



Future global water scarcity partially alleviated by vegetation responses to atmospheric CO₂ and climate change

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Abstract. Accurate water scarcity projections are essential for effective adaptation strategies. Most existing studies rely on hydrology models that often neglect the effects of plant physiological responses to rising CO₂ on the water cycle, such as reduced stomatal opening, which can decrease transpiration and enhance water availability over large scales. Using a land surface model driven by an Earth system model under a high-emission climate scenario, we evaluate how physiological and structural plant responses to rising CO₂ and subsequent climate change affect the Water Scarcity Index (WSI). Our simulations suggest that the combined effects of these plant responses partially alleviate WSI for most regions, largely due to CO₂-induced stomatal closure. However, CO₂- and climate-induced vegetation changes do exacerbate water scarcity in some places, particularly arid regions. By 2076–2095, when incorporating all plant responses in our projections, global median WSI is approximately 12% lower, and among 291 global river basins, median WSI is between 10 and 70% lower in 138 basins, home to 80% of the global population, and between 10% and 60% higher in 11 basins, home to 0.2% of the population. These model results highlight the potential for plant responses to CO₂ to somewhat alleviate water scarcity, noting water scarcity is still projected to worsen in many regions, including highly populated areas. There is an urgent need to gather empirical evidence on the strength of plant responses to CO₂ at large scales to address modelling uncertainties.

Short summary. Plants typically transpire less with rising atmospheric carbon dioxide, leaving more water in the ground for human use, but many future water scarcity assessments ignore this effect. We use a land surface model to examine how plant responses to carbon dioxide and climate change affect future water scarcity. Our results suggest that including these plant responses increases overall water availability for most people, highlighting the importance of their inclusion in future water scarcity studies.

1 Introduction

Water scarcity, where water demand exceeds available supply, is one of the greatest challenges of our time (FAO, 2017). Nearly half of the global population already faces severe water scarcity at some point each year, and as both population and consumption rates rise, water demand is escalating (Caretta et al. 2022). From 1992 to 2015, global freshwater resources per



capita declined by over 25% (Ripple et al., 2017). Water availability, crucial for meeting this rising demand, depends on the balance between land precipitation and evapotranspiration, both of which are strongly affected by human activities, including climate change. Climate change is altering precipitation patterns and near-surface meteorological conditions, driving more frequent hydrological extremes and higher evaporative demand (Seneviratne et al., 2023). Human interventions—such as groundwater over-abstraction, dam construction, and water diversion—further disrupt water supply, while pollution threatens the availability of clean water. Accurately forecasting future water supply and demand remains a complex but vital task for informing long-term adaptation strategies (Caretta et al., 2022). Current impact studies on future water scarcity are typically based on output from hydrology models driven by climate model outputs (e.g., Dolan et al., 2021; Gosling and Arnell, 2016; Greve et al., 2018; Haddeland et al., 2014). While hydrology models are powerful tools for understanding, managing, and planning water resources, they often lack a representation of vegetation response to rising levels of CO₂ and climate change. In this study, we investigate the influence that these vegetation responses have on water scarcity projections.

Vegetation is crucial to the global water cycle and therefore to water availability for humans. Large-scale changes in vegetation type and coverage are already occurring due to climate change and human activities, such as deforestation. Vegetation plays a key role in precipitation generation, with approximately 60% of terrestrial precipitation originating from land via evapotranspiration – primarily through plant transpiration (Schneider et al., 2017; Wei et al., 2017). Vegetation also influences other hydrological processes, including infiltration, interception, and runoff (Caretta et al., 2022). Climate change continues to alter vegetation types and coverage globally, as regions experience more or less favourable conditions. Increased vegetation growth has been observed in many areas (Xu et al., 2017; Yu et al., 2018; Zhu et al., 2016), while droughts and heatwaves have heightened plant stress and mortality (Parmesan et al. 2022).

Rising atmospheric CO₂ concentrations also impact the water cycle by altering plant physiology. Plants continuously adjust the widths of their stomatal openings to maximise photosynthesis while minimising water loss (Cowan, 1978). Under higher atmospheric CO₂, plants typically reduce their stomatal openings, as they can maintain higher rates of photosynthesis at increased leaf-level water-use efficiency, thereby decreasing transpiration (Battipaglia et al., 2013; Field et al., 1995; Norby and Zak, 2011). As less water is lost through transpiration, more water remains in the soil and at the surface, contributing to increased runoff and soil moisture levels (Fowler et al., 2019; Gedney et al., 2006). However, higher CO₂ generally enhances photosynthesis, known as the CO₂ fertilisation effect, leading to increased vegetation growth and thus overall canopy transpiration due to a higher number of stomata, even as individual stomatal openings are reduced (Betts et al., 1997). At the canopy-level, this effect can offset or even reverse the increase in runoff from reduced stomatal openings (Cowling and Field, 2003; Piao et al., 2007; Ukkola et al., 2016). The net effect on canopy transpiration thus depends on the balance between these two opposing factors, which varies greatly between different plant species and climatic biomes (Norby and Zak 2011).



65 Better understanding of vegetation-water-atmosphere interactions, in both historical observations and under future climate
change scenarios (e.g., Betts et al., 2007; Gedney et al., 2006) has been made possible with the introduction of Land Surface
Models (LSMs). LSMs simulate complex interactions between the atmosphere, land surface, and sub-surface, including energy
and water fluxes, carbon cycling, and soil processes. Dynamic vegetation schemes in LSMs have been made increasingly
70 realistic over the past few decades (Fisher and Koven, 2020). They typically simulate vegetation coverage, canopy height and
leaf area index for a limited number of generalised plant functional types, driven by carbon fluxes and vegetation competition.
Including dynamic vegetation in climate models is essential for capturing critical changes in land surface and plant physiology
that influence the climate system and hydrological cycle. Yet, these schemes are still absent from many hydrology models.

Advances in LSMs have improved understanding of how plant physiological response to rising CO₂ (herein ‘physiological
75 forcing’) impact the water cycle. An early study by Wigley and Jones (1985) was one of the first to link CO₂-driven changes
in plant evapotranspiration (ET) to runoff. As land surface and climate models advanced, research incorporated CO₂-induced
vegetation growth alongside stomatal closure. Betts et al. (1997) projected that increased vegetation cover could partially
offset the projected reduction in ET. Gedney et al. (2006) attributed rising historical continental river runoff records to CO₂-
induced stomatal closure. However, Piao et al. (2007) suggested that physiological forcing *reduced* global runoff when CO₂-
80 induced leaf area increases were also considered from 1901 to 1999. Subsequent modelling studies continue to support the
idea that CO₂-induced stomatal closure and leaf area increases together generally increase projected global runoff in the current
generation of models. For instance, doubling CO₂ in climate models led to global mean runoff increases of 6% (Betts et al.,
2007) and 8-9% (Cao et al., 2010) relative to preindustrial; comparable to the impact of radiative forcing. Further studies
suggested physiological forcing effects on the hydrological cycle exhibited large spatial heterogeneity around the globe,
85 although typically suggesting increased runoff, especially in the tropics (Davie et al., 2013; Fowler et al., 2019; Lemordant et
al., 2018; Yang et al., 2019), including reducing drought severity (Swann et al., 2016) and increasing flood risk (Kooperman
et al., 2018). Conversely, runoff reductions are suggested in more arid locations, including the mid-latitudes in model
projections (Mankin et al., 2019) and parts of Australia in observations (Ukkola et al., 2016). Moreover, a recent study by Wei
et al. (2024) suggested physiological forcing had limited effect on observed global streamflow. However, the consensus
90 between most studies currently suggests that the stomatal response to CO₂ has a dominant effect over the structural responses
at the global scale, particularly in future climate projections.

Water scarcity is a complex, multifaceted issue influenced by water availability, demand, and quality. Many future water
scarcity projections rely on standalone hydrology models driven by global climate model outputs (e.g., Dolan et al., 2021;
95 Gosling and Arnell, 2016; Greve et al., 2018; Haddeland et al., 2014; Schewe et al., 2013). These studies have generally
projected worsening water scarcity in many regions due to both climate change and rising demand, with the most affected
areas including parts of northern and southern Africa, south and southeast Asia, Australia, parts of Europe, the Middle East

and the western United States. However, these hydrology models often do not account for vegetation responses to atmospheric CO₂ and climate change.

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Few studies have explored the influence of physiological forcing on water scarcity-related variables. Wiltshire et al. (2013a, b) suggested that when both climate change and CO₂ effects are considered, the number of people experiencing water stress decreases. Notably, Wiltshire et al. (2013a) projected that physiological forcing could reduce the population under high water stress by approximately 200 million by the end of the century, an impact comparable to that of climate change alone. However, while their water stress indicator accounted for population growth, it did not consider varying water demands due to different living standards. Wang and Sun (2023) also examined socioeconomic exposure to drought under various Shared Socioeconomic Pathways finding that physiological forcing could increase extreme drought frequency by around 2% in the 2030s, particularly in arid and semi-arid regions, but this influence shifted to a decrease by the 2050s. However, their study only used fully coupled models and did not replicate the experimental setup typically used in hydrology studies—such as driving standalone hydrology models with climate model outputs—and therefore did not directly address the impact of physiological forcing in hydrological studies, as this research aims to do.

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Understanding the extent to which dynamic plant processes affect metrics like water scarcity remains a critical research gap for the climate and hydrology impacts community. This study is the first to address this by replicating the experimental design of typical hydrology impact studies, i.e., running a standalone hydrology model without dynamic vegetation driven by climate model output, but adjusting plant responses to rising CO₂ and climate change through a land surface model. This approach allows us to estimate how water scarcity would change if hydrology models accounted for both vegetation's physiological and structural responses.

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2 Methodology

120 2.1 The Joint UK Land Environment Simulator (JULES)

The Joint UK Land Environment Simulator (JULES; Best et al., 2011; Clark et al., 2011) simulates fluxes of carbon, water, energy and momentum between the land surface and atmosphere. JULES is used as either an integral part of an Earth system model such as UKESM1 (Sellar et al., 2019) or as an independent land surface model driven by input data from observations or atmospheric models; here we use it in the latter manner.

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JULES is a multi-sectoral land surface model with a dynamic vegetation scheme (Cox, 2001) and global hydrological cycle, including river routing scheme (Falloon et al., 2007), which allows us to effectively explore vegetation-water-atmosphere interactions. Within JULES, the dynamic vegetation model predicts changes in leaf area and the fractional coverage of 13 different Plant Functional Types (PFTs; Harper et al., 2016) where each PFT is categorised by specific physiological traits,



130 and surface fluxes are calculated separately for each PFT. JULES uses a coupled canopy conductance and photosynthesis
model (Cox et al., 1998) which is based on the stomatal conductance model from (Leuning, 1995). Full descriptions of all
JULES model equations can be found in Clark et al. (2011) and Best et al. (2011).

The earth system configuration JULES-ES is used in this study and it follows the setup used for the Inter-Sectoral Impact
135 Model Intercomparison Project (ISIMIP; <https://www.isimip.org/>) version 2b; details of the setup can be found in Mathison et
al. (2023).

In this version of JULES, soil is divided into 4 layers, each with its own water content, which is determined by considering
the inputs, such as precipitation, and outputs such as evapotranspiration and infiltration. The moisture content of each soil
140 layer influences water movement, affecting how much percolates downward to deeper layers or moves horizontally as lateral
flow. Additionally, in this version of JULES a TOPMODEL-type scheme is included, which is based on Clark and Gedney
(2008) and Gedney and Cox (2003). This accounts for the influence of topography on soil moisture and runoff, enhancing
JULES's ability to simulate the sub-grid spatial variability. Surface runoff is generated when precipitation exceeds the soil's
infiltration capacity, when the soil becomes fully saturated, or when sub-grid scale inundation occurs. In TOPMODEL-based
145 schemes, sub-surface runoff, or "baseflow", occurs with lateral flow below the water table, and its magnitude is influenced by
soil moisture and soil type.

2.2 Experimental setup

The experimental setup has been carefully designed to best replicate the process used in water-related impact studies, i.e., a
hydrology model run offline, driven by climate model output. Therefore, JULES is run offline driven by a bias-adjusted
150 (following Lange, 2019) Earth system climate model HadGEM2-ES (Hadley Centre Global Environment Model version 2;
Jones et al., 2011) resampled to 0.5 x 0.5 degrees horizontal resolution as part of the bias correction . We use the historic
simulation from 1861 to 2006 and the "future" period 2006 to 2100 using Representative Concentration Pathway (RCP) 6.0.
Note sea points have been masked out for all variables.

155 Physiological forcing is "switched off" by fixing atmospheric CO₂ in JULES to 277 ppm, representing pre-industrial levels,
following the protocol of the TRENDY project (Sitch et al., 2024). We then quantify the influence of physiological forcing by
calculating the difference between the preindustrial CO₂ simulation and the equivalent JULES run using CO₂ concentrations
from the driving climate model (i.e., RCP 6.0). Note that, in the preindustrial CO₂ simulation, atmospheric CO₂ has been fixed
in JULES only so that physiological forcing is not incorporated in JULES. The atmospheric CO₂ and meteorological input
160 variables such as radiation, temperature, precipitation and windspeed, are identical for all simulations, since they come from
the driving climate model output (Fig. 1), which would be the case for a typical hydrology study.



165 Furthermore, we also examine the influence of climate-induced vegetation distribution changes, including Leaf Area Index (LAI; the ratio of leaf to ground area) changes, by switching the dynamic vegetation scheme on and off in JULES; this fixes the spatial vegetation distribution to that at the start of the simulation. This means that we can isolate the effects of physiological forcing from those on structural vegetation changes. We can also quantify the effects of climate on vegetation. Note that anthropogenic disturbance of land is not included in any of our simulations, so vegetation can be affected by changes in climate and CO₂ only.

170 Using a combination of fixing CO₂ and dynamic vegetation in JULES gives the four simulations outlined in Table 1a, all with the same climate. Table 1b clarifies which vegetation responses are included for each simulation. By taking the difference between these simulations, the distinct impacts of dynamic plant responses to CO₂ and/or climate change can be isolated, as indicated in Tables 1a,b. For example, to assess the influence of the CO₂-induced stomatal response, S1 is subtracted from S3, and to estimate the combined effect of all dynamic plant processes, S1 is subtracted from S4. The relative differences are
175 displayed in Figs. 2,5,9,10 and are calculated by dividing the difference by the initial value, following the formula: $\frac{b-a}{a}$. Note that we do not analyse the influence of climate change alone in this study.

Note the naming conventions used in this study for each simulation and isolated factor follow the generic format: <Forcing factor(s)>: <Responding factor(s)>. The following acronyms have been used: ‘CLIM’ represents climate changes, ‘CO₂’
180 represents the CO₂ changes for plants, ‘VEG’ represents vegetation cover and LAI responses and ‘STOM’ represents stomatal responses. S1. CLIM: STOM represents a typical hydrology model with fixed vegetation and plant physiology, with only the climate effects on the stomata included, and S4. CLIM+CO₂: STOM+VEG includes all physiological and structural responses to CO₂ and climate.

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| | | Vegetation distribution (includes coverage, LAI and canopy height) | | Calculations for isolated factor(s): |
|---|--|--|--|---|
| | | Dynamic vegetation off (fixed at preindustrial) | Dynamic vegetation on | |
| Plant physiology | 277 ppm (fixed at preindustrial) | S1. CLIM: STOM | S2. CLIM: STOM+VEG | S2 - S1. CLIM: VEG |
| CO₂ levels in JULES | RCP 6.0 | S3. CLIM+CO ₂ : STOM | S4. CLIM+CO ₂ : STOM+VEG | <i>Not used</i> |
| Calculations for isolated factor(s): | | S3 - S1. CO₂: STOM | S4 - S2. CO₂: STOM+VEG | S4 - S1. CO₂: STOM & CLIM+CO₂: VEG |

Table 1a: The four JULES simulations driven by identical climate model output, and a combination of fixing plant CO₂ and structural vegetation responses to include the following effects: S1: climate effects on stomata (closest to typical hydrology study), S2: climate effects on stomata and vegetation coverage/LAI, S3: climate and CO₂ effects on stomata, and S4: climate and CO₂ effects on stomata and vegetation coverage/LAI. The isolated factors are combined by taking the differences between simulations: S2 – S1: Climate effects on vegetation coverage/LAI, S3 – S1: CO₂ effects on stomata, S4 – S2: CO₂ effects on stomata and vegetation coverage/LAI and S4 – S1: CO₂ effects on stomata and climate plus CO₂ effects on vegetation coverage/LAI.

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| Simulation | Name | Climate-induced stomatal changes | Climate-induced veg. changes | CO ₂ -induced stomatal changes | CO ₂ -induced veg. changes |
|------------|---|----------------------------------|------------------------------|---|---------------------------------------|
| S1 | CLIM: STOM | ✓ | | | |
| S2 | CLIM: STOM+VEG | ✓ | ✓ | | |
| S3 | CLIM+CO ₂ : STOM | ✓ | | ✓ | |
| S4 | CLIM+CO ₂ : STOM+VEG | ✓ | ✓ | ✓ | ✓ |
| S2 - S1 | CLIM: VEG | | ✓ | | |
| S3 - S1 | CO ₂ : STOM | | | ✓ | |
| S4 - S2 | CO ₂ : STOM+VEG | | | ✓ | ✓ |
| S4 - S1 | CO ₂ : STOM & CLIM+CO ₂ : VEG | | ✓ | ✓ | ✓ |

Table 1b: Details of dynamic processes included in each of the simulations and isolated factors.

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2.3 Data

2.3.1 Water supply (runoff)

Water supply is represented using the total runoff from the output of the simulations, which includes both surface and sub-surface runoff at the grid box scale.

205 2.3.2 Water demand

Water demand data has been downloaded from the ISIMIP database (<https://data.isimip.org/>), specifically ISIMIP2b from the global water sector (Gosling et al., 2023). The hydrology model used is H08 (Hanasaki et al., 2008a, b, 2018) driven by HadGEM2-ES, RCP 6.0 and shared socioeconomic pathway SSP2, which represents population and gross domestic product for the ‘middle of the road’ scenario (Riahi et al., 2017). Total water demand is represented by summing water withdrawal for irrigation (assuming unlimited water supply), domestic use and manufacturing.

This water demand data was found to display a small number of negative demand values. For simplicity and to avoid negative values of water scarcity, these areas have been masked out in any plots incorporating water demand, including those on water scarcity.

215 2.3.3 Water Scarcity Index

In this study, we calculate the Water Scarcity Index (WSI) to be the ratio of water demand to water supply (Falkenmark et al., 1989). The WSI is chosen as it is a simple and widely used indicator of water scarcity. We use a WSI of 0.2-0.4 to indicate mild or emerging water scarcity, and $WSI \geq 0.4$ for severe water scarcity, in line with Raskin and Gleick (1997) and Greve et al. (2018).

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Different approaches can be used to calculate the average WSI over space and time, which can considerably influence the results. Mostly, we have chosen to calculate WSI at the most granular spatial and temporal scale, which is monthly and by grid-box. The exception is when analysing by river basins in Fig. 9, where the sum of total supply and demand is computed for each basin before calculating WSI. The rationale is that, generally, all water within a river basin could ideally be used for all the population within that basin, noting in real life this is not always the case.

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Since WSI is calculated as water demand divided by water supply, it can yield extremely high values where supply values are very low relative to demand. To mitigate the impact of these extreme values, the median WSI is used for spatial and temporal averaging in this study, as it provides a more robust measure less influenced by outliers.

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2.3.4 Population

Gridded (0.5 degree) annual population projections database for SSP2 from the ISIMIP2b data library (Piontek and Geiger, 2017), plotted in Fig. S1, is used to calculate projected population numbers by river basin in Table 2 and Figure 9.

2.4 Regions and River Basins

235 In this study, we utilise the climate regions outlined by the Intergovernmental Panel on Climate Change (IPCC) in its Sixth Assessment Report (AR6), consisting of 46 land regions (Fig. S2; Iturbide et al., 2020). These regions are defined based on a combination of geographic, climatic, and socio-economic criteria, ensuring a comprehensive representation of global climatic variability.

240 River basin shapefiles are from Hydrosheds (<https://www.hydrosheds.org/products/hydrobasins> ; Lehner and Grill, 2013).

2.5 Terminology

- Isolated factors: factors that have been isolated by taking difference between simulations, as outlined in Table 1.
- Physiological forcing: the combined response of stomata and change in plant functional types and leaf area due to rising CO₂.
- 245 • Stomatal response: the response of plant stomata due to rising CO₂ and/or climate.
- Vegetation distribution change: spatial and temporal change in plant functional type , as well as leaf area.

3. Results

3.1 Vegetation and water cycle variables

250 The climate-only simulation (S1) which represents a typical hydrology study with fixed vegetation and plant physiology, suggests relatively small changes in most global mean water cycle variables from 1900 to 2100 (Fig. 2). However, there is a notable decline in soil moisture, coinciding with a slight upward trend in transpiration (Fig. 2d,i), likely driven by increasing temperatures through the 21st century (Fig. 1a). Despite soil drying, total runoff is projected to slightly increase in the second half of the century (Fig. 2a), coinciding with similar increases in global mean precipitation (Fig. 1b). In contrast, subsurface runoff shows a gradual downward trend (Fig. 2c).

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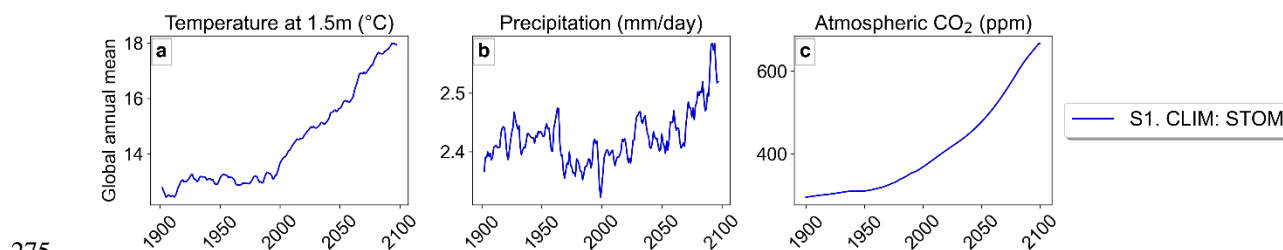
The relative difference when the CO₂-induced stomatal response (S3) compared to the simulation without CO₂-induced stomatal response (S1), shown by CO₂: STOM, suggests an exponential decrease in both transpiration and stomatal conductance, reduced by approximately 20% by 2100 (Fig. 2l,m), along with an increase in runoff of 10-15% (Fig. 2e) and 20-30% for sub-surface runoff (Fig. 2g) by 2100. The CO₂-induced stomatal response appears to dominate over the CO₂-



260 induced LAI increases for the global mean, since, as shown in CO₂: STOM+VEG, increases in total runoff occur despite a
nearly 30% rise in LAI (Fig. 2e,n).

Climate-induced changes in vegetation distribution drives LAI decreases by almost 20% by the end of the century shown by
CLIM: VEG (Fig. 2n;), leading to a modest decrease in transpiration of about 3-5% (Fig. 2l). This decrease in transpiration
265 results in a slight increase in total runoff (Fig. 2e), though these changes are much smaller and more stable over time compared
to the CO₂-induced plant responses. Additionally, reductions in soil moisture are projected at subsurface levels, as indicated
by subsurface runoff and soil moisture, implying more total evaporation (Fig. 2g,h).

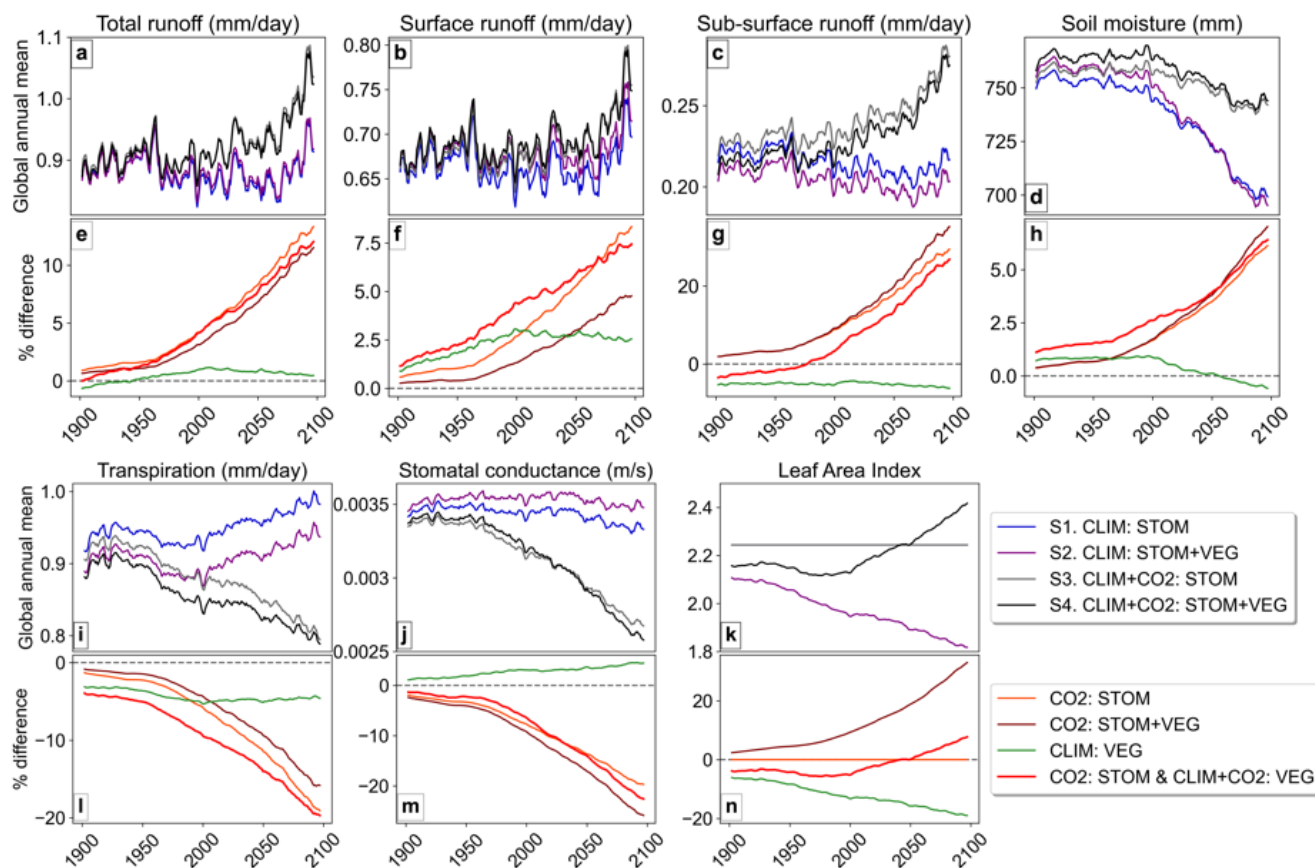
When all processes associated with dynamic vegetation and physiological forcing are included in S4, compared to the climate-
270 only scenario S1, there is a pronounced decrease in transpiration and stomatal conductance, along with growing increases in
runoff (Fig. 2a,i,j). At the global mean level, these differences in water cycle variables appear to be primarily driven by CO₂-
induced stomatal closure, as all simulations including 'STOM' exhibit similar trends, with its influence growing rapidly through
the 21st century.



275 **Figure 1: Global annual mean timeseries for climate variables from HadGEM2-ES used as input to JULES simulations (rolling 5-
year mean for precipitation and temperature).**

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290 **Figure 2: Global annual mean timeseries (rolling 5-year mean) in water cycle and vegetation variables in each simulation and the relative (%) difference between simulations.**

While the CO₂-induced stomatal response drives overall surface wetting at the global mean scale (Fig. 2), this pattern is not uniform across the globe and the influence of the various processes exhibits considerable spatial variation). The climate-induced changes in runoff from the present (2006-2025) to the future (2076-2095) largely align with shifts in precipitation (Fig. 3; right), varying greatly in both magnitude and direction (Fig. 4a,c). Regions such as South Asia and the high latitudes are projected to experience large increases in runoff, while decreases are expected in areas like the Amazon, northern Europe, and central Africa. Soil moisture trends follow a similar pattern to runoff, although the northern latitudes show substantial soil drying despite increased runoff (Fig. 4b), likely an artefact of the thawing of frozen surfaces.

300 When all vegetation and physiological changes are included in S4, more widespread wetting is observed in both runoff and soil moisture across many regions (Fig. 4e,f) compared to the climate-only scenario (Fig. 4a,b). These differences can be attributed to the inclusion of CO₂-induced stomatal responses, as shown by the isolated factors which include “STOM”. For instance, in CO₂: STOM+VEG, runoff is projected to increase in many regions (Fig. 4i), particularly in the tropics and high



northern latitudes, corresponding with decreases in transpiration (Fig. 4k). In areas predicted to become drier, the stomatal
305 response helps to mitigate the drying, such as in the Amazon, parts of the USA, northern and eastern Europe, and even shifts
projected drying to wetting in regions such as central Africa. Moreover, in many regions, runoff increases despite CO₂-induced
LAI increases (Fig. 4l). This indicates that runoff increases from CO₂-induced stomatal closure is dominant over any drying
caused by CO₂-induced LAI increases. However, in many parts of the globe, particularly in semi-arid and arid climates such
as the Middle East and mid-latitude regions such as the western USA, CO₂-induced LAI increases are driving small decreases
310 in runoff (Fig. 4i, l).

In contrast, vegetation distribution changes driven by climate in CLIM: VEG have relatively little impact on runoff,
transpiration, and stomatal conductance, despite significant changes in LAI in parts of the tropics and high latitudes (Fig. 4m-
p).

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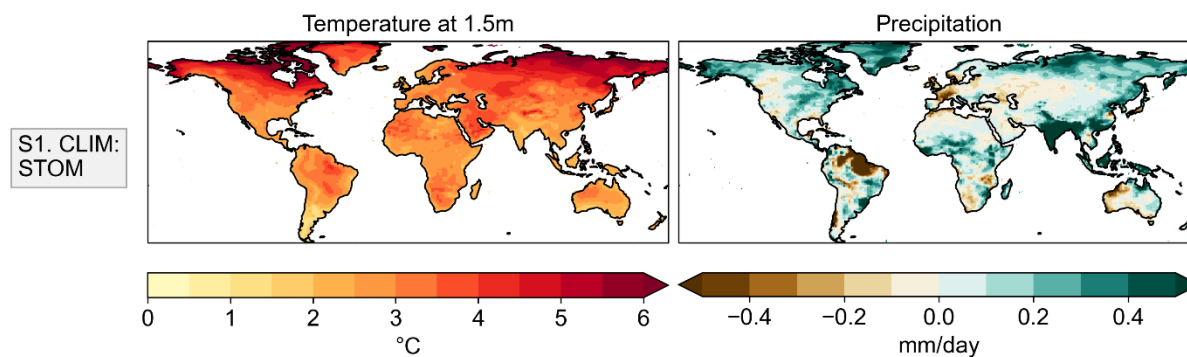
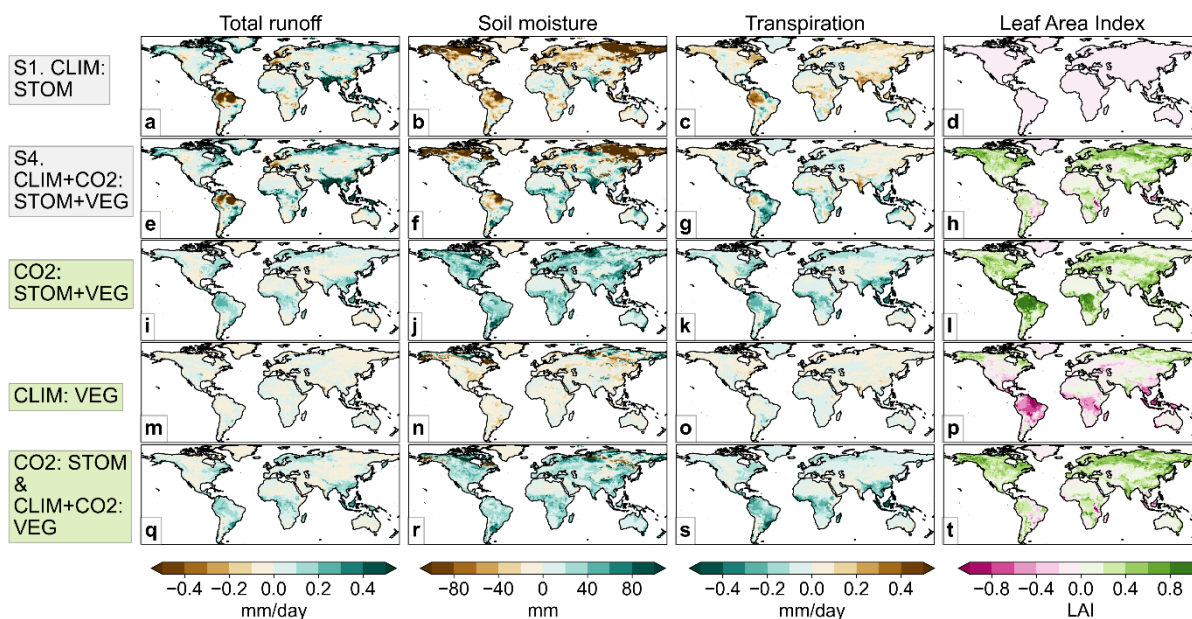


Figure 3: Global mean changes from present (2006-2025) to future (2076-2095) for precipitation and 1.5m temperature. Note these outputs are from the driving climate model and thus the same in all simulations.



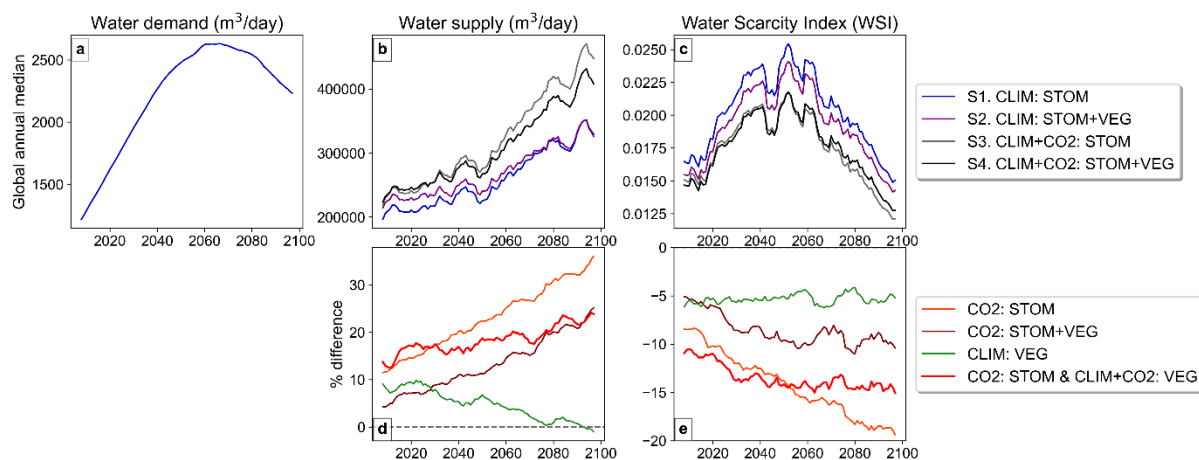
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Figure 4: Global mean changes from present (2006-2025) to future (2076-2095) period in the climate-only simulation (top row), and the absolute difference when the various isolated factors are included.

3.2 Water demand, supply and the Water Scarcity Index

Global median water demand, supply, and WSI are projected to increase over the coming decades under the SSP2 and RCP
 325 6.0 (Fig. 5a-c). However, water demand and WSI are projected to peak and then decline later in the century, while JULES
 projects global water supply to continue to increase, particularly in simulations S3 and S4 that incorporate CO₂ impacts on
 stomata (Fig. 5b). The isolated effect of increased CO₂ on plant stomata is illustrated by CO₂: STOM (Fig. 5d), which indicates
 a 30% increase in global median water supply by the end of the century. Even when CO₂-induced leaf area changes are
 considered, shown in CO₂: STOM+VEG, a 20% increase in water supply is still projected by the century's end. In contrast, the
 330 climate effects on vegetation have a comparatively small influence on the global scale which becomes even smaller in the
 coming decades (Fig. 5d; CLIM: VEG).

These water supply increases correspond with consistent projected reductions in global median WSI throughout the century
 (Fig. 5c,e). The CO₂-induced stomatal response appears to ameliorate WSI by 15-20% toward the century-end shown by CO₂:
 335 STOM (Fig. 5e). However, when CO₂-induced LAI increases are also allowed in CO₂: STOM+VEG, the reduction in WSI is
 notably less at 8-10% in the second half of the century. Climate-induced vegetation changes also reduce global median WSI
 by around 5%, remaining consistent throughout the period. When all processes are included, the combined influence shown
 by S4 – S1 (Fig. 5e) results in a 10-15% reduction in WSI throughout the century.



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Figure 5: Annual global-median timeseries (rolling 5-year mean) of a) water demand, b) water supply, c) WSI in the four simulations and the % difference in d) supply and e) WSI due to the various isolated factors. Note, water demand is the same across all simulations.

345 Under RCP 6.0 and SSP2, water demand for the present period is high in much of Europe, South and Southeast Asia and the USA (Fig. 6a). Water demand increases for most places, especially in the highly populated and developing regions of South Asia, as well as parts of Africa, but decreases are also seen for parts of Europe and China (Fig. 7a). Regions experiencing severe water scarcity ($WSI \geq 0.4$; Raskin, et al., 1997) in the present period (2006 - 2025), include most of India, the Middle East, eastern China and parts of South Africa, USA, and Europe (Fig. 6c). Large swathes of northern Africa are also
350 experiencing severe water scarcity despite low demand (Fig. 6a). Even though global median WSI reduces later this century in Fig. 5c, many of the already water scarce regions are projected to become even more water scarce by the future period (2076-2095; Fig. 7c), as the demand grows, including in highly populated regions such as India.

The plots comparing the change in median WSI from the present (2006-2025) to the future (2076-2095) under scenarios with
355 and without plant processes (Fig. 7c,e) appear quite similar, suggesting that water demand and meteorological factors driving water supply are the primary influences on WSI. Interestingly, the changes in supply between the S1 and S4 simulations (Fig. 7b,d) show greater difference than those for WSI, since the supply differences mainly occur in areas with low levels of water scarcity, and therefore have less impact on WSI.

360 Despite the similarities between simulations with (Fig. 7e) and without (Fig. 7c) plant responses to CO₂ and climate, the effect of plant responses on WSI is not negligible. The CO₂-induced stomatal response increases water supply in most regions, especially in the tropics (Fig. 7f), resulting in corresponding reductions in WSI (Fig. 7g). When CO₂-induced vegetation increases are factored in (CO₂: STOM+VEG; Fig. 7h,i), supply continues to show an overall increase, which may be because the decreases are relatively small and thus less visible on the plot. However, even small decreases can mean large increases on



365 WSI in arid regions like the Middle East, northern and southern Africa. Climate-induced vegetation changes shown in CLIM:
VEG appear to have minimal impact on supply (Fig. 7j), yet there are substantial changes in WSI in some areas, with increases
in some places, including western India, although parts of southern and northern Africa show some reductions (Fig. 7k).
Finally, when all processes are combined in CO2: STOM & CLIM+CO2: VEG, supply predominantly increases (Fig. 7l), even
though WSI increases in many arid and semi-arid regions.

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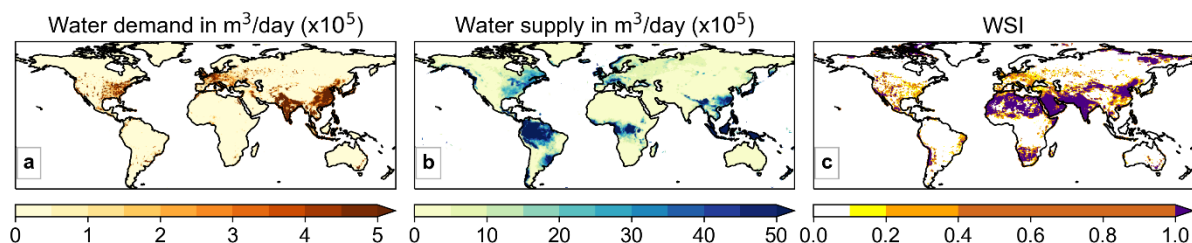
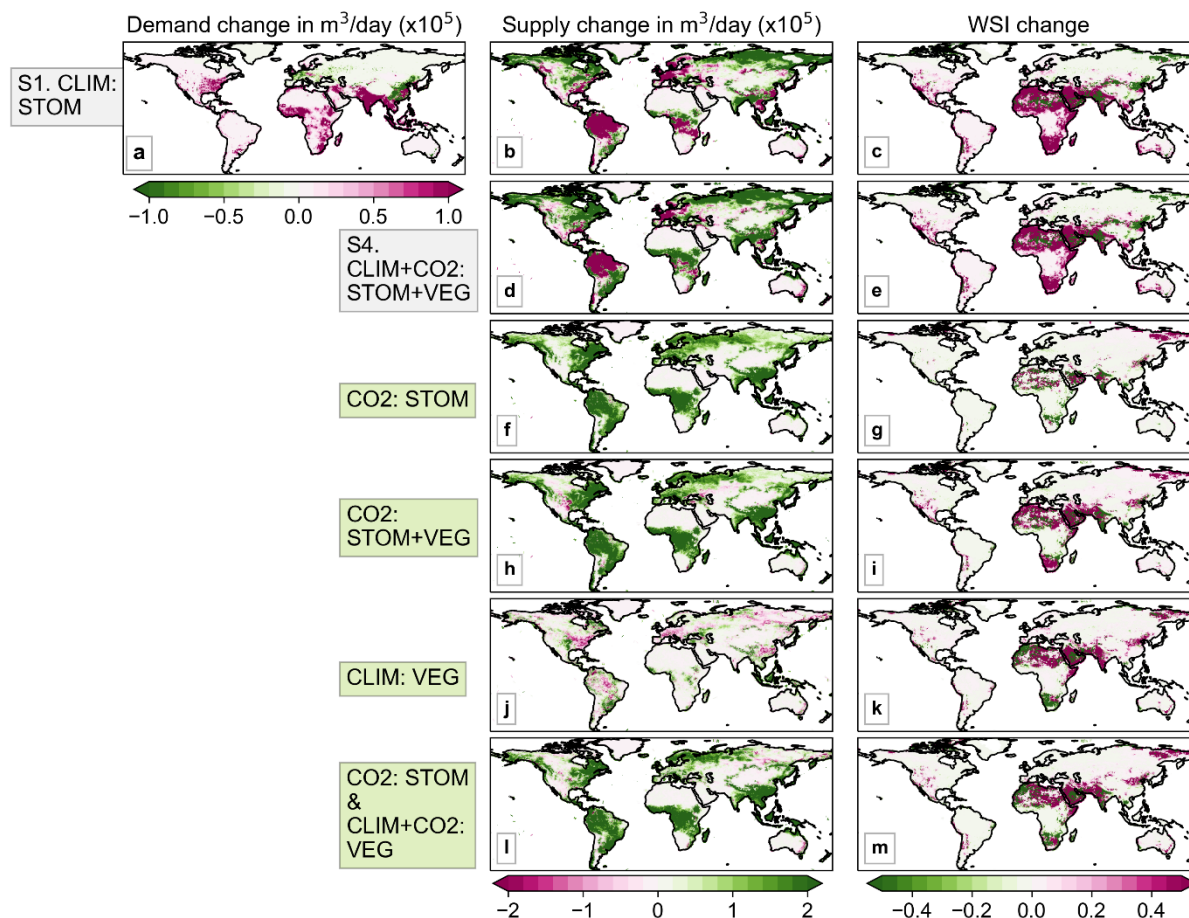


Figure 6: Median a) water demand, b) supply and c) Water Scarcity Index (WSI) for the period 2006-2025 in S1. CLIM: STOM.



375 **Figure 7: Median water demand, supply and Water Scarcity Index (WSI) change from the present (2006-2025) to future (2076-2095) period in simulations S1 and S4 (a-e), and the difference in supply and WSI when including the various isolated factors (f-m).**

The 25 IPCC AR6 climate regions with the highest monthly median WSI between 2076-2095 are shown in Fig. 8. The Arabian Peninsula region is projected to experience the highest median WSI, and South Asia is predicted to have the second highest
 380 (Fig. 8; left panel). Comparing with the 2006-2025 present period (Fig. S3), nearly all these regions are projected to increase in median WSI by the end of the century, with the largest increases in the East and West Southern Africa and Western Africa regions.

Comparing the fixed vegetation processes simulation (S1) with the dynamic vegetation processes simulation (S4) (Fig 8; left
 385 panel), there is a reduction in median WSI for all regions, except for East Central Asia and the Sahara. The CO₂-induced reductions in stomatal aperture appear to be driving the largest reductions indicated by CO₂: STOM and CO₂: STOM+VEG (Fig. 8; right panel). Reductions of 30-40% are projected for Madagascar, East Southern Africa and South-Eastern Africa



regions, and 20-30% reductions in Western Africa, Northeast South America, and South and East Asia. These regions are predominantly in tropical climates, aligning with the areas of increased water supply shown in Fig. 7b. However, CO₂: STOM+VEG also indicates increases in median WSI, likely due to CO₂-induced vegetation growth in regions like North Central America, East Central Asia, and South and East Australia. Climate-induced vegetation changes (CLIM: VEG) appear to drive WSI reductions in almost all regions, likely due to decreased leaf area encouraging additional water supply in these regions. These reductions are considerable in some areas, with ~45% decreases in East and South Australia. When all dynamic vegetation responses are considered in CO₂: STOM & CLIM+CO₂: VEG, the majority of these most water scarce regions see a 20-40% reduction.

These results are reinforced by alternative WSI measures; both the number of severely water scarce months (Fig. S4a) and % area in severe water scarcity (Fig. S4b), indicate that incorporating dynamic plant processes leads to a reduction in both the temporal and spatial extent of water scarcity for most regions. These reductions are also primarily driven by the CO₂-induced reduction in stomatal aperture, particularly in the tropical regions such as East Asia and South-Eastern Africa.

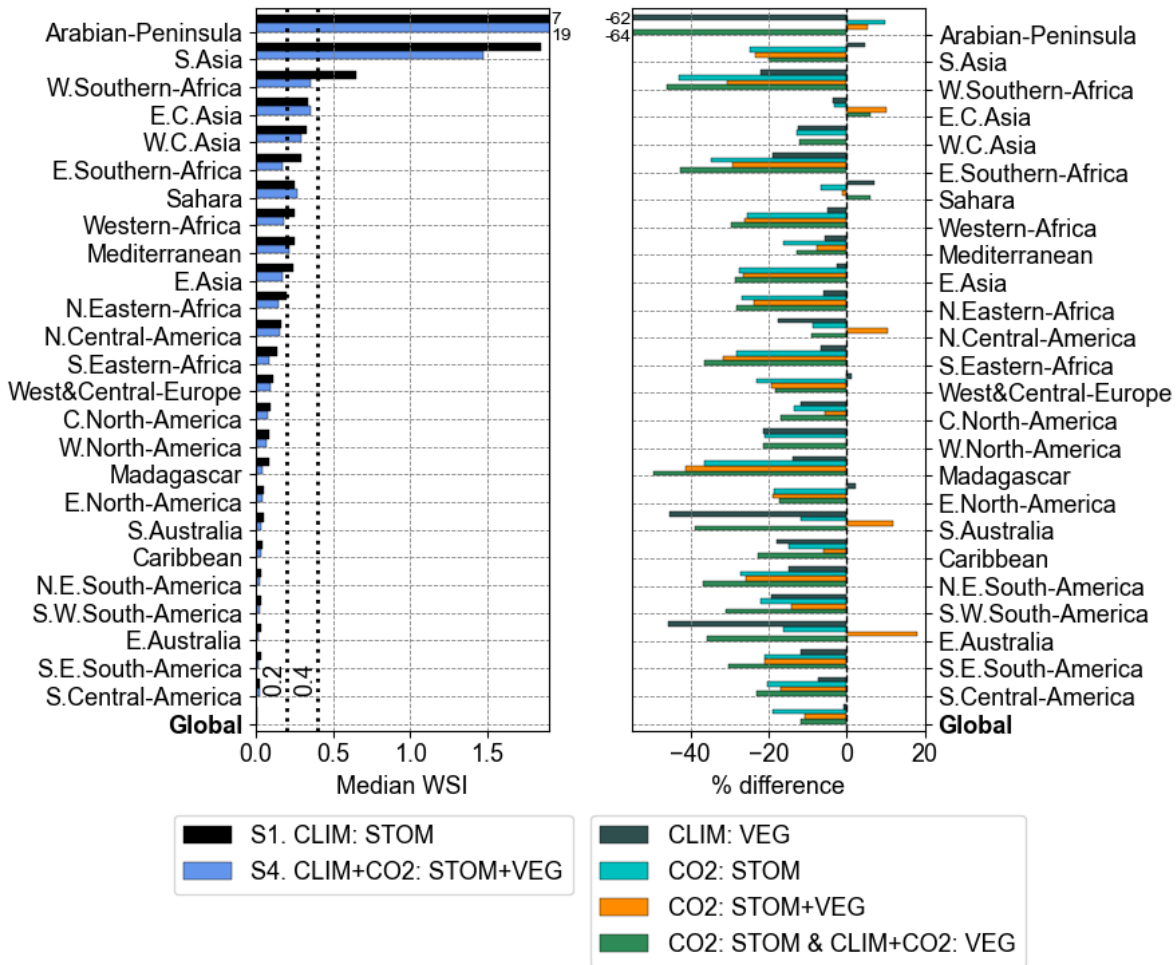


Figure 8: Median monthly WSI in simulations S1 and S4 (left) and % difference of median WSI when including the various isolated factors (right) by IPCC AR6 regions for the future period 2076-2095. The grey dashed lines (left) indicate the thresholds for mild water scarcity ($WSI \geq 0.2$) and severe water scarcity ($WSI \geq 0.4$). Only the 25 regions with the highest median WSI, according to the S1. CLIM: STOM simulation, are shown, sorted from the most water scarce region (top) to the least (bottom). The global median is also presented at the bottom. Out-of-range values for the Arabian-Peninsula are printed at the top.

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When analysing median WSI by river basins for the future period (2076 – 2095; Fig. 9), the findings become clearer compared to the grid-cell analysis in Fig. 7. Similar to the bar plots in Fig. 8, the comparison of median WSI between scenarios S1 and S4 (Fig. 9a, b) suggests that dynamic plant processes results in limited overall changes. However, WSI category shifts are suggested for several basins, including in central, southern, and northern Africa, Southeast Asia, and eastern Australia. Supporting our existing findings, the CO₂-induced stomatal response reduces WSI in many basins (Fig. 9c,d,f). Median WSI decreases by at least 20% in numerous basins, including in Europe, central and southern Africa, and South and East Asia, with



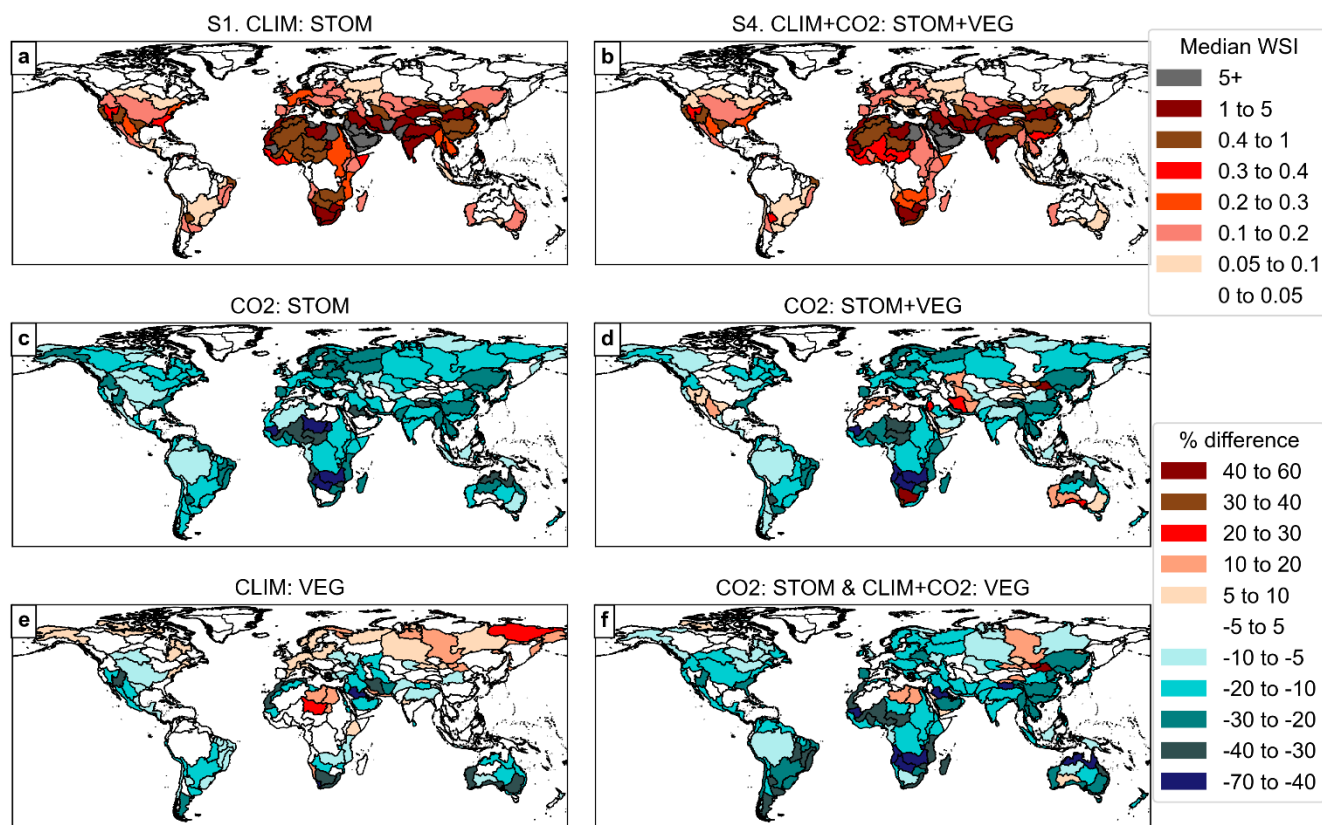
415 reductions exceeding 40% in basins in part of Africa. When CO₂ effects on vegetation are also included in CO₂: STOM+VEG, median WSI increases by more than 10% in 18 basins (Table 2) including in the Middle East, Australia, Southern and Northwestern Africa, and the western USA (Fig. 9d), likely due to CO₂-induced vegetation increases enhancing drying. However, the supply increases from stomatal responses due to enhanced CO₂ appear to dominate, resulting in WSI reductions by at least 10% in 122 basins (Table 2).

420 The impact of climate-induced changes on vegetation is more varied with modest increases in WSI (<10%) in much of Europe and larger increases (10-30%) in central-northern Africa. However, reductions are more common, particularly around arid and semi-arid regions (Fig. 9e), also supported by Table 2, which suggests more increases than decreases in median WSI across all the thresholds.

425 Considering all factors combined in CO₂: STOM & CLIM+CO₂: VEG, decreases in WSI outweigh increases (Fig. 9f). Out of 291 basins, 139 show reductions of at least 10% (maximum 67%), affecting 80% of the global population, while only 11 basins see increases over 10% (maximum 59%), affecting just 0.2% of the population (Table 2).

430 Most of the population are seeing small percentage changes compared with large ones, shown by the higher numbers in the lower thresholds (e.g., 5% and 10%) in Table 2. For example, when all processes are included in CO₂: STOM & CLIM+CO₂: VEG, median WSI will reduce by at least 5% for 88% of the population compared with reductions of at least 40% for only 2% of the population.

435 Figure S5 shows the number of months in severe water scarcity (WSI \geq 0.4), with the CO₂-induced stomatal response again driving small reductions of mainly 1 to 2 months in many basins, in similar regions to those seen in Fig. 9f, including southern South America, central and southern Africa southeast Asia and coastal Australia. The results are also consistent when dividing into seasons, which show overwhelming reductions in median WSI across all seasons in the future period (Fig. S6).



440 **Figure 9: Median WSI in simulations S1 and S4 (top row) and the relative (%) difference in median WSI when including the various isolated factors by river basin for the future period 2076-2095.**



| | Threshold (%) | Factor | Basin count above Threshold | Basin count below -Threshold | Percentage of population above Threshold | Percentage of population below -Threshold |
|-----|---------------|--|-----------------------------|------------------------------|--|---|
| 445 | 5 | CO ₂ : STOM | 0 | 198 | 0.0 | 90.1 |
| | | CO ₂ : STOM+VEG | 26 | 169 | 4.4 | 83.5 |
| | | CLIM: VEG | 51 | 76 | 7.3 | 33.4 |
| | | CO₂: STOM & CLIM+CO₂: VEG | 17 | 176 | 1.1 | 87.8 |
| 450 | 10 | CO ₂ : STOM | 0 | 156 | 0.0 | 81.4 |
| | | CO ₂ : STOM+VEG | 18 | 122 | 2.7 | 62.0 |
| | | CLIM: VEG | 21 | 43 | 0.4 | 9.3 |
| | | CO₂: STOM & CLIM+CO₂: VEG | 11 | 139 | 0.2 | 80.2 |
| 455 | 20 | CO ₂ : STOM | 0 | 67 | 0.0 | 24.7 |
| | | CO ₂ : STOM+VEG | 7 | 56 | 1.0 | 21.4 |
| | | CLIM: VEG | 5 | 15 | 0.1 | 2.6 |
| | | CO₂: STOM & CLIM+CO₂: VEG | 4 | 68 | 0.0 | 26.4 |
| 460 | 40 | CO ₂ : STOM | 0 | 9 | 0.0 | 1.6 |
| | | CO ₂ : STOM+VEG | 2 | 6 | 0.3 | 1.9 |
| | | CLIM: VEG | 1 | 2 | 0.0 | 0.2 |
| | | CO₂: STOM & CLIM+CO₂: VEG | 3 | 11 | 0.0 | 2.1 |

Table 2. Total number of river basins and the percentage of the total projected global population affected by changes in median WSI relative to specific percentage thresholds, driven by various isolated factors for the period 2076–2095.

The annual cycles of median WSI for the period 2076 to 2095 across several major river basins are illustrated in Fig. 10, along with the relative differences when the isolated factors are included. These basins were selected based on their population and water scarcity levels, ensuring a fair geographic distribution across all continents (excluding the poles).

All basins experience periods of water scarcity during parts of the year. Consistent with previous findings, the inclusion of the CO₂-induced stomatal response mitigates WSI in all basins throughout the year, and especially during water-scarce periods. In some basins, this effect reduces WSI by over 40% during certain times of the year. For instance, in the northwest Africa and Tigris-Euphrates basins (Fig. 10a,c), the WSI is projected to be at least 50% lower during the most water-scarce periods. The basin in southern Africa presents contrasting results to the other basins and to our existing results; when including the CO₂-induced vegetation increases in CO₂: STOM+VEG, median WSI is 50% higher, which is the case for much of the year. Interestingly, climate-induced vegetation changes drive 40-50% reduction in WSI over the year. These two processes appear to be balancing one another out, as the combined effect of all processes results in minimal net change in WSI.



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Otherwise, including all plant responses to CO₂ and climate in S4, consistently mitigates WSI across the year in most basins, with the magnitude of this effects varying across the year. These findings suggest that plant responses to CO₂ have the most substantial impact during periods of water scarcity, highlighting their importance in future water scarcity projections.

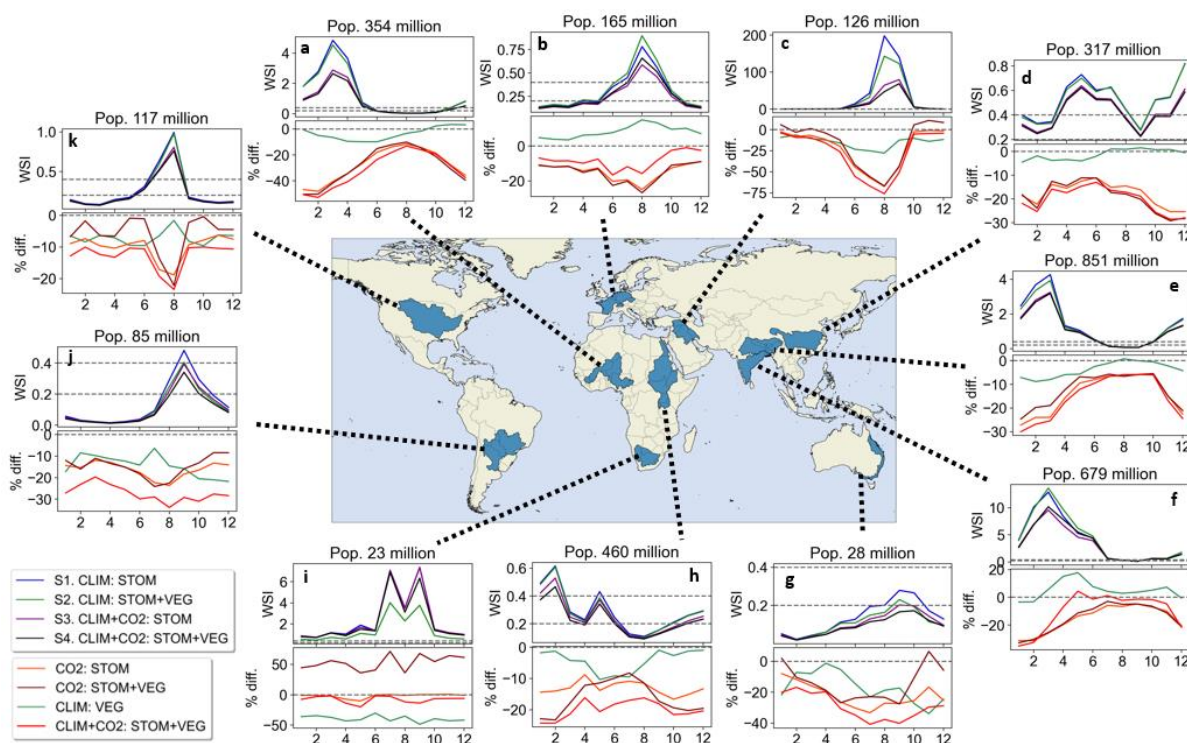


Figure 10: Annual cycles of median WSI, and the relative (%) difference in median WSI when including the various isolated factors for various river basins around the world for the future period 2076-2095. Total population of the basin is noted above each plot.

4 Discussion

485 Existing studies on the socioeconomic impacts of water scarcity are typically based on hydrology models that do not include plant physiological or structural responses to CO₂ or climate change (e.g., Dolan et al., 2021; Gosling and Arnell, 2016; Greve et al., 2018; Haddeland et al., 2014; Schewe et al., 2013). By replicating the common approach, i.e., driving a standalone impacts model with climate model output, this study investigates the influence of incorporating these plant responses in such analyses.

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Numerous observational and modelling studies have demonstrated the impact of physiological forcing on the water cycle. In line with many of these studies (e.g., Betts et al., 2007; Cao et al., 2010; Gedney et al., 2006), our results suggest that, for the overall global mean, rising CO₂ decreases stomatal conductance and transpiration, leading to higher soil moisture and increased



runoff (Figs. 2,4). Projected total runoff increases of 10-12% by the end of the century (Fig. 2e) are analogous with the global
495 mean values suggested in Betts et al. (2007) and Cao et al. (2010). Interestingly, the relative increase due to physiological
forcing is much higher for sub-surface runoff than surface runoff (Fig. 2f,g), likely because surface runoff in the model is
mostly driven by intense precipitation, i.e., where precipitation rate exceeds infiltration rate. The runoff increases from the
stomatal response are most pronounced in the tropics (Fig. 4i), corroborating the findings of several studies (e.g., Davie et al.,
2013; Fowler et al., 2019; Lemordant et al., 2018; Yang et al., 2019). Furthermore, also supported by these studies, our results
500 suggest that global mean LAI increases with rising CO₂ (Fig. 2k,n), but, at the global scale, any reductions in runoff due to
increased vegetation cover and LAI is outweighed by the increases in runoff due to the CO₂-induced stomatal response, since
CO₂: STOM+VEG shows relative increases for global mean runoff and soil moisture (Fig. 2e-h). However, CO₂- and climate-
induced vegetation increases are still projected to drive small decreases in runoff change across large areas of the globe,
especially in semi-arid and arid regions, west USA, parts of mid-latitudes and Australia, supported by some studies (e.g., Piao
505 et al., 2007; Ukkola et al., 2016). Even though these decreases appear negligible in number, water supply is already low in
many of these regions and therefore a small decrease can greatly exacerbate water scarcity in these areas.

As expected, the increase in global water supply due to the various plant responses analysed in our simulations translates to
overall reductions in global median WSI. Our results suggest that the stomatal response to rising CO₂ has the dominating
510 influence over vegetation growth in most places, especially when analysing by IPCC climate regions and river basins.
However, the impact on water supply is relatively larger than the reduction in WSI (Fig. 5). For the global median, by 2100,
the CO₂-induced stomatal response (CO₂: STOM) results in a ~35% increase in water supply (Fig. 5d) but only ~20% reduction
in WSI (Fig. 5e). The lesser influence on WSI is likely because the most substantial increases in water supply are primarily
due to the CO₂-induced stomatal response, which has most influence in non-water scarce regions with abundant water supply,
515 such as tropical regions like the Amazon and Southeast Asia (Fig. 7f,g).

The areas currently experiencing and projected to face severe water scarcity highlighted in our study align with those indicated
in previous studies (e.g., Dolan et al., 2021; Gosling and Arnell, 2016; Greve et al., 2018; Mekonnen and Hoekstra, 2016).
Under RCP 6.0 and SSP2 middle of the road scenarios, global median WSI increases until around the middle of the century
520 and then declines (Fig. 5c), although the maps of projected change suggest many places will still experience worsening water
scarcity throughout the century (Fig. 7c). Water scarcity projections with and without dynamic plant processes (Figs. 7-9) do
not present drastic differences since the primary drivers are clearly water demand and climate effects on supply, like
precipitation and temperature. However, the influence of plant responses, particularly the stomatal response to rising CO₂, is
not completely negligible when the results are collated over larger areas. Overall median WSI for the majority of IPCC AR6
525 regions and river basins are projected to be alleviated when all plant responses are included in CO₂: STOM & CLIM+CO₂:
VEG, with a much smaller number projected to be exacerbated (Figs. 8,9; Table 2).



The estimation for water supply for the WSI calculation in this study has inherent limitations. We use surface and sub-surface runoff for a proxy of water supply, giving an indication of how much water is available. In reality, water supply is taken from sources such as groundwater from aquifers and wells, glacier and ice melt, desalinated seawater or even imported water. Consequently, WSI values may be overestimated in certain regions, particularly in arid areas with limited surface water availability, such as the Middle East. To address the uncertainties surrounding water supply sources, we calculate WSI at multiple spatial scales: by grid-box (Figs. 6,7), IPCC AR6 climate regions (Fig. 8) and river basins (Figs. 9,10). At the grid-box level, WSI tends to be higher in many places, particularly in urban areas where demand substantially exceeds the supply within the grid-box. In contrast, when aggregating supply and demand by river basin before computing WSI, we assume that total runoff in the basin will be accessible for all the population within the basin. While neither calculating WSI at the grid-box or river basin scales fully captures the complexity of water distribution and accessibility, this is not a critical limitation for the objective of this study, which focuses on assessing the relative impacts of vegetation responses on WSI rather than providing precise WSI values. There are notable difference when computing WSI by grid-box on maps like in Fig. 7 which suggest that plant responses lead to *increases* in median WSI across many areas; a trend not corroborated when calculating WSI by larger spatial scales (Figs. 8,9).

As a multi-sectoral model, JULES is a suitable model for this study, since it allows us to explore how the water cycle responds to the combined effects of vegetation responses to both atmospheric CO₂ and subsequent climate change. This capability enables us to assess the sensitivity of water scarcity metrics to these critical processes, making JULES an invaluable tool for our analysis. However, there are some limitations. Firstly, while JULES includes detailed physiological, vegetation dynamics and hydrological processes, it was not specifically designed as a hydrology model. As a result, the Earth System version of JULES used in this study lacks key components essential for accurate water scarcity projections, such as the integration of water quality factors and water management practices like reservoirs and irrigation. Additionally, JULES does not account for the water needs of ecosystems, such as rivers and wetlands, which could lead to an overestimation of water supply. However, there are versions of JULES, such as Hydro-JULES (Dadson et al., 2019), that are being developed to address these limitations.

Secondly, due to limitations on resolution of climate models, many hydrological and biophysical processes occur on much smaller scales than models can resolve, and thus these interactions are parameterised in JULES. Consequently, the intricacies of the Earth system are simplified, and our projections are dependent on the accuracy of these parameterisation schemes, some of which may not reflect the most recent scientific advancements. Notably, recent progress in plant ecophysiology has established links between xylem hydraulic functioning and stomatal responses to climate. A new stomatal optimisation model has been developed for JULES, which has demonstrated improved alignment with observational data, particularly under drought conditions (Eller et al., 2020). Incorporating the updated stomatal conductance parameterisation in future similar analysis could therefore enhance the accuracy of the results. Furthermore, scientific advancements in observations, such as through the Free Air CO₂ Enrichment (FACE) studies, will likely offer further insights into changes in stomatal conductance,

water use efficiency, and growth patterns under higher atmospheric CO₂. Such findings could refine the representations of vegetation and hydrological processes under future climate conditions in the land surface schemes of climate models resulting in more accurate model projections.

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In this study, we have not directly verified output from our simulations against observations, as the key variables for our analysis have been evaluated in Mathison et al., (2023), which uses the same ISIMIP2b setup of JULES. For the period 1980 – 2006, their findings indicate that runoff output from HadGEM2-ES exhibits negligible biases for most basins, with slight underestimations in China and northern high latitudes, and slight overestimations in eastern USA. Given that our study focuses on the influence of plant responses – comparing the differences from two simulations with similar biases - HADGEM2-ES and this version of JULES are deemed suitable for our purposes, despite the runoff biases.

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Another common limitation in many impact studies relying on hydrology or other impact models run offline, is that they are not coupled to the driving climate model, as is the case with JULES in this study. This can lead to unrealistic inconsistencies, because changes in energy and water fluxes at the surface simulated by the offline model, can potentially influence atmospheric circulations, including temperature and precipitation patterns. When models are run offline, these critical feedbacks to the atmosphere are lost, resulting in inconsistencies between the offline impacts model and the driving climate model. Further research into the significance of these inconsistencies for water scarcity projections could highlight the importance of using hydrology models that are coupled to the atmosphere, improving the accuracy and reliability of such studies, which is especially important in a changing climate.

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Another inconsistency in our study occurs between the water demand and supply data, since the hydrology model ‘H08’ used to simulate water demand projections does not account for physiological forcing. As atmospheric CO₂ rises, crops are likely to become more water-efficient, lowering water required for irrigation. This discrepancy creates inconsistencies between water supply data that includes physiological forcing and demand data that does not. Future research could reveal an even greater influence of physiological forcing if increased crop water-use efficiency under elevated CO₂ were also incorporated into water demand projections.

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5 Conclusions

Our results suggest that plant physiological and structural responses to rising CO₂ concentrations and associated climate change are likely to alleviate water scarcity in many regions throughout this century. Enhanced water-use efficiency driven by CO₂-induced stomatal closure contributes to increased water availability in many regions, particularly the tropics. The supply increase translates to decreases in WSI in many regions, although the largest increases in water supply occur in regions that already experience abundant rainfall, such as the tropics, which are typically areas that do not suffer from water scarcity. Thus,

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595 when averaged globally, the CO₂-induced stomatal response drives relatively smaller reductions in WSI than increases in water supply. Our projections also indicate potential increases in WSI in certain semi-arid and arid regions, attributed to CO₂- and climate-induced expansions in vegetation cover and leaf area, reducing water availability in already water-limited areas. When WSI is calculated across IPCC climate regions and river basins, the incorporation of all dynamic plant responses alleviates projected WSI for most of the global population, highlighting the importance of accounting for vegetation dynamics in water scarcity assessments.

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We note that there are limitations inherent in modelling the complex interactions between the biosphere and hydrosphere under changing climate conditions. The results presented here are based on assumptions and parameterisations within the JULES land surface model. Further research is needed to refine these findings, particularly through the use of more advanced representations of plant responses to elevated CO₂ and climate change, supported by observational data. Such efforts will enhance the accuracy and reliability of future water scarcity projections, improving their utility for policymakers and water resource managers.

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Code availability

Analyses have been done using Python. Code is available on GitHub at <https://github.com/jessica-stacey/water-scarcity-plants-jules>.

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Data availability

Output from JULES simulations can be made available upon request. Water demand data is available from the ISIMIP database (e.g., https://data.isimip.org/search/query/amanww/tree/ISIMIP2b/OutputData/water_global/h08/hadgem2-es/). Population data is also available from the ISIMIP database (<https://data.isimip.org/datasets/6eee7c61-4baa-4b1d-aa81-d854f217f07e/>).

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Author contributions

JS: Conceptualisation, investigation, methodology, formal analysis, visualisation, writing draft

RAB: Conceptualisation, methodology, supervision, writing (review and editing)

620 AH: Supervision, methodology, validation, writing (review and editing)

LM: Supervision, writing (review and editing)

NG: Writing (review and editing)

Competing interests

625 The authors declare that they have no conflict of interest.

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