



Review Article

The uncertain role of rising atmospheric CO₂ on global plant transpiration

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ABSTRACT

As CO₂ 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 CO₂ 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 CO₂ will impact plant transpiration, the exact nature of this impact remains unclear due to complex interactions between CO₂ 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 CO₂ 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 CO₂ 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

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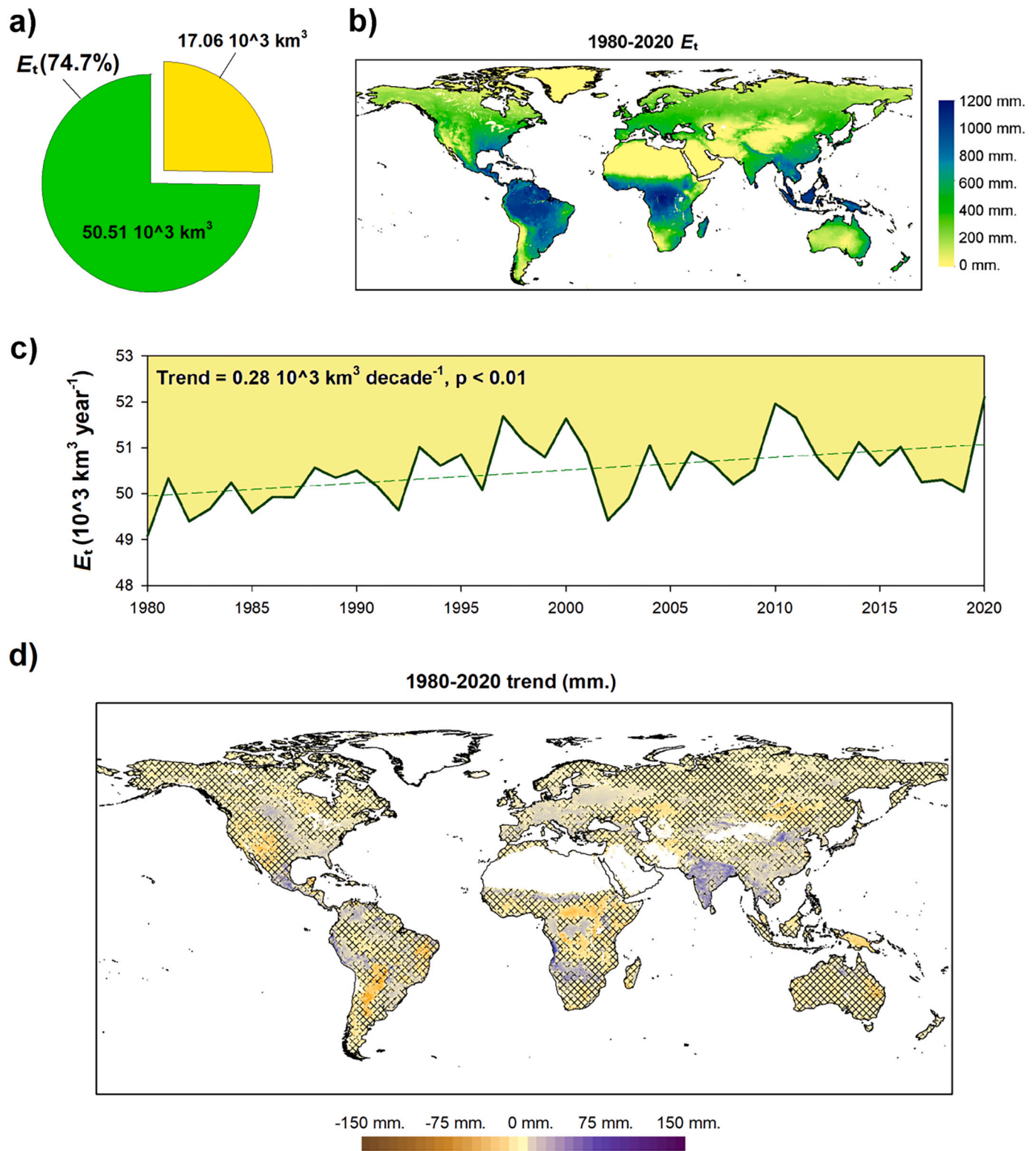


Fig. 1. a) 1980-2020 global average of annual magnitude of E_t and percentage regarding total E . The data is obtained from a combined remote sensing and modelling-based approach to obtain the GLEAM v3 dataset (<https://www.gleam.eu/>) (Miralles et al., 2011), b) Spatial distribution of 1980-2020 average annual E_t (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)

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

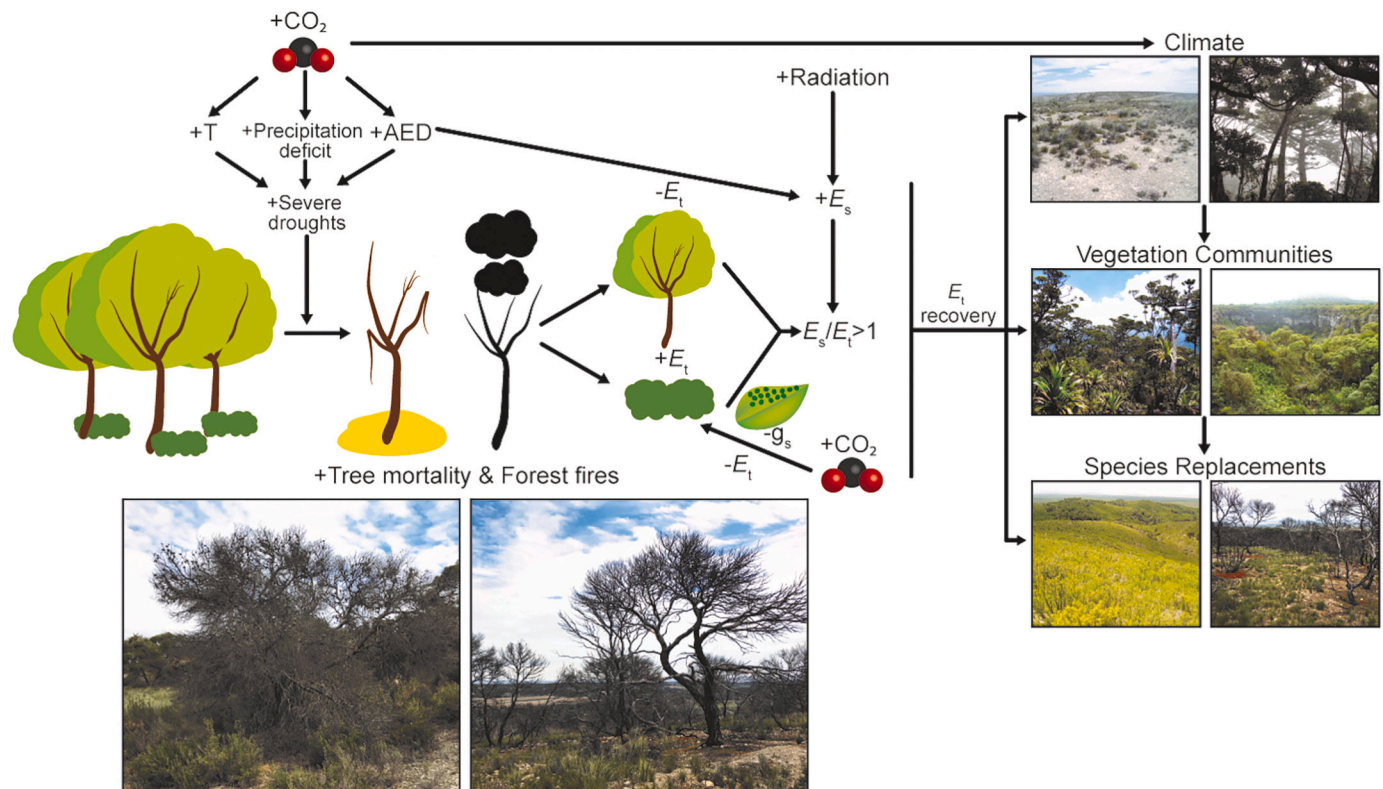


Fig. 3. Effects of tree mortality and forest fires associated to the influence of enhanced $a\text{CO}_2$. After disturbance the period of E_t recovery will depend on different factors, which are also connected with direct and indirect atmospheric CO_2 effects.

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 $a\text{CO}_2$ 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 $a\text{CO}_2$. On the other hand, increased radiative effects associated with enhanced $a\text{CO}_2$ 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 $a\text{CO}_2$ 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) 1pctCO₂, which represents the effects of CO_2 increases at a rate of 1% per year until quadrupling of the preindustrial concentrations considering coupled CO_2 effects in both carbon cycle and radiation; (b) 1pctCO₂-bgc, which represents 1% per year increasing CO_2 coupled to the carbon-cycle while radiative forcing is kept at the preindustrial CO_2 and (c) 1pctCO₂-rad, which represents 1% per year increasing CO_2 coupled to the radiation forcing while the carbon cycle responds to the preindustrial CO_2 . 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 1pctCO₂-

bgc and 1pctCO₂-rad in the projections of E_t for 2050 and 2100 (Fig. 4b). The 1pctCO₂-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 1pctCO₂-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 1pctCO₂-bgc experiment in these areas suggests a dominance of the g_s decline in ESMs.

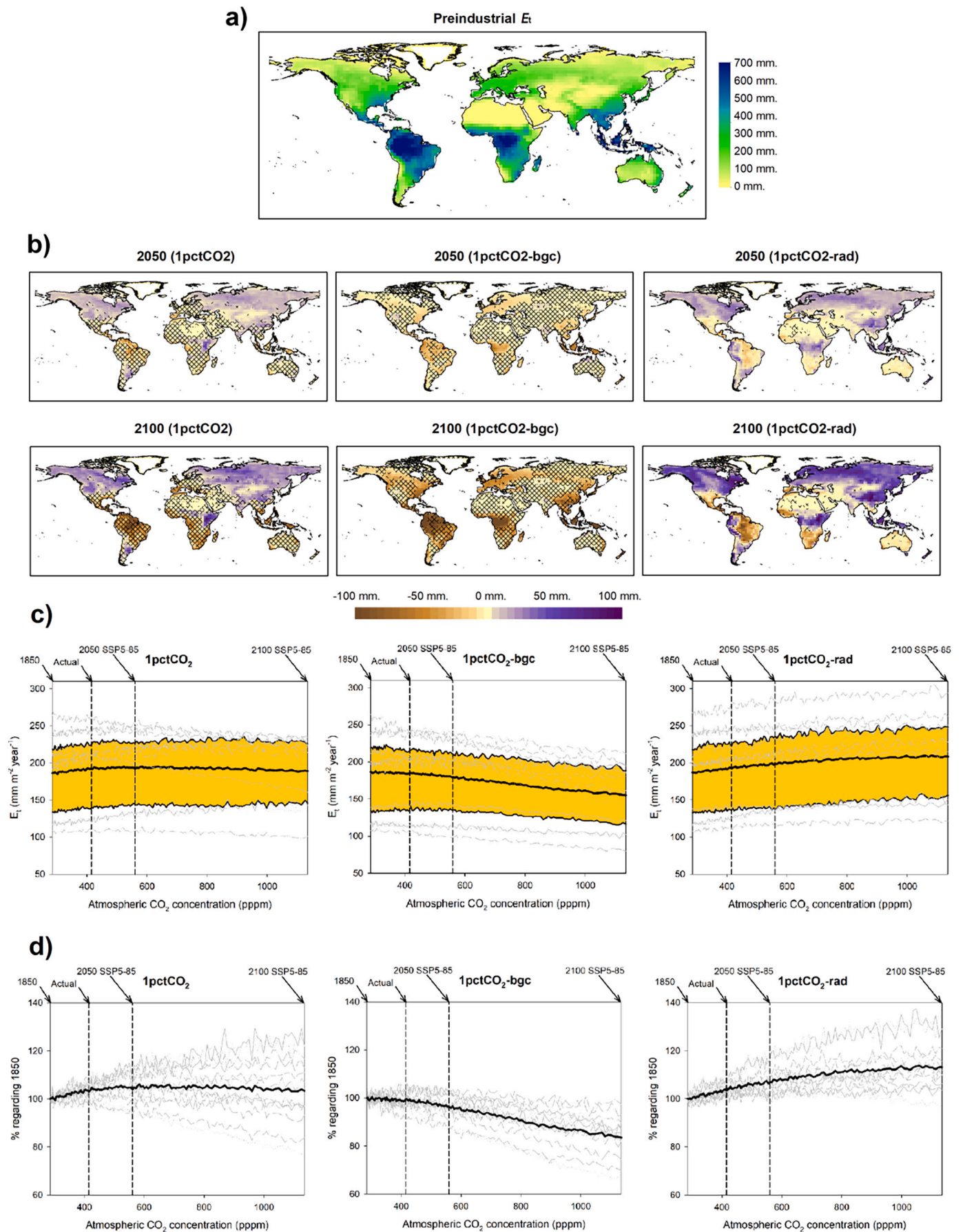
The projections of the 1pctCO₂-rad experiment, which isolates the effect of enhanced aCO_2 on the radiative forcing, show dominant global increase of E_t , which would affect mid-latitudes of the Northern and Southern Hemispheres, central Africa and southeast Asia. Exceptions are the Mediterranean, southern 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 (1pctCO₂ 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 1pctCO₂-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 1pctCO₂-bgc experiment show larger spread among the models and notably this problem propagates to the coupled experiment 1pctCO₂, 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 (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 CO_2 in the three simulation experiments. Black lines represent the global average and in color the 25th and 75th 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 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

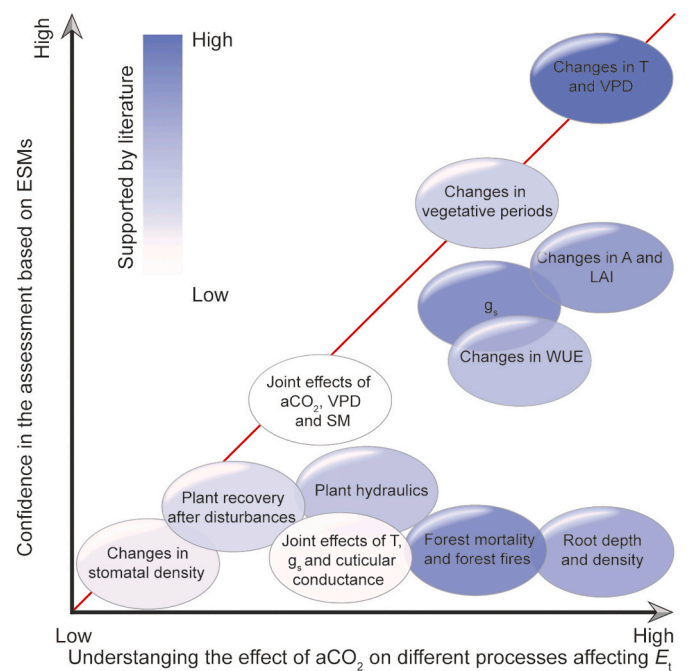


Fig. 5. Relationship between current understanding of the effect of aCO_2 on different processes that control E_t changes and the confidence of their representation in ESMs.

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.

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Declaration of Competing Interest

None declared

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