $aCO_2$ , reinforcing the network of  $E_t$  observations over different regions should be a priority (Beven et al., 2020; Poyatos et al., 2016; Stoy et al., 2019). However, it is necessary to stress that given the uncertainty of  $E_t$  measurements from different sources (sapflow measurements, eddy covariance towers, water budgets at the basin scale), dedicated and controlled experiments to observe  $E_t$  precisely would be needed, and better methodologies for upscaling these observations also need to be developed. Likewise, continuing the efforts to derive  $E_t$  estimates from the current and future wealth of satellite observations must remain in the agenda (Fisher et al., 2017). International efforts and coordination are necessary, and international programs such as the World Integrated Global Observing System of the World Meteorological Organization should promote  $E_t$  observation as one of the main points in climate observation; along those lines, the Global Climate Observing System (GCOS) has recently included  $E_t$  among the list of Essential Climate Variable (ECV) products (Dorigo et al., 2021).

To better understand the direct plant physiological response to enhanced  $aCO_2$  is another priority. Of particular importance is to



**Fig. 5.** Relationship between current understanding of the effect of  $aCO_2$  on different processes that control  $E_t$  changes and the confidence of their representation in ESMs.

improve our understanding of the response of  $g_s$  to  $aCO_2$ -induced warming. For this reason, controlled experimental studies should address the joint contribution of direct and indirect physiological and radiative  $aCO_2$  influences for different vegetation types and environmental conditions. These coupled processes may generate complex spatial mosaics in which it can be very difficult to assess possible  $E_t$  changes. In addition, the assessment of the role of vegetation dynamics related to climate change on global  $E_t$  is a high priority, with the need for a better understanding of how abrupt vegetation changes (tree mortality and forest fires) and gradual changes (secondary succession and land degradation) may affect changes in  $E_t$  and its relation to  $aCO_2$ . Better understanding of these processes would lead to insights into the partitioning between  $E_t$  and  $E_s$  from ecosystems to global scales, which currently remains highly uncertain.

Finally, there is a clear need for improvements in the representation of all these processes in ESMs to reduce the uncertainties in the assessment of future trends in  $E_t$  (e.g., including whole plant hydraulic regulation). A scientific priority should be to better understand ecohydrological processes, which are strongly connected with climate change and have notable societal, economic, and ecological implications. This improved understanding can guide the establishment of better adaptation practices to the large and complex implications of the virtually certain enhancement of  $aCO_2$  in the future.

## Funding

This work was supported by the research projects CGL2017-82216-R, PCI2019-103631 and PID2019-108589RA-I00, financed by the Spanish Ministry of Science and FEDER; CROSSDRO project financed by the AXIS (Assessment of Cross(X) - sectorial climate Impacts and pathways for Sustainable transformation), JPI-Climate co-funded call of the European Commission; NGM and LRL were supported by the Department of Energy's Next Generation Ecosystem Experiment-Tropics. DGM acknowledges support from the European Research Council (ERC) under grant agreement no. 715254 (DRY-2-DRY). AK acknowledges support from the European Union Horizon 2020 program, project no. 869550 (DOWN2EARTH).

## Declaration of Competing Interest

None declared

## References

- Adams, H., Luce, C., Breshears, D., Allen, C., Weiler, M., Hale, V., Smith, A., Huxman, T., 2012. Ecohydrological consequences of drought- and infestation- triggered tree die-off: Insights and hypotheses. *Ecohydrology* 5, 145–159. <https://doi.org/10.1002/eco.233>.
- Adams, M.A., Buckley, T.N., Turnbull, T.L., 2020. Diminishing CO<sub>2</sub>-driven gains in water-use efficiency of global forests. *Nat. Clim. Chang.* 10, 466–471. <https://doi.org/10.1038/s41558-020-0747-7>.
- Ainsworth, E.A., Long, S.P., 2005. What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytol.* 165, 351–372. <https://doi.org/10.1111/j.1469-8137.2004.01224.x>.
- Ainsworth, E.A., Rogers, A., 2007. The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]: mechanisms and environmental interactions. *Plant Cell Environ.* 30, 258–270. <https://doi.org/10.1111/j.1365-3040.2007.01641.x>.
- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* 3, 30–36. <https://doi.org/10.1038/nclimate1635>.
- Anderegg, W., Martinez-Vilalta, J., Cailleret, M., Camarero, J.J., Ewers, B.E., Galbraith, D., Gessler, A., Grote, R., Huang, C., Levick, S.R., Powell, T.L., Rowland, L., Sánchez-Salguero, R., Trotsiuk, V., 2016. When a tree dies in the forest: scaling climate-driven tree mortality to ecosystem water and carbon fluxes. *Ecosystems* 19, 1133–1147. <https://doi.org/10.1007/s10021-016-9982-1>.
- Anderegg, W.R.L., Konings, A.G., Trugman, A.T., Yu, K., Bowling, D.R., Gabbitas, R., Karp, D.S., Pacala, S., Sperry, J.S., Sulman, B.N., Zenes, N., 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* 561, 538–541. <https://doi.org/10.1038/s41586-018-0539-7>.
- Anderegg, W.R.L., Trugman, A.T., Bowling, D.R., Salvucci, G., Tuttle, S.E., 2019. Plant functional traits and climate influence drought intensification and land-atmosphere feedbacks. *Proc. Natl. Acad. Sci. U. S. A.* 116, 14071–14076. <https://doi.org/10.1073/pnas.1904747116>.
- Aphalo, P.J., Jarvis, P.G., 1991. Do stomata respond to relative humidity? *Plant Cell Environ.* 14, 127–132. <https://doi.org/10.1111/j.1365-3040.1991.tb01379.x>.
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, U.K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.* [https://doi.org/10.1175/1520-0477\(2001\)082<2415:FANTTS>2.3.CO;2](https://doi.org/10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2).
- Ball, J., Woodrow, I., Berry, J., 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. *Prog. Photosynth. Res.* 4, 221–224. [https://doi.org/10.1007/978-94-017-0519-6\\_48](https://doi.org/10.1007/978-94-017-0519-6_48).
- Batke, S.P., Yiotti, C., Elliott-Kingston, C., Holohan, A., McElwain, J., 2020. Plant responses to decadal scale increments in atmospheric CO<sub>2</sub> concentration: comparing two stomatal conductance sampling methods. *Planta* 251, 52. <https://doi.org/10.1007/s00425-020-03343-z>.
- Batllori, E., Lloret, F., Aakala, T., Anderegg, W.R.L., Aynekulu, E., Bendixsen, D.P., Bentouati, A., Bigler, C., Burk, C.J., Camarero, J.J., Colangelo, M., Coop, J.D., Fensham, R., Floyd, M.L., Galiano, L., Ganey, J.L., Gonzalez, P., Jacobsen, A.L., Kane, J.M., Kitzberger, T., Linares, J.C., Marchetti, S.B., Matusick, G., Michaelian, M., Navarro-Cerrillo, R.M., Pratt, R.B., Redmond, M.D., Rigling, A., Ripullone, F., Sangüesa-Barreda, G., Sasal, Y., Saura-Mas, S., Suarez, M.L., Veblen, T. T., Vilà-Cabrera, A., Vincke, C., Zeeman, B., 2020. Forest and woodland replacement patterns following drought-related mortality. *Proc. Natl. Acad. Sci.* 117, 29720–29729. <https://doi.org/10.1073/pnas.2002314117>.
- Bearup, L.A., Maxwell, R.M., Clow, D.W., McCray, J.E., 2014. Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. *Nat. Clim. Chang.* 4, 481–486. <https://doi.org/10.1038/nclimate2198>.
- Beer, C., Ciais, P., Reichstein, M., Baldocchi, D., Law, B.E., Papale, D., Soussana, J.-F., Ammann, C., Buchmann, N., Frank, D., Gianelle, D., Janssens, I.A., Knohl, A., Köstner, B., Moors, E., Rouspard, O., Verbeeck, H., Vesala, T., Williams, C.A., Wohlfahrt, G., 2009. Temporal and among-site variability of inherent water use efficiency at the ecosystem level. *Glob. Biogeochem. Cycles* 23, GB2018.
- Bennett, K.E., Bohn, T.J., Solander, K., McDowell, N.G., Xu, C., Vivoni, E., Middleton, R. S., 2018. Climate-driven disturbances in the San Juan River sub-basin of the Colorado River. *Hydrol. Earth Syst. Sci.* 22, 709–725. <https://doi.org/10.5194/hess-22-709-2018>.
- Berg, A., McColl, K.A., 2021. No projected global drylands expansion under greenhouse warming. *Nat. Clim. Chang.* 11, 331–337. <https://doi.org/10.1038/s41558-021-01007-8>.
- Berg, A., Sheffield, J., 2018. Climate change and drought: the soil moisture perspective. *Curr. Clim. Chang. Rep.* 4, 180–191. <https://doi.org/10.1007/s40641-018-0095-0>.
- Bernacchi, C.J., Kimball, B.A., Quarles, D.R., Long, S.P., Ort, D.R., 2007. Decreases in stomatal conductance of soybean under open-air elevation of [CO<sub>2</sub>] are closely coupled with decreases in ecosystem evapotranspiration. *Plant Physiol.* 143, 134–144.
- Betts, R.A., Boucher, O., Collins, M., Cox, P.M., Falloon, P.D., Gedney, N., Hemming, D. L., Huntingford, C., Jones, C.D., Sexton, D.M.H., Webb, M.J., 2007. Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* 448, 1037–1041. <https://doi.org/10.1038/nature06045>.
- Beven, K., Asadullah, A., Bates, P., Blyth, E., Chappell, N., Child, S., Cloke, H., Dadson, S., Everard, N., Fowler, H.J., Freer, J., Hannah, D.M., Heppell, K., Holden, J., Lamb, R., Lewis, H., Morgan, G., Parry, L., Wagener, T., 2020. Developing observational methods to drive future hydrological science: can we make a start as a community? *Hydrol. Process.* 34, 868–873. <https://doi.org/10.1002/hyp.13622>.
- Biederman, J.A., Harpold, A.A., Gochis, D.J., Ewers, B.E., Reed, D.E., Papuga, S.A., Brooks, P.D., 2014. Increased evaporation following widespread tree mortality limits streamflow response. *Water Resour. Res.* 50, 5395–5409. <https://doi.org/10.1002/2013WR014994>.
- Biederman, J.A., Somor, A.J., Harpold, A.A., Gutmann, E.D., Breshears, D.D., Troch, P.A., Gochis, D.J., Scott, R.L., Meddens, A.J.H., Brooks, P.D., 2015. Recent tree die-off has little effect on streamflow in contrast to expected increases from historical studies. *Water Resour. Res.* 51, 9775–9789. <https://doi.org/10.1002/2015WR017401>.
- Bobich, E.G., Barron-Gafford, G.A., Rascher, K.G., Murthy, R., 2010. Effects of drought and changes in vapour pressure deficit on water relations of *Populus deltoides* growing in ambient and elevated CO<sub>2</sub>. *Tree Physiol.* <https://doi.org/10.1093/treephys/tpq036>.
- Bourbia, I., Pritzkow, C., Brodribb, T.J., 2021. Herb and conifer roots show similar high sensitivity to water deficit. *Plant Physiol.* <https://doi.org/10.1093/plphys/kiab207>.
- Brodribb, T.J., Feild, T.S., 2010. Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecol. Lett.* 13, 175–183. <https://doi.org/10.1111/j.1461-0248.2009.01410.x>.
- Brodribb, T.J., McAdam, S.A.M., 2017. Evolution of the stomatal regulation of plant water content. *Plant Physiol.* 174, 639–649. <https://doi.org/10.1104/pp.17.00078>.
- Brodribb, T.J., McAdam, S.A.M., Jordan, G.J., Feild, T.S., 2009. Evolution of stomatal responsiveness to CO<sub>2</sub> and optimization of water-use efficiency among land plants. *New Phytol.* 183, 839–847. <https://doi.org/10.1111/j.1469-8137.2009.02844.x>.
- Brodribb, T.J., Powers, J., Cochard, H., Choat, B., 2020. Hanging by a thread? Forests and drought. *Science (80- )* 368, 261–266. <https://doi.org/10.1126/science.aat7631>.
- Brutsaert, W., 2017. Global land surface evaporation trend during the past half century: Corroboration by Clausius-Clapeyron scaling. *Adv. Water Resour.* 106, 3–5. <https://doi.org/10.1016/j.advwatres.2016.08.014>.
- Buckley, T.N., 2019. How do stomata respond to water status? *New Phytol.* 224, 21–36. <https://doi.org/10.1111/nph.15899>.
- Bueno, A., Alfarhan, A., Arand, K., Burghardt, M., Deininger, A.-C., Hedrich, R., Leide, J., Seufert, P., Staiger, S., Riederer, M., 2019. Effects of temperature on the cuticular transpiration barrier of two desert plants with water-spender and water-saver strategies. *J. Exp. Bot.* 70, 1613–1625. <https://doi.org/10.1093/jxb/erz018>.
- Byrne, M.P., O’Gorman, P.A., 2018. Trends in continental temperature and humidity directly linked to ocean warming. *Proc. Natl. Acad. Sci. U. S. A.* 115, 4863–4868. <https://doi.org/10.1073/pnas.1722312115>.
- Cernusak, L.A., Haverd, V., Brendel, O., Le Thiec, D., Guehl, J.-M., Cuntz, M., 2019. Robust response of terrestrial plants to rising CO<sub>2</sub>. *Trends Plant Sci.* 24, 578–586. <https://doi.org/10.1016/j.tplants.2019.04.003>.
- Certini, G., 2005. Effects of fire on properties of forest soils: a review. *Oecologia*. <https://doi.org/10.1007/s00442-004-1788-8>.
- Ceulemans, R., Mousseau, M., 1994. Tansley review No. 71. effects of elevated atmospheric CO<sub>2</sub> on woody plants. *New Phytol.* 127, 425–446.
- Chaves, M.M., Costa, J.M., Zarrouk, O., Pinheiro, C., Lopes, C.M., Pereira, J.S., 2016. Controlling stomatal aperture in semi-arid regions—the dilemma of saving water or being cool? *Plant Sci.* 251, 54–64. <https://doi.org/10.1016/j.plantsci.2016.06.015>.
- Cheng, L., Zhang, L., Wang, Y.-P., Canadell, J.G., Chiew, F.H.S., Terrestrial, J., Li, L., Miralles, D.G., Piao, S., Zhang, Y., 2017. Recent increases in birch carbon uptake at little cost to the water cycle. *Nat. Commun.* 8, 110. <https://doi.org/10.1038/s41467-017-00114-5>.
- Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. *Nature* 558, 531–539. <https://doi.org/10.1038/s41586-018-0240-x>.
- Christoffersen, B.O., Gloor, M., Fauset, S., Fyllas, N.M., Galbraith, D.R., Baker, T.R., Kruijt, B., Rowland, L., Fisher, R.A., Binks, O.J., Sevanto, S., Xu, C., Jansen, S., Choat, B., Mencuccini, M., McDowell, N.G., Meir, P., 2016. Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS~v.1-Hydro). *Geosci. Model Dev.* 9, 4227–4255. <https://doi.org/10.5194/gmd-9-4227-2016>.
- Clark, D.B., Mercado, L.M., Sitch, S., Jones, C.D., Gedney, N., Best, M.J., Pryor, M., Rooney, G.G., Essery, R.L.H., Blyth, E., Boucher, O., Harding, R.J., Huntingford, C., Cox, P.M., 2011. The Joint UK Land Environment Simulator (JULES), model description – Part 2: carbon fluxes and vegetation dynamics. *Geosci. Model Dev.* 4, 701–722. <https://doi.org/10.5194/gmd-4-701-2011>.
- Cook, B., Mankin, J., Anchukaitis, K., 2018. Climate change and drought: from past to future. *Curr. Clim. Chang. Rep.* 4, 164–179. <https://doi.org/10.1007/s40641-018-0093-2>.
- Costa, M.H., Biajoli, M.C., Sanches, L., Malhado, A.C.M., Hutryra, L.R., da Rocha, H.R., Aguiar, R.G., de Araújo, A.C., 2010. Atmospheric versus vegetation controls of Amazonian tropical rain forest evapotranspiration: are the wet and seasonally dry rain forests any different? *J. Geophys. Res. Biogeosci.* 115 <https://doi.org/10.1029/2009JG001179>.
- Dai, A., Zhao, T., Chen, J., 2018. Climate change and drought: a precipitation and evaporation perspective. *Curr. Clim. Chang. Rep.* 4, 301–312. <https://doi.org/10.1007/s40641-018-0101-6>.



- De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Hickler, T., Jain, A. K., Luo, Y., Parton, W.J., Prentice, I.C., Smith, B., Thornton, P.E., Wang, S., Wang, Y.-P., Wärlind, D., Weng, E., Crous, K.Y., Ellsworth, D.S., Hanson, P.J., Seok Kim, H., Warren, J.M., Oren, R., Norby, R.J., 2013. Forest water use and water use efficiency at elevated CO<sub>2</sub>: a model-data intercomparison at two contrasting temperate forest FACE sites. *Glob. Chang. Biol.* 19, 1759–1779. <https://doi.org/10.1111/gcb.12164>.
- De Kauwe, M.G., Medlyn, B.E., Tissue, D.T., 2021. To what extent can rising [CO<sub>2</sub>] ameliorate plant drought stress? *New Phytol.* <https://doi.org/10.1111/nph.17540>.
- Decker, M., Or, D., Pitman, A., Ukkola, A., 2017. New turbulent resistance parameterization for soil evaporation based on a pore-scale model: Impact on surface fluxes in CABLE. *J. Adv. Model. Earth Syst.* 9, 220–238. <https://doi.org/10.1002/2016MS000832>.
- Dong, J., Lei, F., Crow, W.T., 2022. Land transpiration-evaporation partitioning errors responsible for modeled summertime warm bias in the central United States. *Nat. Commun.* 13, 336. <https://doi.org/10.1038/s41467-021-27938-6>.
- Dore, S., Montes-Helu, M., Hart, S.C., Hungate, B.A., Koch, G.W., Moon, J.B., Finkral, A. J., Kolb, T.E., 2012. Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. *Glob. Chang. Biol.* 18, 3171–3185. <https://doi.org/10.1111/j.1365-2486.2012.02775.x>.
- Dorigo, W., Dietrich, S., Aires, F., Brocca, L., Carter, S., Cretaux, J.-F., Dunkerley, D., Enomoto, H., Forsberg, R., Güntner, A., Hegglin, M.I., Hollmann, R., Hurst, D.F., Johannessen, J.A., Kummerow, C., Lee, T., Luojus, K., Looser, U., Miralles, D.G., Pellet, V., Recknagel, T., Ruz Vargas, C., Schneider, U., Schoeneich, P., Schröder, M., Tapper, N., Vuglinsky, V., Wagner, W., Yu, L., Zappa, L., Zemp, M., Aich, V., 2021. Closing the water cycle from observations across scales: where do we stand? *Bull. Am. Meteorol. Soc.* 1–95. <https://doi.org/10.1175/BAMS-D-19-0316.1>.
- Douville, H., Raghavan, K., Renwick, J., 2021. Water cycle changes. *Climate Change 2021: The Physical Climate, Basis*. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.
- Drake, B.G., González-Meler, M.A., Long, S.P., 1997. More efficient plants: a Consequence of Rising Atmospheric CO<sub>2</sub>? *Annu. Rev. Plant Biol.* 48, 609–639.
- Drake, J.E., Tjoelker, M.G., Vårhammar, A., Medlyn, B.E., Reich, P.B., Leigh, A., Pfautsch, S., Blackman, C.J., López, R., Aspinwall, M.J., Crous, K.Y., Duursma, R.A., Kumarathunge, D., De Kauwe, M.G., Jiang, M., Nicotra, A.B., Tissue, D.T., Choat, B., Atkin, O.K., Barton, C.V.M., 2018. Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. *Glob. Chang. Biol.* 24, 2390–2402. <https://doi.org/10.1111/gcb.14037>.
- Duan, H., Duursma, R.A., Huang, G., Smith, R.A., Choat, B., O'Grady, A.P., Tissue, D.T., 2014. Elevated [CO<sub>2</sub>] does not ameliorate the negative effects of elevated temperature on drought-induced mortality in *Eucalyptus radiata* seedlings. *Plant Cell Environ.* 37, 1598–1613.
- Duan, H., Chazsar, B., Lewis, J.D., Smith, R.A., Huxman, T.E., Tissue, D.T., 2018. CO<sub>2</sub> and temperature effects on morphological and physiological traits affecting risk of drought-induced mortality. *Tree Physiol.* 38, 1138–1151. <https://doi.org/10.1093/treephys/tpy037>.
- Fang, Y., Leung, L.R., Wolfe, B.T., Detto, M., Knox, R.G., McDowell, N.G., Grossiord, C., Xu, C., Christoffersen, B.O., Gentine, P., Koven, C.D., Chambers, J.Q., 2021. Disentangling the effects of vapor pressure deficit and soil water availability on canopy conductance in a seasonal tropical forest during the 2015 El Niño drought. *J. Geophys. Res. Atmos.* 126. <https://doi.org/10.1029/2021JD035004>.
- Faticchi, S., Sebastian, L., Athanasios, P., Adam, L.J., Alicia, D.B.J.H.M., 2016. Partitioning direct and indirect effects reveals the response of water-limited ecosystems to elevated CO<sub>2</sub>. *Proc. Natl. Acad. Sci.* 113, 12757–12762. <https://doi.org/10.1073/pnas.1605036113>.
- Filoso, S., Bezerra, M.O., Weiss, K.C.B., Palmer, M.A., 2017. Impacts of forest restoration on water yield: a systematic review. *PLoS One* 12, e0183210.
- Fisher, J.B., Melton, F., Middleton, E., Hain, C., Anderson, M., Allen, R., McCabe, M.F., Hook, S., Baldocchi, D., Townsend, P.A., Kilic, A., Tu, K., Miralles, D.D., Perret, J., Lagouarde, J.-P., Waliser, D., Purdy, A.J., French, A., Schimel, D., Famiglietti, J.S., Stephens, G., Wood, E.F., 2017. The future of evapotranspiration: global requirements for ecosystem functioning, carbon and climate feedbacks, agricultural management, and water resources. *Water Resour. Res.* 53, 2618–2626. <https://doi.org/10.1002/2016WR020175>.
- Fisher, R.A., Koven, C.D., Anderegg, W.R.L., Christoffersen, B.O., Dietze, M.C., Farrior, C. E., Holm, J.A., Hurr, G.C., Knox, R.G., Lawrence, P.J., Lichstein, J.W., Longo, M., Matheny, A.M., Medvigy, D., Muller-Landau, H.C., Powell, T.L., Serbin, S.P., Sato, H., Shuman, J.K., Smith, B., Trugman, A.T., Viskari, T., Verbeeck, H., Weng, E., Xu, C., Xu, X., Zhang, T., Moorcroft, P.R., 2018. Vegetation demographics in Earth System Models: a review of progress and priorities. *Glob. Chang. Biol.* 24, 35–54. <https://doi.org/10.1111/gcb.13910>.
- Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S.C., Collins, W., Cox, P., Driouech, F., Emori, S., Eyring, V., Forest, C., Gleckler, P., Guilyardi, E., Jakob, C., Kattsov, V., Reason, C., Rummukainen, M., 2013. Evaluation of climate models BT. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Doschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 741–882.
- Flo, V., Martínez-Vilalta, J., Mencuccini, M., Granda, V., Anderegg, W.R.L., Poyatos, R., 2021. Climate and functional traits jointly mediate tree water-use strategies. *New Phytol.* 231, 617–630. <https://doi.org/10.1111/nph.17404>.
- Forkel, M., Driike, M., Thurner, M., Dorigo, W., Schaphoff, S., Thonicke, K., von Bloh, W., Carvalhais, N., 2019. Constraining modelled global vegetation dynamics and carbon turnover using multiple satellite observations. *Sci. Rep.* 9, 18757. <https://doi.org/10.1038/s41598-019-55187-7>.
- Forzieri, G., Miralles, D.G., Ciais, P., Alkama, R., Ryu, Y., Duveiller, G., Zhang, K., Robertson, E., Kautz, M., Martens, B., Jiang, C., Arneth, A., Georgievski, G., Li, W., Ceccherini, G., Anthoni, P., Lawrence, P., Wiltshire, A., Pongratz, J., Piao, S., Sitch, S., Goll, D.S., Arora, V.K., Lienert, S., Lombardozi, D., Kato, E., Nabel, J.E.M. S., Tian, H., Friedlingstein, P., Cescatti, A., 2020. Increased control of vegetation on global terrestrial energy fluxes. *Nat. Clim. Chang.* 10, 356–362. <https://doi.org/10.1038/s41558-020-0717-0>.
- Fowler, M.D., Kooperman, G.J., Randerson, J.T., Pritchard, M.S., 2019. The effect of plant physiological responses to rising CO<sub>2</sub> on global streamflow. *Nat. Clim. Chang.* 9, 873–879. <https://doi.org/10.1038/s41558-019-0602-x>.
- Frank, D.C., Poulter, B., Saurer, M., Esper, J., Huntington, C., Helle, G., Treydte, K., Zimmermann, N.E., Schleser, G.H., Ahlström, A., Ciais, P., Friedlingstein, P., Levis, S., Lomas, M., Sitch, S., Viovy, N., Andreu-Hayles, L., Bednarz, Z., Berninger, F., Boettger, T., D'alessandro, C.M., Daux, V., Filot, M., Grabner, M., Gutierrez, E., Haupt, M., Hilasvuori, E., Jungner, H., Kalela-Brundin, M., Krapiec, M., Leuenberger, M., Loader, N.J., Marah, H., Masson-Delmotte, V., Pazzur, A., Pawelczyk, S., Pierre, M., Planells, O., Pukiene, R., Reynolds-Henne, C.E., Rinne, K. T., Saracino, A., Sonninen, E., Stievenard, M., Switsur, V.R., Szczepanek, M., Szychowska-Krapiec, E., Todoru, L., Waterhouse, J.S., Weigl, M., 2015. Water-use efficiency and transpiration across European forests during the Anthropocene. *Nat. Clim. Chang.* 5, 579–583. <https://doi.org/10.1038/nclimate2614>.
- Franks, P.J., Berry, J.A., Lombardozi, D.L., Bonan, G.B., 2017. Stomatal function across temporal and spatial scales: deep-time trends, land-atmosphere coupling and global models. *Plant Physiol.* 174, 583–602.
- Franzaring, J., Högy, P., Erbs, M., Fangmeier, A., 2010. Responses of canopy and soil climate in a six year free-air CO<sub>2</sub> enrichment study with spring crops. *Agric. For. Meteorol.* <https://doi.org/10.1016/j.agrformet.2009.11.018>.
- García-Amorena, I., Wagner, F., van Hoof, T.B., Gómez-Manzanaque, F., 2006. Stomatal responses in deciduous oaks from southern Europe to the anthropogenic atmospheric CO<sub>2</sub> increase; refining the stomatal-based CO<sub>2</sub> proxy. *Rev. Palaeobot. Palynol.* 141, 303–312. <https://doi.org/10.1016/j.revpalbo.2006.06.002>.
- Gentine, P., Green, J., Guerin, M., Humphrey, V., Seneviratne, S., Zhang, Y., Zhou, S., 2019. Coupling between the terrestrial carbon and water cycles - a review. *Environ. Res. Lett.* 14, 083003. <https://doi.org/10.1088/1748-9326/ab22d6>.
- Ghimire, C.P., Bruijnzeel, L.A., Lubczynski, M.W., Zwartendijk, B.W., Odongo, V.O., Ravelona, M., van Meerveld, H.J. (Ilja), 2018. Transpiration and stomatal conductance in a young secondary tropical montane forest: contrasts between native trees and invasive understorey shrubs. *Tree Physiol.* 38, 1053–1070. <https://doi.org/10.1093/treephys/tpy004>.
- Gimeno, T.E., Crous, K.Y., Cooke, J., O'Grady, A.P., Ósváldsson, A., Medlyn, B.E., Ellsworth, D.S., 2016. Conserved stomatal behaviour under elevated CO<sub>2</sub> and varying water availability in a mature woodland. *Funct. Ecol.* 30, 700–709. <https://doi.org/10.1111/1365-2435.12532>.
- Goeking, S.A., Tarboton, D.G., 2020. Forests and water yield: a synthesis of disturbance effects on streamflow and snowpack in western coniferous forests. *J. For.* 118, 172–192. <https://doi.org/10.1093/jofore/fvz069>.
- Gotsch, S.G., Asbjornsen, H., Goldsmith, G.R., 2016. Plant carbon and water fluxes in tropical montane cloud forests. *J. Trop. Ecol.* 32, 404–420. <https://doi.org/10.1017/S0266467416000341>.
- Graniar, A., Hue, R., Barigah, S.T., 1996. Transpiration of natural rain forest and its dependence on climatic factors. *Agric. For. Meteorol.* 78, 19–29. [https://doi.org/10.1016/0168-1923\(95\)02252-X](https://doi.org/10.1016/0168-1923(95)02252-X).
- Green, J.K., Berry, J., Ciais, P., Zhang, Y., Gentine, P., 2020. Amazon rainforest photosynthesis increases in response to atmospheric dryness. *Sci. Adv.* 6. <https://doi.org/10.1126/sciadv.abb7232>.
- Greve, P., Roderick, M.L., Ukkola, A.M., Wada, Y., 2019. The aridity Index under global warming. *Environ. Res. Lett.* 14, 124006. <https://doi.org/10.1088/1748-9326/ab5046>.
- Grossiord, C., 2020. Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytol.* 228, 42–49. <https://doi.org/10.1111/nph.15667>.
- Grossiord, C., Gessler, A., Granier, A., Berger, S., Bréchet, C., Hentschel, R., Hommel, R., Scherer-Lorenzen, M., Bonal, D., 2014. Impact of interspecific interactions on the soil water uptake depth in a young temperate mixed species plantation. *J. Hydrol.* 519, 3511–3519. <https://doi.org/10.1016/j.jhydrol.2014.11.011>.
- Grossiord, C., Christoffersen, B., Alonso-Rodríguez, A.M., Anderson-Teixeira, K., Asbjornsen, H., Aparecido, L.M.T., Carter Berry, Z., Baraloto, C., Bonal, D., Borrego, I., Burban, B., Chambers, J.Q., Christianson, D.S., Detto, M., Faybishenko, B., Fontes, C.G., Fortunel, C., Gimenez, B.O., Jardine, K.J., Kueppers, L., Miller, G.R., Moore, G.W., Negron-Juarez, R., Stahl, C., Swenson, N.G., Trotsiuk, V., Varadharajan, C., Warren, J.M., Wolfe, B.T., Wei, L., Wood, T.E., Xu, C., McDowell, N.G., 2019. Precipitation mediates sap flow sensitivity to evaporative demand in the neotropics. *Oecologia* 191, 519–530. <https://doi.org/10.1007/s00442-019-04513-x>.
- Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. *New Phytol.* 226, 1550–1566. <https://doi.org/10.1111/nph.16485>.
- Guerrieri, R., Belmecheri, S., Ollinger, S.V., Asbjornsen, H., Jennings, K., Xiao, J., Stocker, B.D., Martin, M., Hollinger, D.Y., Bracho-Garrillo, R., Clark, K., Dore, S., Kolb, T., Munger, J.W., Novick, K., Richardson, A.D., 2019. Disentangling the role of photosynthesis and stomatal conductance on rising forest water-use efficiency. *Proc. Natl. Acad. Sci.* 116, 16909–16914.
- Hao, G.-Y., Holbrook, N.M., Zwieniecki, M.A., Gutschick, V.P., BassiriRad, H., 2018. Coordinated responses of plant hydraulic architecture with the reduction of stomatal conductance under elevated CO<sub>2</sub> concentration. *Tree Physiol.* 38, 1041–1052. <https://doi.org/10.1093/treephys/tpy001>.

- Hasper, T.B., Wallin, G., Lamba, S., Hall, M., Jaramillo, F., Laudon, H., Linder, S., Medhurst, J.L., Råntfors, M., Sigurdsson, B.D., Uddling, J., 2016. Water use by Swedish boreal forests in a changing climate. *Funct. Ecol.* 30, 690–699. <https://doi.org/10.1111/1365-2435.12546>.
- Holden, Z.A., Swanson, A., Luce, C.H., Jolly, W.M., Maneta, M., Oyler, J.W., Warren, D. A., Parsons, R., Affleck, D., 2018. Decreasing fire season precipitation increased recent western US forest wildfire activity. *Proc. Natl. Acad. Sci. U. S. A.* <https://doi.org/10.1073/pnas.1802316115>.
- Huang, J., Yu, H., Guan, X., Wang, G., Guo, R., 2016a. Accelerated dryland expansion under climate change. *Nat. Clim. Chang.* <https://doi.org/10.1038/nclimate2837>.
- Huang, Y., Gerber, S., Huang, T., Lichstein, J.W., 2016b. Evaluating the drought response of CMIP5 models using global gross primary productivity, leaf area, precipitation, and soil moisture data. *Glob. Biogeochem. Cycles* 30, 1827–1846. <https://doi.org/10.1002/2016GB005480>.
- Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T., Jackson, R.B., 2005. Ecological implications of woody plant encroachment. *Ecology* 86, 308–319.
- Igarashi, Y., Katul, G.G., Kumagai, T., Yoshifuji, N., Sato, T., Tanaka, N., Tanaka, K., Fujinami, H., Suzuki, M., Tantisirin, C., 2015. Separating physical and biological controls on long-term evapotranspiration fluctuations in a tropical deciduous forest subjected to monsoonal rainfall. *J. Geophys. Res. G Biogeosci.* 120, 1262–1278. <https://doi.org/10.1002/2014JG002767>.
- IPCC, 2021. IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.
- Iversen, C.M., 2010. Digging deeper: fine-root responses to rising atmospheric CO<sub>2</sub> concentration in forested ecosystems. *New Phytol.* 186, 346–357. <https://doi.org/10.1111/j.1469-8137.2009.03122.x>.
- Jasechko, S., Sharp, Z.D., Gibson, J.J., Birks, S.J., Yi, Y., Fawcett, P.J., 2013. Terrestrial water fluxes dominated by transpiration. *Nature* 496, 347–350. <https://doi.org/10.1038/nature11983>.
- Jiang, M., Medlyn, B.E., Drake, J.E., Duursma, R.A., Anderson, I.C., Barton, C.V.M., Boer, M.M., Carrillo, Y., Castañeda-Gómez, L., Collins, L., Crous, K.Y., De Kauwe, M. G., dos Santos, B.M., Emmerson, K.M., Facey, S.L., Gherlenda, A.N., Gimeno, T.E., Hasegawa, S., Johnson, S.N., Kännaste, A., Macdonald, C.A., Mahmud, K., Moore, B. D., Nazaries, L., Neilson, E.H.J., Nielsen, U.N., Niinemets, Ü., Noh, N.J., Ochoa-Hueso, R., Pathare, V.S., Pendall, E., Pihlblad, J., Pineiro, J., Powell, J.R., Power, S. A., Reich, P.B., Renchon, A.A., Riegler, M., Rinnan, R., Rymer, P.D., Salomón, R.L., Singh, B.K., Smith, B., Tjoelker, M.G., Walker, J.K.M., Wujeska-Klaue, A., Yang, J., Zaehle, S., Ellsworth, D.S., 2020. The fate of carbon in a mature forest under carbon dioxide enrichment. *Nature* 580, 227–231. <https://doi.org/10.1038/s41586-020-2128-9>.
- Jiang, M., Kelly, J.W.G., Atwell, B.J., Tissue, D.T., Medlyn, B.E., 2021. Drought by CO<sub>2</sub> interactions in trees: a test of the water savings mechanism. *New Phytol.* 230, 1421–1434.
- Jiao, X.-C., Song, X.-M., Zhang, D.-L., Du, Q.-J., Li, J.-M., 2019. Coordination between vapor pressure deficit and CO<sub>2</sub> on the regulation of photosynthesis and productivity in greenhouse tomato production. *Sci. Rep.* 9, 8700. <https://doi.org/10.1038/s41598-019-45232-w>.
- Jordan, G.J., Carpenter, R.J., Holland, B.R., Beeton, N.J., Woodhams, M.D., Brodribb, T. J., 2020. Links between environment and stomatal size through evolutionary time in Proteaceae. *Proc. R. Soc. B Biol. Sci.* 287, 20192876. <https://doi.org/10.1098/rspb.2019.2876>.
- Katul, G.G., Oren, R., Manzoni, S., Higgins, C., Parlange, M.B., 2012. Evapotranspiration: a process driving mass transport and energy exchange in the soil-plant-atmosphere-climate system. *Rev. Geophys.* 50, RG3002.
- Keel, S.G., Pepin, S., Leuzinger, S., Körner, C., 2006. Stomatal conductance in mature deciduous forest trees exposed to elevated CO<sub>2</sub>. *Trees* 21, 151. <https://doi.org/10.1007/s00468-006-0106-y>.
- Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., Bennett, A. F., Buckland, S.T., Canelles, Q., Clarke, M.F., Fortin, M.-J., Hermoso, V., Herrando, S., Keane, R.E., Lake, F.K., McCarthy, M.A., Morán-Ordóñez, A., Parr, C.L., Pausas, J.G., Penman, T.D., Regos, A., Rumpff, L., Santos, J.L., Smith, A.L., Syphard, A.D., Tingley, M.W., Brotons, L., 2020. Fire and biodiversity in the Anthropocene. *Science* (80-) 370, 929.
- Kennedy, D., Swenson, S., Oleson, K.W., Lawrence, D.M., Fisher, R., Lola da Costa, A.C., Gentile, P., 2019. Implementing plant hydraulics in the community land model, version 5. *J. Adv. Model. Earth Syst.* <https://doi.org/10.1029/2018MS001500>.
- Kirschbaum, M., Mcmillan, A., 2018. Warming and elevated CO<sub>2</sub> have opposing influences on transpiration. Which is more important? *Curr. For. Rep.* 4, 1–21. <https://doi.org/10.1007/s40725-018-0073-8>.
- Klein, T., 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct. Ecol.* 28, 1313–1320. <https://doi.org/10.1111/1365-2435.12289>.
- Klein, T., Ramon, U., 2019. Stomatal sensitivity to CO<sub>2</sub> diverges between angiosperm and gymnosperm tree species. *Funct. Ecol.* 33, 1411–1424. <https://doi.org/10.1111/1365-2435.13379>.
- Knauer, J., Werner, C., Zaehle, S., 2015. Evaluating stomatal models and their atmospheric drought response in a land surface scheme: A multi-biome analysis. *J. Geophys. Res. Biogeosci.* 120, 1894–1911. <https://doi.org/10.1002/2015JG003114>.
- Knauer, J., Zaehle, S., Reichstein, M., Medlyn, B.E., Forkel, M., Hagemann, S., Werner, C., 2017. The response of ecosystem water-use efficiency to rising atmospheric CO<sub>2</sub> concentrations: sensitivity and large-scale biogeochemical implications. *New Phytol.* 213, 1654–1666. <https://doi.org/10.1111/nph.14288>.
- Konrad, W., Roth-Nebelsick, A., Grein, M., 2008. Modelling of stomatal density response to atmospheric CO<sub>2</sub>. *J. Theor. Biol.* 253, 638–658. <https://doi.org/10.1016/j.jtbi.2008.03.032>.
- Körner, C., 2017. When meta-analysis fails: a case about stomata. *Glob. Chang. Biol.* 23, 2533–2534. <https://doi.org/10.1111/gcb.13700>.
- Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W., Zotz, G., 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO<sub>2</sub>. *Science* (80-) 309, 1360–1362.
- Körner, C., Morgan, J., Norby, R., 2007. CO<sub>2</sub> Fertilization: when, where, how much?. In: *Terrestrial Ecosystems in a Changing World*, pp. 9–21. [https://doi.org/10.1007/978-3-540-32730-1\\_2](https://doi.org/10.1007/978-3-540-32730-1_2).
- Kosugi, Y., Takanashi, S., Tani, M., Ohkubo, S., Matsuo, N., Itoh, M., Noguchi, S., Nik, A. R., 2012. Effect of inter-annual climate variability on evapotranspiration and canopy CO<sub>2</sub> exchange of a tropical rainforest in Peninsular Malaysia. *J. For. Res.* 17, 227–240. <https://doi.org/10.1007/s10310-010-0235-4>.
- Krich, C., Mahecha, M.D., Migliavacca, M., De Kauwe, M.G., Griebel, A., Runge, J., Miralles, D.G., 2022. Decoupling between ecosystem photosynthesis and transpiration: a last resort against overheating. *Environ. Res. Lett.* 17, 044013. <https://doi.org/10.1088/1748-9326/ac583e>.
- Lammertsma, E.I., de Boer, H.J., Dekker, S.C., Dilcher, D.L., Lotter, A.F., Wagner-Cremer, F., 2011. Global CO<sub>2</sub> rise leads to reduced maximum stomatal conductance in Florida vegetation. *Proc. Natl. Acad. Sci.* 108, 4035–4040.
- Lansu, E.M., van Heerwaarden, C.C., Stegehuis, A.L., Teuling, A.J., 2020. Atmospheric aridity and apparent soil moisture drought in European forest during heat waves. *Geophys. Res. Lett.* 47, e2020GL087091.
- Lauriks, F., Salomon, R.L., Steppe, K., 2020. Temporal variability in tree responses to elevated atmospheric CO<sub>2</sub>. *Plant Cell Environ.* 44, 1292–1310.
- Lawrence, D.M., Thornton, P.E., Oleson, K.W., Bonan, G.B., 2007. The Partitioning of evapotranspiration into transpiration, soil evaporation, and canopy evaporation in a GCM: impacts on land-atmosphere interaction. *J. Hydrometeorol.* 8, 862–880. <https://doi.org/10.1175/JHM596.1>.
- Leakey, A.D.B., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., Ort, D.R., 2009. Elevated CO<sub>2</sub> effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J. Exp. Bot.* 60, 2859–2876. <https://doi.org/10.1093/jxb/erp096>.
- Lemordant, L., Gentile, P., Stéfanon, M., Drobinski, P., Faticchi, S., 2016. Modification of land-atmosphere interactions by CO<sub>2</sub> effects: Implications for summer dryness and heat wave amplitude. *Geophys. Res. Lett.* 43, 10240–10248.
- Lemordant, L., Gentile, P., Swann, A.S., Cook, B.I., Scheff, J., 2018. Critical impact of vegetation physiology on the continental hydrologic cycle in response to increasing CO<sub>2</sub>. *Proc. Natl. Acad. Sci. U. S. A.* 115, 4093–4098. <https://doi.org/10.1073/pnas.1720712115>.
- Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C<sub>3</sub> plants. *Plant Cell Environ.* 18, 339–355. <https://doi.org/10.1111/j.1365-3040.1995.tb00370.x>.
- Leuzinger, S., Körner, C., 2007. Water savings in mature deciduous forest trees under elevated CO<sub>2</sub>. *Glob. Chang. Biol.* 13, 2498–2508. <https://doi.org/10.1111/j.1365-2486.2007.01467.x>.
- Leuzinger, S., Körner, C., 2010. Rainfall distribution is the main driver of runoff under future CO<sub>2</sub>-concentration in a temperate deciduous forest. *Glob. Chang. Biol.* 16, 246–254. <https://doi.org/10.1111/j.1365-2486.2009.01937.x>.
- Li, J., Huo, R., Chen, H., Zhao, Y., Zhao, T., 2021. Comparative assessment and future prediction using CMIP6 and CMIP5 for annual precipitation and extreme precipitation simulation. *Front. Earth Sci.* 9, 430. <https://doi.org/10.3389/feart.2021.687976>.
- Lian, X., Piao, S., Huntingford, C., Li, Y., Zeng, Z., Wang, X., Ciais, P., McVicar, T.R., Peng, S., Otlé, C., Yang, H., Yang, Y., Zhang, Y., Wang, T., 2018. Partitioning global land evapotranspiration using CMIP5 models constrained by observations. *Nat. Clim. Chang.* 8, 640–646. <https://doi.org/10.1038/s41558-018-0207-9>.
- Lian, X., Piao, S., Li, L.Z.X., Li, Y., Huntingford, C., Ciais, P., Cescatti, A., Janssens, I.A., Peñuelas, J., Buermann, W., Chen, A., Li, X., Myneni, R.B., Wang, X., Wang, Y., Yang, Y., Zeng, Z., Zhang, Y., McVicar, T.R., 2020. Summer soil drying exacerbated by earlier spring greening of northern vegetation. *Sci. Adv.* 6 <https://doi.org/10.1126/sciadv.aax0255>.
- Lian, X., Piao, S., Chen, A., Huntingford, C., Fu, B., Li, L.Z.X., Huang, J., Sheffield, J., Berg, A.M., Keenan, T.F., McVicar, T.R., Wada, Y., Wang, X., Wang, T., Yang, Y., Roderick, M.L., 2021. Multifaceted characteristics of dryland aridity changes in a warming world. *Nat. Rev. Earth Environ.* 2, 232–250. <https://doi.org/10.1038/s43017-021-00144-0>.
- Liu, Z., Ballantyne, A.P., Cooper, L.A., 2019. Biophysical feedback of global forest fires on surface temperature. *Nat. Commun.* 10, 214.
- Liu, Y., Kumar, M., Katul, G.G., Feng, X., Konings, A.G., 2020. Plant hydraulics accentuates the effect of atmospheric moisture stress on transpiration. *Nat. Clim. Chang.* 10, 691–695. <https://doi.org/10.1038/s41558-020-0781-5>.
- Liu, J., You, Y., Li, J., Stith, S., Gu, X., Nabel, J.E.M.S., Lombardozzi, D., Luo, M., Feng, X., Arneth, A., Jain, A.K., Friedlingstein, P., Tian, H., Poulter, B., Kong, D., 2021. Response of global land evapotranspiration to climate change, elevated CO<sub>2</sub>, and land use change. *Agric. For. Meteorol.* 311, 108663. <https://doi.org/10.1016/j.agrformet.2021.108663>.
- Long, S.P., Ainsworth, E.A., Rogers, A., Ort, D.R., 2004. Rising atmospheric carbon dioxide: plants FACE the future. *Annu. Rev. Plant Biol.* 55, 591–628. <https://doi.org/10.1146/annurev.arplant.55.031903.141610>.
- Ma, Q., Bales, R.C., Rungee, J., Conklin, M.H., Collins, B.M., Goulden, M.L., 2020. Wildfire controls on evapotranspiration in California's Sierra Nevada. *J. Hydrol.* 590, 125364. <https://doi.org/10.1016/j.jhydrol.2020.125364>.

- Mahowald, N., Lo, F., Zheng, Y., Harrison, L., Funk, C., Lombardozzi, D., Goodale, C., 2016. Projections of leaf area index in earth system models. *Earth Syst. Dyn.* 7, 211–229. <https://doi.org/10.5194/esd-7-211-2016>.
- Mankin, J.S., Seager, R., Smerdon, J.E., Cook, B.I., Williams, A.P., Horton, R.M., 2018. Blue water trade-offs with vegetation in a CO<sub>2</sub>-enriched climate. *Geophys. Res. Lett.* 45, 3115–3125. <https://doi.org/10.1002/2018GL077051>.
- Mankin, J.S., Seager, R., Smerdon, J.E., Cook, B.I., Williams, A.P., 2019. Mid-latitude freshwater availability reduced by projected vegetation responses to climate change. *Nat. Geosci.* 12, 983–988. <https://doi.org/10.1038/s41561-019-0480-x>.
- Manusch, C., Bugmann, H., Heiri, C., Wolf, A., 2012. Tree mortality in dynamic vegetation models – a key feature for accurately simulating forest properties. *Ecol. Model.* 243, 101–111. <https://doi.org/10.1016/j.ecolmodel.2012.06.008>.
- Marchand, W., Girardin, M.P., Hartmann, H., Depardieu, C., Isabel, N., Gauthier, S., Boucher, É., Bergeron, Y., 2020. Strong overestimation of water-use efficiency responses to rising CO<sub>2</sub> in tree-ring studies. *Glob. Chang. Biol.* 26, 4538–4558. <https://doi.org/10.1111/gcb.15166>.
- Marengo, R.A., Nascimento, H.C.S., Magalhães, N.S., 2014. Stomatal conductance in Amazonian tree saplings in response to variations in the physical environment. *Photosynthetica* 52, 493–500. <https://doi.org/10.1007/s11099-014-0056-3>.
- Martínez-Vilalta, J., Poyatos, R., Aguadé, D., Retana, J., Mencuccini, M., 2014. A new look at water transport regulation in plants. *New Phytol.* 204, 105–115. <https://doi.org/10.1111/nph.12912>.
- Martins, S.C.V., McAdam, S.A.M., Deans, R.M., DaMatta, F.M., Brodrribb, T.J., 2016. Stomatal dynamics are limited by leaf hydraulics in ferns and conifers: results from simultaneous measurements of liquid and vapour fluxes in leaves. *Plant Cell Environ.* 39, 694–705. <https://doi.org/10.1111/pce.12668>.
- Massmann, A., Gentine, P., Lin, C., 2019. When does vapor pressure deficit drive or reduce evapotranspiration? *J. Adv. Model. Earth Syst.* 11, 3305–3320. <https://doi.org/10.1029/2019MS001790>.
- Mathias, J.M., Thomas, R.B., 2021. Global tree intrinsic water use efficiency is enhanced by increased atmospheric CO<sub>2</sub> and modulated by climate and plant functional types. *Proc. Natl. Acad. Sci.* 118, e2014286118.
- Mccarthy, H., Oren, R., FINZI, A., Ellsworth, D., KIM, H.-S., Johnsen, K., MILLAR, B., 2007. Temporal dynamics and spatial variability in the enhancement of canopy leaf area under elevated atmospheric CO<sub>2</sub>. *Glob. Chang. Biol.* 13, 2479–2497. <https://doi.org/10.1111/j.1365-2486.2007.01455.x>.
- McDowell, N.G., Williams, A.P., Xu, C., Pockman, W.T., Dickman, L.T., Sevanto, S., Pangle, R., Limousin, J., Plaut, J., Mackay, D.S., Ogee, J., Domec, J.C., Allen, C.D., Fisher, R.A., Jiang, X., Muss, J.D., Breshears, D.D., Rauscher, S.A., Koven, C., 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nat. Clim. Chang.* 6, 295–300. <https://doi.org/10.1038/nclimate2873>.
- McDowell, N.G., Brodrribb, T.J., Nardini, A., 2019. Hydraulics in the 21st century. *New Phytol.* 224, 537–542. <https://doi.org/10.1111/nph.16151>.
- McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurr, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. *Science (80-)* 368 eaaz9463.
- McJannet, D., Fitch, P., Disher, M., Wallace, J., 2007. Measurements of transpiration in four tropical rainforest types of north Queensland. *Australia. Hydrol. Process.* 21, 3549–3564. <https://doi.org/10.1002/hyp.6576>.
- Medlyn, B.E., Barton, C.V.M., Broadmeadow, M.S.J., Ceulemans, R., De Angelis, P., Forstreuter, M., Freeman, M., Jackson, S.B., Kellomäki, S., Laitat, E., Rey, A., Roberntz, P., Sigurdsson, B.D., Strassmeyer, J., Wang, K., Curtis, P.S., Jarvis, P.G., 2001. Stomatal conductance of forest species after long-term exposure to elevated CO<sub>2</sub> concentration: a synthesis. *New Phytol.* 149, 247–264. <https://doi.org/10.1046/j.1469-8137.2001.00028.x>.
- Medlyn, B.E., Duursma, R.A., Eamus, D., Ellsworth, D.S., Prentice, I.C., Barton, C.V.M., Crous, K.Y., De Angelis, P., Freeman, M., Wingate, L., 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Glob. Chang. Biol.* 17, 2134–2144. <https://doi.org/10.1111/j.1365-2486.2010.02375.x>.
- Medlyn, B.E., De Kauwe, M.G., Duursma, R.A., 2016. New developments in the effort to model ecosystems under water stress. *New Phytol.* 212, 5–7. <https://doi.org/10.1111/nph.14082>.
- Medlyn, B.E., De Kauwe, M.G., Lin, Y.-S., Knauer, J., Duursma, R.A., Williams, C.A., Arneeth, A., Clement, R., Isaac, P., Limousin, J.-M., Linderson, M.-L., Meir, P., Martin-StPaul, N., Wingate, L., 2017. How do leaf and ecosystem measures of water-use efficiency compare? *New Phytol.* 216, 758–770. <https://doi.org/10.1111/nph.14626>.
- Mendes, K.R., Marengo, R.A., 2017. Stomatal opening in response to the simultaneous increase in vapor pressure deficit and temperature over a 24-h period under constant light in a tropical rainforest of the central Amazon. *Theor. Exp. Plant Physiol.* 29, 187–194. <https://doi.org/10.1007/s40626-017-0094-x>.
- Menezes-Silva, P.E., Loram-Lourenço, L., Alves, R.D.F.B., Sousa, L.F., da Almeida, S.E.S., Farnese, F.S., 2019. Different ways to die in a changing world: Consequences of climate change for tree species performance and survival through an ecophysiological perspective. *Ecol. Evol.* 9, 11979–11999.
- Milly, P.C.D., Dunne, K.A., 2016. Potential evapotranspiration and continental drying. *Nat. Clim. Chang.* 6, 946–949. <https://doi.org/10.1038/nclimate3046>.
- Miralles, D.G., Holmes, T.R.H., De Jeu, R.A.M., Gash, J.H., Meesters, A.G.C.A., Dolman, A.J., 2011. Global land-surface evaporation estimated from satellite-based observations. *Hydrol. Earth Syst. Sci.* 15, 453–469. <https://doi.org/10.5194/hess-15-453-2011>.
- Miralles, D.G., van den Berg, M.J., Gash, J.H., Parinussa, R.M., de Jeu, R.A.M., Beck, H. E., Holmes, T.R.H., Jiménez, C., Verhoest, N.E.C., Dorigo, W.A., Teuling, A.J., Johannes Dolman, A., 2014. El Niño–La Niña cycle and recent trends in continental evaporation. *Nat. Clim. Chang.* 4, 122–126. <https://doi.org/10.1038/nclimate2068>.
- Miralles, D., Gentine, P., Seneviratne, S.I., Teuling, A.J., 2019. Land-atmospheric feedbacks during droughts and heatwaves: state of the science and current challenges. *Ann. N. Y. Acad. Sci.* 8, 469.
- Monin, A.S., Obukhov, A.M., 1954. Basic Laws of Turbulent Mixing in the Ground Layer of the Atmosphere. *Tr. Geofiz. Inst. Akad. Nauk SSSR*.
- Morgan, J.A., Pataki, D.E., Körner, C., Clark, H., Del Grosso, S.J., Grünzweig, J.M., Knapp, A.K., Mosier, A.R., Newton, P.C.D., Niklaus, P.A., Nippert, J.B., Nowak, R.S., Parton, W.J., Polley, H.W., Shaw, M.R., 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO<sub>2</sub>. *Oecologia* 140, 11–25.
- Morgan, J.A., LeCain, D.R., Pendall, E., Blumenthal, D.M., Kimball, B.A., Carrillo, Y., Williams, D.G., Heisler-White, J., Dijkstra, F.A., West, M., 2011. C4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* 476, 202–205. <https://doi.org/10.1038/nature10274>.
- Morillas, L., Pangle, R.E., Maurer, G.E., Pockman, W.T., McDowell, N., Huang, C.-W., Krofcheck, D.J., Fox, A.M., Sinsabaugh, R.L., Rahn, T.A., Litvak, M.E., 2017. Tree Mortality Decreases Water Availability and Ecosystem Resilience to Drought in Piñon-Juniper Woodlands in the Southwestern U.S. *J. Geophys. Res. Biogeosci.* 122, 3343–3361. <https://doi.org/10.1002/2017JG004095>.
- Morris, L.R., Monaco, T.A., Sheley, R.L., 2011. Land-Use legacies and vegetation recovery 90 years after cultivation in great basin sagebrush ecosystems. *Rangel. Ecol. Manag.* <https://doi.org/10.2111/REM-D-10-00147.1>.
- Motzer, T., Munz, N., Küppers, M., Schmitt, D., Anhuif, D., 2005. Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes. *Tree Physiol.* 25, 1283–1293. <https://doi.org/10.1093/treephys/25.10.1283>.
- Mou, P., Fahey, T.J., Hughes, J.W., 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. *J. Appl. Ecol.* <https://doi.org/10.2307/2404245>.
- Naumburg, E., Housman, D.C., Huxman, T.E., Charlet, T.N., Loik, M.E., Smith, S.D., 2003. Photosynthetic responses of Mojave Desert shrubs to free air CO<sub>2</sub> enrichment are greatest during wet years. *Glob. Chang. Biol.* 9, 276–285. <https://doi.org/10.1046/j.1365-2486.2003.00580.x>.
- Nelson, J.A., Pérez-Priego, O., Zhou, S., Poyatos, R., Zhang, Y., Blanken, P.D., Gimeno, T. E., Wohlfahrt, G., Desai, A.R., Gioli, B., Limousin, J.-M., Bonal, D., Paul-Limoges, E., Scott, R.L., Varlagin, A., Fuchs, K., Montagnani, L., Wolf, S., Delpiere, N., Berveiller, D., Gharun, M., Belleli Marchesini, L., Gianelle, D., Šigut, L., Mammarella, I., Siebicke, L., Andrew Black, T., Knohl, A., Hörtnagl, L., Magliulo, V., Besnard, S., Weber, U., Carvalhais, N., Migliavacca, M., Reichstein, M., Jung, M., 2020. Ecosystem transpiration and evaporation: Insights from three water flux partitioning methods across FLUXNET sites. *Glob. Chang. Biol.* 26, 6916–6930. <https://doi.org/10.1111/gcb.15314>.
- Nie, M., Lu, M., Bell, J., Raut, S., Pendall, E., 2013. Altered root traits due to elevated CO<sub>2</sub>: a meta-analysis. *Glob. Ecol. Biogeogr.* 22, 1095–1105. <https://doi.org/10.1111/gcb.12062>.
- Norby, R.J., Wulfscheger, S.D., Gundersson, C.A., Johnson, D.W., Ceulemans, R., 1999. Tree responses to rising CO<sub>2</sub> in field experiments: implications for the future forest. *Plant Cell Environ.* 22, 683–714. <https://doi.org/10.1046/j.1365-3040.1999.00391.x>.
- Oki, T., Kanae, S., 2006. Global hydrological cycles and world water resour. *Science (80-)* 313, 1068–1072.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ.* 22, 1515–1526. <https://doi.org/10.1046/j.1365-3040.1999.00513.x>.
- Pan, Y., Jackson, R.B., Hollinger, D.Y., Phillips, O.L., Nowak, R.S., Norby, R.J., Oren, R., Reich, P.B., Lüscher, A., Mueller, K.E., Owensby, C., Birdsey, R., Hom, J., Luo, Y., 2022. Contrasting responses of woody and grassland ecosystems to increased CO<sub>2</sub> as water supply varies. *Nat. Ecol. Evol.* 6, 315–323. <https://doi.org/10.1038/s41559-021-01642-6>.
- Park, H., Jeong, S., 2021. Leaf area index in Earth system models: how the key variable of vegetation seasonality works in climate projections. *Environ. Res. Lett.* 16, 034027. <https://doi.org/10.1088/1748-9326/abe2cf>.
- Park, S.-W., Kim, J.-S., Kug, J.-S., 2020. The intensification of Arctic warming as a result of CO<sub>2</sub> physiological forcing. *Nat. Commun.* 11, 2098. <https://doi.org/10.1038/s41467-020-15924-3>.
- Parnesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. <https://doi.org/10.1038/nature01286>.
- Paschalis, A., Faticchi, S., Pappas, C., Or, D., 2018. Covariation of vegetation and climate constrains present and future T/ET variability. *Environ. Res. Lett.* 13, 104012. <https://doi.org/10.1088/1748-9326/aae267>.
- Pataki, D.E., Huxman, T.E., Jordan, D.N., Zitzer, S.F., Coleman, J.S., Smith, S.D., Nowak, R.S., Seemann, J.R., 2000. Water use of two Mojave desert shrubs under elevated CO<sub>2</sub>. *Glob. Chang. Biol.* 6, 889–897. <https://doi.org/10.1046/j.1365-2486.2000.00360.x>.
- Peña-Angulo, D., Vicente-Serrano, S.M., Domínguez-Castro, F., Noguera, I., Tomas-Burguera, M., López-Moreno, J.I., Lorenzo-Lacruz, J., El Kenawy, A., 2021. Unravelling the role of vegetation on the different trends between climatic and hydrologic drought in headwater catchments of Spain. *Anthropocene* 36, 100309. <https://doi.org/10.1016/j.ancene.2021.100309>.
- Pendergrass, A.G., Knutti, R., Lehner, F., Deser, C., Sanderson, B.M., 2017. Precipitation variability increases in a warmer climate. *Sci. Rep.* 7, 17966.
- Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., Van Der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M., Janssens, I.A., 2013. Human-induced nitrogen-phosphorus imbalances alter natural



- and managed ecosystems across the globe. *Nat. Commun.* <https://doi.org/10.1038/ncomms3934>.
- Powell, T.L., Galbraith, D.R., Christoffersen, B.O., Harper, A., Imbuzeiro, H.M.A., Rowland, L., Almeida, S., Brandão, P.M., da Costa, A.C.L., Costa, M.H., Levine, N.M., Malhi, Y., Saleska, S.R., Sotta, E., Williams, M., Meir, P., Moorcroft, P.R., 2013. Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytol.* 200, 350–365. <https://doi.org/10.1111/nph.12390>.
- Poyatos, R., Granda, V., Molowny-Horas, R., Mencuccini, M., Steppe, K., Martínez-Vilalta, J., 2016. SAPFLUXNET: towards a global database of sap flow measurements. *Tree Physiol.* <https://doi.org/10.1093/treephys/tpw110>.
- Pritarch, S., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., Oren, R.A.M., 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO<sub>2</sub>-enrichment: a six-year-minirhizotron study. *Glob. Chang. Biol.* 14, 588–602. <https://doi.org/10.1111/j.1365-2486.2007.01523.x>.
- Purcell, C., Batke, S.P., Yiotis, C., Caballero, R., Soh, W.K., Murray, M., McElwain, J.C., 2018. Increasing stomatal conductance in response to rising atmospheric CO<sub>2</sub>. *Ann. Bot.* 121, 1137–1149. <https://doi.org/10.1093/aob/mcx208>.
- Raczka, B., Duarte, H.F., Koven, C.D., Ricciuto, D., Thornton, P.E., Lin, J.C., Bowling, D. R., 2016. An observational constraint on stomatal function in forests: evaluating coupled carbon and water vapor exchange with carbon isotopes in the Community Land Model (CLM4.5). *Biogeosciences* 13, 5183–5204. <https://doi.org/10.5194/bg-13-5183-2016>.
- Raz-Yaseef, N., Rotenberg, E., Yakir, D., 2010. Effects of spatial variations in soil evaporation caused by tree shading on water flux partitioning in a semi-arid pine forest. *Agric. For. Meteorol.* 150, 454–462. <https://doi.org/10.1016/j.agrformet.2010.01.010>.
- Reid, C.D., Maherali, H., Johnson, H.B., Smith, S.D., Wullschlegel, S.D., Jackson, R.B., 2003. On the relationship between stomatal characters and atmospheric CO<sub>2</sub>. *Geophys. Res. Lett.* 30, 1983.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., De Soyza, A.G., Tremmel, D.C., 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecol. Monogr.* 69, 69–106.
- Riederer, M., 2006. Thermodynamics of the water permeability of plant cuticles: characterization of the polar pathway. *J. Exp. Bot.* 57, 2937–2942. <https://doi.org/10.1093/jxb/erl053>.
- Rind, D., Chiou, E.-W., Chu, W., Larsen, J., Oltmans, S., Lerner, J., McCormick, M.P., McMaster, L., 1991. Positive water vapour feedback in climate models confirmed by satellite data. *Nature* 349, 500–503. <https://doi.org/10.1038/349500a0>.
- Roderick, M.L., Greve, P., Farquhar, G.D., 2015. On the assessment of aridity with changes in atmospheric CO<sub>2</sub>. *Water Resour. Res.* 51, 5450–5463. <https://doi.org/10.1002/2015WR017031>.
- Sardans, J., Peñuelas, J., 2012. The role of plants in the effects of global change on nutrient availability and stoichiometry in the plant-soil system. *Plant Physiol.* <https://doi.org/10.1104/pp.112.208785>.
- Sato, H., Kumagai, T., Takahashi, A., Katul, G.G., 2015. Effects of different representations of stomatal conductance response to humidity across the African continent under warmer CO<sub>2</sub>-enriched climate conditions. *J. Geophys. Res. Biogeosci.* 120, 979–988. <https://doi.org/10.1002/2014JG002838>.
- Saxe, H., Ellsworth, D., Heath, J., 1998. Tree and forest functioning in an enriched CO<sub>2</sub> atmosphere. *New Phytol.* 139, 395–436. <https://doi.org/10.1046/j.1469-8137.1998.00221.x>.
- Scheff, J., 2018. Drought indices, drought impacts, CO<sub>2</sub>, and warming: a historical and geologic perspective. *Curr. Clim. Chang. Rep.* 4, 202–209. <https://doi.org/10.1007/s40641-018-0094-1>.
- Schoennagel, T., Balch, J.K., Brenkert-Smith, H., Dennison, P.E., Harvey, B.J., Krawchuk, M.A., Mietkiewicz, N., Morgan, P., Moritz, M.A., Rasker, R., Turner, M.G., Whitlock, C., 2017. Adapt to wildfire in western North American forests as climate changes. *Proc. Natl. Acad. Sci. U. S. A.* <https://doi.org/10.1073/pnas.1617464114>.
- Scholten, R.C., Jandt, R., Miller, E.A., Rogers, B.M., Veraverbeke, S., 2021. Overwintering fires in boreal forests. *Nature* 593, 399–404. <https://doi.org/10.1038/s41586-021-03437-y>.
- Schreiber, L., 2001. Effect of temperature on cuticular transpiration of isolated cuticular membranes and leaf discs. *J. Exp. Bot.* 52, 1893–1900. <https://doi.org/10.1093/jxb/52.362.1893>.
- Sellers, P.J., Dickinson, R.E., Randall, D.A., Betts, A.K., Hall, F.G., Berry, J.A., Collatz, G. J., Denning, A.S., Mooney, H.A., Nobre, C.A., Sato, N., Field, C.B., Henderson-Sellers, A., 1997. Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science* (80-) 275, 502–509. <https://doi.org/10.1126/science.275.5299.502>.
- Seneviratne, S.I., Donat, M.G., Mueller, B., Alexander, L.V., 2014. No pause in the increase of hot temperature extremes. *Nat. Clim. Chang.* 4, 161–163. <https://doi.org/10.1038/nclimate2145>.
- Siddiq, Z., Cao, K.-F., 2016. Increased water use in dry season in eight dipterocarp species in a common plantation in the northern boundary of Asian tropics. *Ecology* 9, 871–881. <https://doi.org/10.1002/eco.1689>.
- Siddiq, Z., Chen, Y.-J., Zhang, Y.-J., Zhang, J.-L., Cao, K.-F., 2017. More sensitive response of crown conductance to VPD and larger water consumption in tropical evergreen than in deciduous broadleaf timber trees. *Agric. For. Meteorol.* 247, 399–407. <https://doi.org/10.1016/j.agrformet.2017.08.028>.
- Sinclair, T.R., Devi, J., Shekoofa, A., Choudhary, S., Sadok, W., Vadez, V., Riar, M., Ruffy, T., 2017. Limited-transpiration response to high vapor pressure deficit in crop species. *Plant Sci.* 260, 109–118. <https://doi.org/10.1016/j.plantsci.2017.04.007>.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob. Chang. Biol.* 9, 161–185. <https://doi.org/10.1046/j.1365-2486.2003.00569.x>.
- Skinner, C.B., Poulsen, C.J., Mankin, J.S., 2018. Amplification of heat extremes by plant CO<sub>2</sub> physiological forcing. *Nat. Commun.* 9, 1094. <https://doi.org/10.1038/s41467-018-03472-w>.
- Slot, M., Winter, K., 2017. In situ temperature relationships of biochemical and stomatal controls of photosynthesis in four lowland tropical tree species. *Plant Cell Environ.* 40, 3055–3068. <https://doi.org/10.1111/pce.13071>.
- Slot, M., Nardwattanawong, T., Hernández, G.G., Bueno, A., Riederer, M., Winter, K., 2021. Large differences in leaf cuticle conductance and its temperature response among 24 tropical tree species from across a rainfall gradient. *New Phytol.* 232, 1618–1631. <https://doi.org/10.1111/nph.17626>.
- Song, X., Wang, D.-Y., Li, F., Zeng, X.-D., 2019. Evaluating the performance of CMIP6 Earth system models in simulating global vegetation structure and distribution. *Adv. Clim. Chang. Res.* 12, 584–595. <https://doi.org/10.1016/j.accre.2021.06.008>.
- Stephens, C.M., Lall, U., Johnson, F.M., Marshall, L.A., 2021. Landscape changes and their hydrologic effects: interactions and feedbacks across scales. *Earth-Sci. Rev.* 212, 103466. <https://doi.org/10.1016/j.earscirev.2020.103466>.
- Stoy, P.C., El-Madany, T.S., Fisher, J.B., Gentile, P., Gerken, T., Good, S.P., Klosterhalfen, A., Liu, S., Miralles, D.G., Perez-Priego, O., Rigden, A.J., Skaggs, T.H., Wohlfahrt, G., Anderson, R.G., Coenders-Gerrits, A.M.J., Jung, M., Maes, W.H., Mammarella, I., Mauder, M., Migliavacca, M., Nelson, J.A., Poyatos, R., Reichstein, M., Scott, R.L., Wolf, S., 2019. Reviews and syntheses: turning the challenges of partitioning ecosystem evaporation and transpiration into opportunities. *Biogeosciences* 16, 3747–3775. <https://doi.org/10.5194/bg-16-3747-2019>.
- Swann, A.L.S., 2018. Plants and drought in a changing climate. *Curr. Clim. Chang. Rep.* 4, 192–201. <https://doi.org/10.1007/s40641-018-0097-y>.
- Swann, A.L.S., Koven, C.D., 2017. A Direct Estimate of the Seasonal Cycle of Evapotranspiration over the Amazon Basin. *J. Hydrometeorol.* 18, 2173–2185. <https://doi.org/10.1175/JHM-D-17-0004.1>.
- Swann, A.L.S., Hoffman, F.M., Koven, C.D., Randerson, J.T., 2016. Plant responses to increasing CO<sub>2</sub> reduce estimates of climate impacts on drought severity. *Proc. Natl. Acad. Sci. U. S. A.* 113, 10019–10024. <https://doi.org/10.1073/pnas.1604581113>.
- Teklehaimanot, Z., Jarvis, P.G., 1991. Direct measurement of evaporation of intercepted water from forest canopies. *J. Appl. Ecol.* <https://doi.org/10.2307/2404571>.
- Trenberth, K.E., Smith, L., Qian, T., Dai, A., Fasullo, J., 2007. Estimates of the global water budget and its annual cycle using observational and model data. *J. Hydrometeorol.* 8, 758–769. <https://doi.org/10.1175/JHM600.1>.
- Tricker, P.J., Trewin, H., Kull, O., Clarkson, G.J., Eensalu, E., Tallis, M.J., Colella, A., Doncaster, C.P., Sabatti, M., Taylor, G., 2005. Stomatal conductance and not stomatal density determines the long-term reduction in leaf transpiration of poplar in elevated CO<sub>2</sub>. *Oecologia* 143, 652–660. <https://doi.org/10.1007/s00442-005-0025-4>.
- Tsamir, M., Gottlieb, S., Preisler, Y., Rotenberg, E., Tatarinov, F., Yakir, D., Tague, C., Klein, T., 2019. Stand density effects on carbon and water fluxes in a semi-arid forest, from leaf to stand-scale. *For. Ecol. Manag.* 453, 117573. <https://doi.org/10.1016/j.foreco.2019.117573>.
- Uddin, S., Löw, M., Parvin, S., Fitzgerald, G.J., Tausz-Posch, S., Armstrong, R., O'Leary, G., Tausz, M., 2018. Elevated [CO<sub>2</sub>] mitigates the effect of surface drought by stimulating root growth to access sub-soil water. *PLoS One* 13, e0198928. <https://doi.org/10.1371/journal.pone.0198928>.
- Urban, J., Ingwers, M.W., McGuire, M.A., Teskey, R.O., 2017. Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in *Pinus taeda* and *Populus deltoides* × *nigra*. *J. Exp. Bot.* 68, 1757–1767. <https://doi.org/10.1093/jxb/erx052>.
- Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Bugería, S., Trigo, R., López-Moreno, J.I., Azorín-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Morán-Tejeda, E., Sanchez-Lorenzo, A., 2013. Response of vegetation to drought time-scales across global land biomes. *Proc. Natl. Acad. Sci. U. S. A.* 110, 52–57. <https://doi.org/10.1073/pnas.1207068110>.
- Vicente-Serrano, S., McVicar, T.R., Miralles, D.G., Yang, Y., Tomas-Burguera, M., 2020a. Unravelling the influence of atmospheric evaporative demand on drought and its response to climate change. *WIREs Clim. Chang.* 11, e632. <https://doi.org/10.1002/wcc.632>.
- Vicente-Serrano, S.M., Quiring, S., Peña-Gallardo, M., Domínguez-castro, F., Yuan, S., 2020b. A review of environmental droughts: Increased risk under global warming? *Earth Sci. Rev.* 201, 102953.
- Vicente-Serrano, S.M., Domínguez-Castro, F., Murphy, C., Peña-Angulo, D., Tomas-Burguera, M., Noguera, I., López-Moreno, J.I., Juez, C., Grainger, S., Eklundh, L., Conrad, T., Azorín-Molina, C., El Kenawy, A., 2021. Increased vegetation in mountainous headwaters amplifies water stress during dry periods. *Geophys. Res. Lett.* 48. <https://doi.org/10.1029/2021GL094672>.
- Vourlitis, G.L., De Souza Nogueira, J., De Almeida Lobo, F., Sendall, K.M., De Paulo, S.R., Antunes Dias, C.A., Pinto Jr., O.B., De Andrade, N.L.R., 2008. Energy balance and canopy conductance of a tropical semi-deciduous forest of the southern Amazon Basin. *Water Resour. Res.* 44. <https://doi.org/10.1029/2006WR005526>.
- Walker, A.P., De Kauwe, M.G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R.F., McMahon, S.M., Medlyn, B.E., Moore, D.J.P., Norby, R.J., Zaehle, S., Anderson-Teixeira, K.J., Battipaglia, G., Brienen, R.J.W., Cabugao, K.G., Cailleret, M., Campbell, E., Canadell, J.G., Ciais, P., Craig, M.E., Ellsworth, D.S., Farquhar, G.D., Fattichi, S., Fisher, J.B., Frank, D.C., Graven, H., Gu, L., Haverd, V., Heilmann, K., Heimann, M., Hungate, B.A., Iversen, C.M., Joo, F., Jiang, M., Keenan, T.F.,

- Knauer, J., Körner, C., Leshyk, V.O., Leuzinger, S., Liu, Y., MacBean, N., Malhi, Y., McVicar, T.R., Penuelas, J., Pongratz, J., Powell, A.S., Riutta, T., Sabot, M.E.B., Schleucher, J., Sitch, S., Smith, W.K., Sulman, B., Taylor, B., Terrer, C., Torn, M.S., Treseder, K.K., Trugman, A.T., Trumbore, S.E., van Mantgem, P.J., Voelker, S.L., Whelan, M.E., Zuidema, P.A., 2020. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO<sub>2</sub>. *New Phytol.* 229, 2413–2445.
- Wallace, J., McJannet, D., 2010. Processes controlling transpiration in the rainforests of north Queensland, Australia. *J. Hydrol.* 384, 107–117. <https://doi.org/10.1016/j.jhydrol.2010.01.015>.
- Wang, K., Dickinson, R.E., 2012. A review of global terrestrial evapotranspiration: Observation, modeling, climatology, and climatic variability. *Rev. Geophys.* 50, RG2005 <https://doi.org/10.1029/2011RG000373>.
- Wang, C., He, J., Zhao, T.-H., Cao, Y., Wang, G., Sun, B., Yan, X., Guo, W., Li, M.-H., 2019. The smaller the leaf is, the faster the leaf water loses in a temperate forest. *Front. Plant Sci.* 10, 58. <https://doi.org/10.3389/fpls.2019.00058>.
- Ward, E.J., Oren, R., Bell, D.M., Clark, J.S., McCarthy, H.R., Kim, H.-S., Domec, J.-C., 2013. The effects of elevated CO<sub>2</sub> and nitrogen fertilization on stomatal conductance estimated from 11 years of scaled sap flux measurements at Duke FACE. *Tree Physiol.* 33, 135–151. <https://doi.org/10.1093/treephys/tps118>.
- Warren, J.M., Pötzelberger, E., Wullschlegel, S.D., Thornton, P.E., Hasenauer, H., Norby, R.J., 2011. Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO<sub>2</sub>. *Ecohydrology* 4, 196–210. <https://doi.org/10.1002/eco.173>.
- Wei, Z., Yoshimura, K., Wang, L., Miralles, D.G., Jasechko, S., Lee, X., 2017. Revisiting the contribution of transpiration to global terrestrial evapotranspiration. *Geophys. Res. Lett.* 44, 2792–2801. <https://doi.org/10.1002/2016GL072235>.
- Werner, C., Meredith, L.K., Ladd, S.N., Ingrischi, J., Kübert, A., van Haren, J., Bahn, M., Bailey, K., Bamberger, I., Beyer, M., Blomdahl, D., Byron, J., Daber, E., Deleeu, J., Dippold, M.A., Fudyma, J., Gil-Loaiza, J., Honeker, L.K., Hu, J., Huang, J., Klüpfel, T., Krechmer, J., Kreuzwieser, J., Kühnhammer, K., Lehmann, M.M., Meeran, K., Misztal, P.K., Ng, W.R., Pfannerstill, E., Pugliese, G., Purser, G., Roscioli, J., Shi, L., Tfaily, M., Williams, J., 2021. Ecosystem fluxes during drought and recovery in an experimental forest. *Science* (80-) 374, 1514–1518. <https://doi.org/10.1126/science.abj6789>.
- Wesolowski, A., Blackman, C.J., Smith, R.A., Tissue, D.T., Pfautsch, S., 2020. Elevated CO<sub>2</sub> did not stimulate stem growth in 11 provenances of a globally important hardwood plantation species. *Front. For. Glob. Chang.* 3 <https://doi.org/10.3389/ffgc.2020.00066>.
- Wu, H., Fu, C., Wu, H., Zhang, L., 2020. Plant hydraulic stress strategy improves model predictions of the response of gross primary productivity to drought across China. *J. Geophys. Res. Atmos.* 125, e2020JD033476.
- Wullschlegel, S.D., Epstein, H.E., Box, E.O., Euskirchen, E.S., Goswami, S., Iversen, C.M., Kattge, J., Norby, R.J., Van Bodegom, P.M., Xu, X., 2014. Plant functional types in Earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Ann. Bot.* 114, 1–16. <https://doi.org/10.1093/aob/mcu077>.
- Xu, Z., Shimizu, H., Yagasaki, Y., Ito, S., Zheng, Y., Zhou, G., 2013. Interactive effects of elevated CO<sub>2</sub>, drought, and warming on plants. *J. Plant Growth Regul.* 32, 692–707. <https://doi.org/10.1007/s00344-013-9337-5>.
- Xu, X., Medvigy, D., Powers, J.S., Becknell, J.M., Guan, K., 2016a. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytol.* 212, 80–95. <https://doi.org/10.1111/nph.14009>.
- Xu, Z., Jiang, Y., Jia, B., Zhou, G., 2016b. Elevated-CO<sub>2</sub> response of stomata and its dependence on environmental factors. *Front. Plant Sci.* 657, 1–15.
- Yang, Y., Roderick, M.L., Zhang, S., McVicar, T.R., Donohue, R.J., 2019. Hydrologic implications of vegetation response to elevated CO<sub>2</sub> in climate projections. *Nat. Clim. Chang.* 9, 44–48. <https://doi.org/10.1038/s41558-018-0361-0>.
- Yang, Y., Roderick, M.L., Yang, D., Wang, Z., Ruan, F., McVicar, T.R., Zhang, S., Beck, H. E., 2021. Streamflow stationarity in a changing world. *Environ. Res. Lett.* 16, 064096.
- Yoshifuji, N., Kumagai, T., Ichie, T., Kume, T., Tateishi, M., Inoue, Y., Yoneyama, A., Nakashizuka, T., 2020. Limited stomatal regulation of the largest-size class of *Dryobalanops aromatica* in a Bornean tropical rainforest in response to artificial soil moisture reduction. *J. Plant Res.* 133, 175–191. <https://doi.org/10.1007/s10265-019-01161-3>.
- Zeng, Z., Piao, S., Li, L.Z.X., Wang, T., Ciais, P., Lian, X., Yang, Y., Mao, J., Shi, X., Myneni, R.B., 2018. Impact of Earth greening on the terrestrial water cycle. *J. Clim.* 31, 2633–2650. <https://doi.org/10.1175/JCLI-D-17-0236.1>.
- Zhang, M., Wei, X., 2021. Deforestation, forestation, and water supply. *Science* (80-) 371, 990–991. <https://doi.org/10.1126/science.abc7821>.
- Zhang, X., Zwiers, F.W., Hegerl, G.C., Lambert, F.H., Gillett, N.P., Solomon, S., Stott, P. A., Nozawa, T., 2007. Detection of human influence on twentieth-century precipitation trends. *Nature*. <https://doi.org/10.1038/nature06025>.
- Zhang, Y., Peña-Arancibia, J.L., McVicar, T.R., Chiew, F.H.S., Vaze, J., Liu, C., Lu, X., Zheng, H., Wang, Y., Liu, Y., Miralles, D.G., Pan, M., 2016. Multi-decadal trends in global terrestrial evapotranspiration and its components. *Sci. Rep.* 6, 19124. <https://doi.org/10.1038/srep19124>.
- Zhang, Y., Parazoo, N.C., Williams, A.P., Zhou, S., Gentile, P., 2020. Large and projected strengthening moisture limitation on end-of-season photosynthesis. *Proc. Natl. Acad. Sci.* 117, 9216–9222. <https://doi.org/10.1073/pnas.1914436117>.
- Zhao, Q., Zhu, Z., Zeng, H., Zhao, W., Myneni, R.B., 2020. Future greening of the Earth may not be as large as previously predicted. *Agric. For. Meteorol.* 292–293, 108111. <https://doi.org/10.1016/j.agrformet.2020.108111>.
- Zhou, S., Duursma, R.A., Medlyn, B.E., Kelly, J.W.G., Prentice, I.C., 2013. How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress. *Agric. For. Meteorol.* 182–183, 204–214. <https://doi.org/10.1016/j.agrformet.2013.05.009>.
- Zhou, S., Keenan, T.F., Williams, A.P., Lintner, B.R., Zhang, Y., Gentile, P., 2022. Large divergence in tropical hydrological projections caused by model spread in vegetation responses to elevated CO<sub>2</sub>. *Earth's Futur.* <https://doi.org/10.1029/2021EF002457> n/a, e2021EF002457.
- Zhu, K., Zhang, J., Niu, S., Chu, C., Luo, Y., 2018. Limits to growth of forest biomass carbon sink under climate change. *Nat. Commun.* 9, 2709. <https://doi.org/10.1038/s41467-018-05132-5>.