





PRIMARY RESEARCH ARTICLE

Increasing aridity will not offset CO₂ fertilization in fast-growing eucalypts with access to deep soil water

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Abstract

Rising atmospheric [CO₂] (C_a) generally enhances tree growth if nutrients are not limiting. However, reduced water availability and elevated evaporative demand may offset such fertilization. Trees with access to deep soil water may be able to mitigate such stresses and respond more positively to C_a. Here, we sought to evaluate how increased vapor pressure deficit and reduced precipitation are likely to modify the impact of elevated C_a (eC_a) on tree productivity in an Australian *Eucalyptus saligna* Sm. plantation with access to deep soil water. We parameterized a forest growth simulation model (GOTILWA+) using data from two field experiments on *E. saligna*: a 2-year whole-tree chamber experiment with factorial C_a (ambient = 380, elevated = 620 μmol mol⁻¹) and watering treatments, and a 10-year stand-scale irrigation experiment. Model evaluation showed that GOTILWA+ can capture the responses of canopy C uptake to (1) rising vapor pressure deficit (*D*) under both C_a treatments; (2) alterations in tree water uptake from shallow and deep soil layers during soil dry-down; and (3) the impact of irrigation on tree growth. Simulations suggest that increasing C_a up to 700 μmol mol⁻¹ alone would result in a 33% increase in annual gross primary production (GPP) and a 62% increase in biomass over 10 years. However, a combined 48% increase in *D* and a 20% reduction in precipitation would halve these values. Our simulations identify high *D* conditions as a key limiting factor for GPP. They also suggest that rising C_a will compensate for increasing aridity limitations in *E. saligna* trees with access to deep soil water under non-nutrient limiting conditions, thereby reducing the negative impacts of global warming upon this eucalypt species. Simulation models not accounting for water sources available to deep-rooting trees are likely to overestimate aridity impacts on forest productivity and C stocks.

KEYWORDS

deep soil water uptake, *Eucalyptus saligna*, forest productivity, vapor pressure deficit, water availability

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1 | INTRODUCTION

The atmospheric CO₂ concentration (C_a) has increased by about 45% since the Industrial Revolution (Ciais et al., 2014), strongly altering the climate worldwide (IPCC, 2013; Lüthi et al., 2008). Globally, forests buffer the rise in C_a by removing annually ~3.6 PgC from the atmosphere, which corresponds to roughly 34% of anthropogenic greenhouse gas emissions (Canadell et al., 2007; Pan et al., 2011; see Keenan & Williams, 2018 for a review). Recent observations attributed the increase in forest carbon uptake of the last decades to rising C_a (Keenan et al., 2016, 2020; Liu et al., 2019). However, forest C uptake is strongly affected by the water cycle (Denmead & Shaw, 1962; Humphrey et al., 2018; Nemani et al., 2003). Two of its components are primarily limiting: low water available in the soil (e.g., Denmead & Shaw, 1962; Grassi & Magnani, 2005; Van der Molen et al., 2011) and high atmospheric evaporative demand (Novick et al., 2016; Sanginés de Cárcer et al., 2018; see Grossiord et al., 2020 for a review). From now on, we use the term aridity as the hydric stress exerted on the vegetation by low soil water availability (land aridity) and/or by elevated evaporative demand (atmospheric aridity), following Berg et al. (2017).

Over the next decades C_a is projected to keep rising, modifying Earth's climate (IPCC, 2013; Webb & Hennessy, 2015). In the absence of nutrient limitation (see Ellsworth et al., 2017), rising C_a has led to an increase in forest productivity and carbon sequestration during the last few decades (e.g., Cheng et al., 2017; Haverd et al., 2020; Keenan et al., 2013; see Walker et al., 2019). More precisely, eC_a enhances intrinsic water-use efficiency (WUE; De Kauwe et al., 2013; Eamus & Jarvis, 1989; Keenan et al., 2013) due to decreased stomatal conductance (e.g., Ainsworth & Long, 2005; Farquhar & Sharkey, 1982; Medlyn et al., 2001) and increased net assimilation (e.g., Barton et al., 2012; Kelly et al., 2016). Higher WUE may sustain non-limiting soil moisture for a longer period during the growing season, resulting in a further stimulation of gross primary production (GPP). In parallel, the increase in CO₂ and other greenhouse gas concentrations in the atmosphere has led to an overall augment in temperature, 2020 which is expected to keep rising in the next decades. Following temperatures, exponential increases in vapor pressure deficit (*D*) are expected, thus augmenting atmospheric aridity (Berg & Sheffield, 2018; Lin et al., 2018; Scheff & Frierson, 2014). Similarly, changes in annual precipitation amounts and patterns may limit soil water availability particularly during the growing season (Doughty et al., 2015; Gazol et al., 2017; Trenberth et al., 2014; Williams et al., 2010). At declining soil water potential, trees typically close their stomata to avoid losses in hydraulic conductance (Peñuelas et al., 2017; Reich et al., 2018; Sperry & Tyree, 1990). This limits C substrate for photosynthesis, hence reducing assimilation. Additionally, trees may reduce leaf mesophyll conductance and decrease photosynthetic potential under drought stress, which further limits assimilation (Drake et al., 2017; Grassi & Magnani, 2005; Keenan et al., 2011). Trees that are able to mobilize water from deep soil reservoirs have shown to be less affected by episodic drought events and to maintain productivity at a higher rate (e.g., McDowell et al., 2019;

Ripullone et al., 2020). This ability is thought to be key for the persistence of water-demanding eucalypts in the harsh Australian climate (Christina et al., 2017; Laclau et al., 2013; Zeppel et al., 2008). Recent findings suggest that when trees are able to access shallow water tables, even extreme sporadic drought has little impact on tree growth (Sousa et al., 2020). Nevertheless, in the long term, deep soil water availability is tightly linked to precipitation patterns over land (Berg et al., 2017). In addition, increased water consumption by vegetation due to increasing evaporative demand may reduce such deep soil water reservoirs (Mu et al., 2021). In the context of increasing aridity, this may limit productivity and survival of eucalypts relying on such deep soil water reservoirs.

Whether rising C_a will continue to enhance forest productivity during the next decades, or it will be counterbalanced by aridity increases, is still under debate. On the one hand, tree mortality may increase in a hotter and drier world (Allen et al., 2015). This will limit forest C uptake and reduce forest C stock. Recent observations suggest that drought and heat stress is accelerating tree mortality in mature Amazon forests, thus counterbalancing eC_a-driven biomass gains, and reducing carbon sink potential (Brienen et al., 2015). A similar trend is expected for the African tropical forests in the near future (Hubau et al., 2020). Similarly, *D* increases have been suggested to have the potential to offset eC_a fertilization at a global level (Yuan et al., 2019). Furthermore, recent findings suggest that trees do not benefit from eC_a conditions when exposed to a severe hot-drought stress (e.g., Birami et al., 2020; Duan et al., 2014; Gattmann et al., 2020). On the other hand, data from large-scale decadal manipulative fertilizing experiments involving eC_a (FACE experiments) of young forests growing under non-limiting nutrient availability conditions show a persistent stand biomass increase (Walker et al., 2019). A number of process-based models suggest that such eC_a stimulation on forest net productivity will be sustained during the next decades, for environments ranging from semiarid Mediterranean to tropical forests (e.g., De Kauwe et al., 2016; Fatichi et al., 2016; Keenan et al., 2011; Sperry et al., 2019). In all cases, stimulation of photosynthesis and water savings due to reduced *g*_s at eC_a were found to exceed the detrimental effects of increasing aridity (e.g., Keenan et al., 2020; Swann et al., 2016). Also, the aforementioned ability to access water-enriched deep soil layers may contribute to ameliorate stand responses, thus allowing trees to take more advantage of eC_a conditions (e.g., Humphrey et al., 2018; Laclau et al., 2013; Nadal-Sala et al., 2019).

In eucalypts, early experiments with potted *Eucalyptus grandis* seedlings demonstrated that eC_a led to an increase in net assimilation and tree biomass, if N and P were not limiting (Conroy et al., 1992). Subsequently, similar conclusions were drawn from numerous controlled experiments on different eucalypt species grown in non-nutrient limiting conditions (e.g., Duan et al., 2019; Ghannoum, Phillips, Conroy, et al., 2010; Quentin et al., 2015). However, in P-limited soil conditions, mature *E. tereticornis* trees grown in eC_a at EucFACE did not exhibit higher aboveground growth, despite higher leaf-level photosynthesis (Ellsworth et al., 2017; Jiang et al., 2020). In growth chamber studies with saplings, eC_a limited the negative effects of

moderate drought stress by increasing leaf-level water-use efficiency (WUE_l) and stimulating fine root development, which delayed drought stress (e.g., Apgaua et al., 2019; Atwell et al., 2007, 2009; Roden & Ball, 1996). However, eucalypt seedlings exposed to a progressive, intense drought did not exhibit growth enhancement or reduced hydraulic vulnerability due to eC_a (Duan et al., 2014, 2018), again suggesting that the benefit of eC_a was dependent on the duration and intensity of the drought stress. Therefore, whether rising C_a will continue to stimulate forest productivity or will be offset by concomitant aridity increases is yet not solved, with severe implications for forest C cycling.

Here, we used data from two field experiments in a young *E. saligna* plantation in Australia, where trees had access to deep soil water, to calibrate the GOTILWA+ process-based forest simulation model. Then, we quantified the sensitivity of *E. saligna* to several environmental drivers related to climate change. We particularly focused on the main and interactive effects of projected rise in D , reduced precipitation, and increasing C_a , upon tree productivity and transpiration. More specifically our research questions were: (1) To what extent does increasing D and decreasing precipitation limit productivity of *E. saligna*? (2) Will access to deep soil water ameliorate soil and atmospheric aridity impacts on productivity? and (3) How will stand WUE respond to combined aridity and C_a increases?

2 | MATERIAL AND METHODS

2.1 | Site description and experimental setup

All measurements were performed in a monospecific Sydney Blue Gum (*E. saligna* Sm.) plantation located at the Hawkesbury Forest Experiment (HFE) on the Western Sydney University Hawkesbury Campus in Richmond, NSW, Australia (33°36'40"S, 150°44'27"E, 20 m a.s.l.). The climate is temperate-subtropical, with annual mean minimum and maximum temperatures of 10.5 and 23.9°C, respectively, and mean annual precipitation of 801 mm year⁻¹ during the 1980–2010 period (Australian Bureau of Meteorology, <http://www.bom.gov.au/>; Barton et al., 2010; Heroult et al., 2013). Upper soil layers are an alluvial formation of low-fertility sandy loam soils, with low organic matter content. Below 100 cm depth, there is a water-enriched clay layer that limits drainage from the upper parts of the soil and acts as a water reservoir (Duursma et al., 2011). In the HFE, *E. saligna* has been observed to develop deep roots, with capacity to access water to ~4.5 m depth (Duursma et al., 2011).

In the HFE, two separate experiments were co-located and performed using *E. saligna*: a whole-tree chamber experiment (hereafter referred as WTC) and an irrigation experiment (hereafter referred as "Ir"). For the Ir experiment, *E. saligna* seedlings were planted in April 2007 at a density of 1000 trees ha⁻¹. Four square plots per treatment (i.e., Control and Irrigation, size = 38.5 × 41.6 m, ~160 trees per plot) were randomly determined. The plots were laid out and planting rows were ripped to a depth of 30 cm; deeper ripping and mounding was unnecessary in the sandy top soil. A 2-m wide strip was sprayed with herbicide to control weed growth prior to planting.

In each plot, a computerized irrigation system capable of supplying a uniform distribution of water across each plot at a rate of 7 mm h⁻¹ was installed. The irrigation treatment consisted of the application of 15 mm every fourth day (delivered at night). Irrigation was withheld during periods of high rainfall to avoid leaching of nutrients or water-logging. For each plot, we performed 14 measurement campaigns between 2007 and 2018, in which we measured the diameter at breast height (DBH, in cm) at ~1.3 m for each individual tree and then we averaged the DBH per plot.

For the WTC experiment, *E. saligna* saplings were planted in April 2007 into twelve 9 m high and 10 m² ground-based surface area cylindrical WTCs that enclosed individual trees rooted in soil. The WTCs served as controlled environment for temperature, humidity, and atmospheric CO₂ while enabling analysis of gas exchange of CO₂ and water vapor between the individual tree crowns and the chamber air. Trees were grown from April 2007 to March 2009 under a 2 × 2 factorial combination of atmospheric CO₂ and watering treatments. The CO₂ treatment levels were ambient CO₂ (aC_a , 380 μmol mol⁻¹) and elevated CO₂ (eC_a , 620 μmol mol⁻¹); see Barton et al. (2010, 2012) for further details. The watering treatment levels were designated wet (irrigated throughout the monitoring period) and dry-down (water withheld from October 2008 to February 2009+ rain exclusion); see Duursma et al. (2011) for further details. There were three chambers for each C_a × watering treatment. The chambers were surrounded by control trees, planted at a density of 1000 trees ha⁻¹.

2.2 | Leaf gas exchange

Leaf-level gas exchange was measured on WTC trees during nine campaigns, from September 2007 to March 2009. Measurements were made on sun-exposed, fully expanded leaves with three replicates per WTC per measurement campaign, using two portable infrared gas analyzer systems (LI-6400, Li-Cor, Inc.) with a 6 cm² chamber. Measurements were taken at saturating photosynthetic photon flux density (PPFD > 1800 μmol m⁻² s⁻¹). Assimilation in relation to [CO₂] in the intercellular space (A_n/C_i) curves were generated by increasing C_a inside the 6 cm² chamber in nine to 10 steps. The first measurement was taken at ambient C_a . We initially took a measurement at sub-ambient C_a (ca. 37 μmol mol⁻¹, near CO₂ compensation point). We then increased C_a progressively, to a maximum of 2000 μmol mol⁻¹. Leaf temperature (T_{leaf} in °C) and other standard variables were also measured. These measurements were taken under prevailing temperature and humidity conditions within each WTC at the time of measurement.

2.3 | Whole-tree aboveground carbon and water fluxes

For each WTC, aboveground whole-tree net carbon assimilation ($A_{n,tot,inst}$ = carbon assimilation minus aboveground growth and

maintenance respiration, in g C m^{-2} leaf area), and transpiration (E_{inst}) per unit of leaf area ($\text{kg H}_2\text{O m}^{-2}$ leaf area), were recorded at 14-min intervals from April 2008 to March 2009 (Barton et al., 2010). We calculated average daylight D inside each WTC on a daily basis. Daily standing leaf area (L , in m^2) per tree calculation is described elsewhere (Barton et al., 2012). We integrated $A_{n,\text{tot,inst}}$ and E_{inst} daily, from April 2008 to March 2009, in order to obtain $A_{n,\text{tot}}$ (in g C m^{-2} leaf area day^{-1}) and E (in $\text{kg H}_2\text{O m}^{-2}$ leaf area day^{-1}). Periods of equipment failure, failed seals to the chamber, and people entering the chamber for measurements were excluded from the final dataset.

2.4 | Soil water content

Volumetric soil water content (SWC, in %) for each WTC was continuously measured in the top 10 cm of soil with a Theta probe (Delta T instruments) throughout the study period. Additionally, for each WTC, SWC was measured every 2 weeks to a depth of 4.25 m (in steps of 0.25–0.5 m) with a neutron probe (503DR Hydroprobe[®], Instrotek; see Duursma et al., 2011 for further details). To obtain a daily time series of SWC in the upper soil, 38 sampling campaigns of discrete SWC measurements at 0.25, 0.5, and 0.75 m depths were correlated to continuous SWC measurements using a 2 degree of freedom generalized additive model (GAM; Wood, 2017) for each WTC. After calculating daily SWC for each soil depth, we selected 0.5 m as the reference soil depth because the agreement between daily and discrete SWC measurements worsened with depth (see Figure S1). Once daily SWC_{50} was obtained for each WTC, we calculated the relative SWC of the upper 0.5 m soil layer (S_{up}) by dividing daily SWC_{50} by an average of the highest 5% daily SWC_{50} values (i.e., $S_{\text{up}} = \text{SWC}_{50} / \text{SWC}_{50,\text{max}}$). Below 0.5 m, we assumed that trees were able to access the deep soil water reservoir, with a relative SWC (S_{deep}) that was set constant to 0.7 based on the relative SWC below 0.5 m measured before the dry-down experiment (see Figures S2 and S3b).

2.5 | Meteorological data

Daily meteorological data for the 2008–2017 period were obtained from the Richmond RAAF base meteorological station (Station O67105, bom.gov.au; see Figure S4), a meteorological station located about 3 km east of HFE. We accessed data on daily precipitation (P , in mm day^{-1}), maximum and minimum temperature (T_{max} and T_{min} , in $^{\circ}\text{C}$), photosynthetic active solar irradiation (Q , in $\text{MJ m}^{-2} \text{day}^{-1}$), and air relative humidity (RH, in %). One and 2-day gaps in data were linearly interpolated. Wider gaps in T_{max} and T_{min} data were interpolated from Windsor Bridge meteorological station (REF =067095, bom.gov.au), located about 5 km westward from the HFE, by linear regression (T_{max} : $n = 2821$, $t = 455.1$, $R^2 = 0.99$, $p < 0.01$; T_{min} : $n = 2821$, $t = 244.3$, $R^2 = 0.96$, $p < 0.01$).

From RH and T_{min} we calculated daily mean air water vapor pressure (VP, in kPa) according to the Clausius–Clapeyron relationship (Allen et al., 1998). Potential evapotranspiration (PET, in mm day^{-1}) was calculated daily according to the Penman–Monteith equation (Allen et al., 1998).

2.6 | Model

GOTILWA+ is a process-based dynamic model that focuses on forest carbon and water balances (www.creaf.uab.es/gotilwa; Gracia et al., 1999; Keenan et al., 2009; Nadal-Sala et al., 2017). GOTILWA+ has been extensively tested and validated against both flux data and stand data in many previous studies (e.g., Bugmann et al., 2019; Gracia et al., 2007; Keenan et al., 2009, 2010; Kramer et al., 2002; Morales et al., 2005). GOTILWA+ has been applied to project climate change and forest management impacts on forest carbon and water fluxes (e.g., Reyer et al., 2017; Sabaté et al., 2002). Also, Nadal-Sala et al. (2019) found that GOTILWA+ was able to properly capture phreatic water uptake in a Mediterranean riparian forest dominated by *Robinia pseudoacacia* L. Briefly, GOTILWA+ simulates carbon and water fluxes in a monospecific forest stand accounting for environmental drivers (e.g., $[\text{CO}_2]$, temperature, soil water, D , etc.), forest structure, and management, and assuming two leaf layers (e.g., sun and shade leaves) in a “big leaf” approach. For a detailed description of the model's process hierarchy and integration, see the references above. In the following subsections we summarize the main processes involved in our analysis.

2.6.1 | Leaf gas exchange in the absence of drought stress

In GOTILWA+, stomatal conductance (g_s , in $\text{mol m}^{-2} \text{s}^{-1}$) and leaf-level net assimilation (A_n , in $\mu\text{mol m}^{-2} \text{s}^{-1}$) are obtained iteratively at hourly time steps, while closing the leaf energy balance according to Gates (1962, 2012). In contrast to previous versions of GOTILWA+, here g_s was derived from the optimal stomatal behavior model (Medlyn et al., 2011, Equation 1):

$$g_s = g_0 + 1.6 \left(1 + \frac{g_1}{\sqrt{D}} \right) \frac{A_n}{C_a}, \quad (1)$$

where g_0 is the residual conductance (in $\text{mol m}^{-2} \text{s}^{-1}$), A_n is the net assimilation, g_1 is the stomatal operating point parameter (in $\text{kPa}^{0.5}$), D is the vapor pressure deficit (in kPa), and C_a is the atmospheric CO_2 concentration. A_n is calculated according to the Farquhar–von Caemmerer–Berry model (FvCB; De Pury & Farquhar, 1997; Farquhar et al., 1980). V_{cmax} and J_{max} in the FvCB model are leaf temperature dependent (e.g., Farquhar et al., 1980; Harley et al., 1992). Dark respiration (R_d) is assumed to increase exponentially with leaf temperature. K_c , K_o , and Γ^* (Rubisco oxidase and carboxylase kinetic constants, and CO_2 compensation point, respectively) are also temperature dependent.

2.6.2 | Effect of drought stress on gas exchange

Under reduced soil water availability, GOTILWA+ assumes a biochemical limitation on photosynthesis. An empirical β coefficient is applied to the gas exchange FvCB model parameters $V_{c_{\max,25,\text{ref}}}$ and $J_{\max,25,\text{ref}}$ —that is, the reference $V_{c_{\max}}$ and J_{\max} measured at well-watered conditions and corrected at 25°C (e.g., De Kauwe et al., 2015; Drake et al., 2017; Keenan et al., 2010). Changes in mesophyll conductance are assumed to be integrated in changes in the β coefficient as SWC decreases. The resulting leaf gas exchange sub-model is referred as FvCB+ β from now on. The β coefficient is given by:

$$\beta = \left(\frac{S_{\text{tot}} - S_{\text{tot,min}}}{S_{\text{tot,max}} - S_{\text{tot,min}}} \right)^q \quad \text{if } S_{\text{tot}} < S_{\text{tot,max}}, \quad (2)$$

$$\beta = 1 \quad \text{if } S_{\text{tot}} \geq S_{\text{tot,max}},$$

where S_{tot} is the relative soil water content of the whole soil profile, $S_{\text{tot,max}}$ is the value of S_{tot} above which there is no water limitation upon photosynthesis, and $S_{\text{tot,min}}$ is the critical S_{tot} value below which $\beta = 0$. The parameter q describes the nonlinearity of the responses to decreasing relative SWC. For a given S_{tot} , the water-limited values of $V_{c_{\max,25,S}}$ and $J_{\max,25,S}$ are given by the water-unlimited values multiplied by β .

GOTILWA+ considers water uptake in two soil layers. The first and uppermost soil layer requires soil depth, rock fraction, organic carbon fraction, and maximum SWC as inputs. SWC (SWC_{up} , in mm) in this first soil layer is dynamically depleted via transpiration, superficial runoff and drainage, and recharged through rainfall or irrigation. Relative SWC in the upper layer, S_{up} , is then calculated hourly from current SWC_{up} with respect to maximum SWC_{up} . Trees in GOTILWA+ may also mobilize a proportion of its water requirements from deep soil layers, even if the depth is unknown (Nadal-Sala et al., 2019). The relative SWC of the whole soil profile explored by the roots, S_{tot} , is therefore computed as a linear combination of the upper and deep soil relative SWCs (S_{up} and S_{deep} , respectively).

$$S_{\text{tot}} = \alpha S_{\text{deep}} + (1 - \alpha) S_{\text{up}}, \quad (3)$$

where S_{up} is the relative SWC, and S_{deep} (fraction) is the relative SWC in the deep soil layers. Here, as noted above S_{deep} is assumed to be constant, with a stand-specific value of 0.7 in the HFE. Finally, α is the proportion of water uptake from S_{deep} when S_{up} is at field capacity. Close-to-zero α values imply that the tree accesses water from the upper soil layer, while higher α values imply increasingly greater water mobilization from the deep soil (see Figure S4). Other impacts from reductions in S_{tot} considered in GOTILWA+ include increases in leaf temperature due to loss of leaf temperature homeostasis at declining g_s (Gates, 1962; 2012), which increases leaf maintenance respiration and accelerates leaf turnover by reducing mean leaf life span. Similarly, fine root carbon turnover velocity also increases at decreasing S_{tot} , which accounts for observed higher fine root turnover rates (e.g.,

Bloom et al., 1985; Gaul et al., 2008; Meier & Leuschner, 2008) and/or increased root exudates (Preece & Peñuelas, 2016) under drought (but see Drake et al., 2019).

2.7 | Model parameterization

For the stomatal model (Equation 1), g_o and g_1 parameters were obtained from Herault et al. (2013). Photosynthesis activation and deactivation energies for *E. saligna* were obtained from Lin et al. (2013). K_c , K_o , and I^* and their activation and inactivation energies were obtained from Bernacchi et al. (2001). See Table S1 for the source of all relevant parameters.

To obtain $V_{c_{\max,25,\text{ref}}}$ and $J_{\max,25,\text{ref}}$, we applied a Bayesian model inversion to the FvCB model (e.g., Feng & Dietze, 2013). As observations, we used A_n to C_i measurements, PAR and leaf temperature, under well-watered conditions. We split the available data into calibration ($n = 466$) and validation data ($n = 77$). As $V_{c_{\max,25,\text{ref}}}$ and $R_{d,25,\text{ref}}$ were strongly correlated (Pearson's $r > 0.8$, data not shown), we set $R_{d,25,\text{ref}}$ to a constant fraction of $V_{c_{\max,\text{ref}}}$ according to Collatz et al. (1991; $R_{d,25,\text{ref}} = 0.015 \cdot V_{c_{\max,25,\text{ref}}}$). In order to account for photosynthesis downregulation under elevated C_a , we ran two FvCB model calibrations, with A_n/C_i data obtained either at aC_a ($n = 230$) or at eC_a ($n = 236$). Afterward, we linearly interpolated changes in median $V_{c_{\max,25,\text{ref}}}$ and median $J_{\max,25,\text{ref}}$ at eC_a compared to aC_a as a percent change per unit of C_a increase.

To include drought limitations on photosynthesis (FvCB+ β model), we ran a third inverse calibration with the same simulation setup. This time, however, observations were taken from the A_n/C_i curves from the WTC dry-down experiment, and measured at $350 \leq C_a \leq 700 \mu\text{mol mol}^{-1}$ conditions ($n = 137$). We assumed the previously estimated median $V_{c_{\max,25,\text{ref}}}$ and median $J_{\max,25,\text{ref}}$ values as constants, and calibrated the parameters S_{min} , S_{max} , q , and α (Table 1).

For all calibrations, we ran three Markov Monte Carlo chains (MCMC), each consisting 100 k simulations of the model. We assumed a double-exponential (Laplace) error of our likelihood function in order to reduce the weight of outliers (Augustynczik et al., 2017) and applied a differential evolution with a memory snooker update sampling algorithm (DEzs; ter Braak & Vrugt, 2008). We used the "BayesianTools" package (Hartig et al., 2017) to run the MCMCs. The first 50 k simulations for each chain were removed from the posterior as a burn-in. Convergence was assessed by comparing the three chains for each calibration, and under a conservative Gelman–Rubin's test score (Gelman & Rubin, 1992) of 1.1.

2.8 | Model validation

We validated the FvCB model against an independent A_n/C_i dataset of observations under no water limitation ($S_{\text{up}} \geq 0.95$), measured at $350 \leq C_a \leq 700 \mu\text{mol mol}^{-1}$ ($n = 77$; Step 1 in Table S2). We validated

TABLE 1 Prior and posterior distributions for the three Bayesian calibrations performed. For all parameters, a uniform prior distribution was assumed. For each parameter, median values and 5%–95% CI of their posterior marginal distribution are noted. $aV_{\text{cmax},25,\text{ref}}$ and $aJ_{\text{max},25,\text{ref}}$ are V_{cmax} and J_{max} at 25°C under well-watered conditions for the aC_a treatment ($\mu\text{mol m}^{-2} \text{s}^{-1}$). $eV_{\text{cmax},25,\text{ref}}$ and $eJ_{\text{max},25,\text{ref}}$ are V_{cmax} and J_{max} at 25°C under well-watered conditions for the eC_a treatment. S_{min} is the minimum S_{tot} below which $A_n = 0$, and S_{max} is the minimum S_{tot} above which there is no drought limitation on photosynthesis assimilation (A_n , both in %). Q is a unit-less scale coefficient according to Equation (2). α is the fraction of water uptake below 50 cm soil depth when S_{up} is at saturation, according to Equation (3)

C_a ($\mu\text{mol mol}^{-1}$)	Variable	Prior		Posterior		
		Lower	Upper	2.5%	Median	97.5%
380	$aV_{\text{cmax},25,\text{ref}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	60	120	95.0	98.0	99.7
	$aJ_{\text{max},25,\text{ref}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	90	160	152.0	154.3	156.2
620	$eV_{\text{cmax},25,\text{ref}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	60	120	82.6	87.6	92.3
	$eJ_{\text{max},25,\text{ref}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	90	160	142.5	145.1	149.0
	S_{min} (%)	1	10	1.1	4.3	9.6
	S_{max} (%)	70	95	94.6	94.9	95.0
	Q	0.1	0.6	0.34	0.44	0.56
	α	0.1	0.7	0.29	0.45	0.60

the FvCB+ β model with another independent dataset of A_n/C_i curves, including A_n measured under all S_{up} conditions ($n = 310$; Step 2).

GOTILWA+'s ability to reproduce the fraction of water extracted from the upper soil (α) was assessed from $S_{\text{deep}}/S_{\text{total}}$ data during two discrete campaigns, under moderate and extreme drought conditions (data extracted from Figure 7a,b in Duursma et al., 2011; Step 3).

We tested for model sensitivity to the fraction of deep soil water uptake α (Step 4). To do so, we ran four simulations for the original *E. saligna* stand during the 2008–2017 period: (1) ambient climate (Ambien, where $\Delta P = 0$ and $\alpha = 0.45$); (2) reduced precipitation (R_p , $\Delta P = -20\%$); (3) reduced deep soil water uptake (R_α , $\alpha = 0.225$); and (4) reduced precipitation and reduced water uptake ($R_\alpha R_p$, $\Delta P = -20\%$ and $\alpha = 0.225$). We compared simulated $A_{n,\text{tot}}$ corrected at $D = 1$ ($A_{n,\text{tot,corr}}$ g C m⁻² leaf day⁻¹ kPa⁻¹) with the measurements from the dry-down WTC experiment when S_{up} was below 0.3. As a Shapiro–Wilk test confirmed non-normality of the data, significant differences in $A_{n,\text{tot,corr}}$ between scenarios were assessed through the Mann–Whitney–Wilcoxon U nonparametric test.

Modeled gas exchange fluxes at the stand scale were validated against WTC gas exchange data. We ran two simulations for the original *E. saligna* stand during the 2008–2017 period under ambient climate and two experimental C_a conditions (380 and 620 $\mu\text{mol mol}^{-1}$; Step 5). Modeled daily stand $A_{n,\text{tot}}$ and E were correlated with average daily daylight D , and we compared simulation results with observations from single-tree WTC under both C_a treatments.

We validated GOTILWA+ growth projections against data from the Ir experiment. Two separate 10-year simulations, control without irrigation and with irrigation (3.75 mm day⁻¹), were run for the 2008–2017 period in order to evaluate the ability of GOTILWA+ to capture stand-scale responses to irrigation. We compared simulated mean stand DBH against observed mean stand DBH under both irrigation treatments (Step 6). See Figure 1 for a scheme of the approach.

2.9 | Climate sensitivity scenarios

After model validation, the sensitivity of the *E. saligna* plantation to changes in environmental conditions was evaluated. Three environmental drivers were considered in this analysis, with upper boundaries of change based on IPCC (2013) and Webb and Hennessy (2015). Each simulation was 10 years long, which is within the traditional coppice rotation length in fast-growing, highly productive eucalypts (e.g., Ferraz Filho et al., 2014; Whittock et al., 2004).

Five levels of C_a were simulated ($C_a = 350, 400, 500, 600,$ and $700 \mu\text{mol mol}^{-1}$). For each C_a level, photosynthesis downregulation was accounted by linearly extrapolating observed changes in $V_{\text{cmax},25,\text{ref}}$ and in $J_{\text{max},25,\text{ref}}$ at changing C_a (see Supporting Information Notes 1). Additionally, six levels of precipitation were considered: +5%, +0%, -5%, -10%, -15%, and -20% of annual precipitation; no seasonal variations were considered. Although long-term deep soil water dynamics are strongly linked to precipitation patterns (Berg et al., 2017; Berg & Sheffield, 2018 and references therein; Seneviratne et al., 2010), there are still important uncertainties about the dynamics of such soil water reservoirs in SW Australia, mostly driven by the impact of vegetation (Mu et al., 2021). Therefore, for each precipitation reduction scenario, we assumed a linear decrease in S_{deep} proportional to the reduction in precipitation.

To evaluate the effect of increased D , we assumed no changes in atmospheric water vapor pressure (Trenberth et al., 2007). We assumed changes in air temperature of -1, 0, 1, 2, 3, 4°C and calculated D for each air temperature scenario following the Clausius–Clapeyron relationship. Rising D due to increasing temperature is nonlinear; therefore, we report those changes as $\Delta T(D)$, in °C. The mean annual D for the temperature change scenarios (-1°C to 4°C) varied between 1.33 and 2.21 kPa, respectively, which corresponded to a range of -11% to 48% increases in annual average D , respectively.

The initial stand density in the *E. saligna* plantation was 1000 trees ha⁻¹ with initial DBH = 2.6 cm. A total of 180 simulation

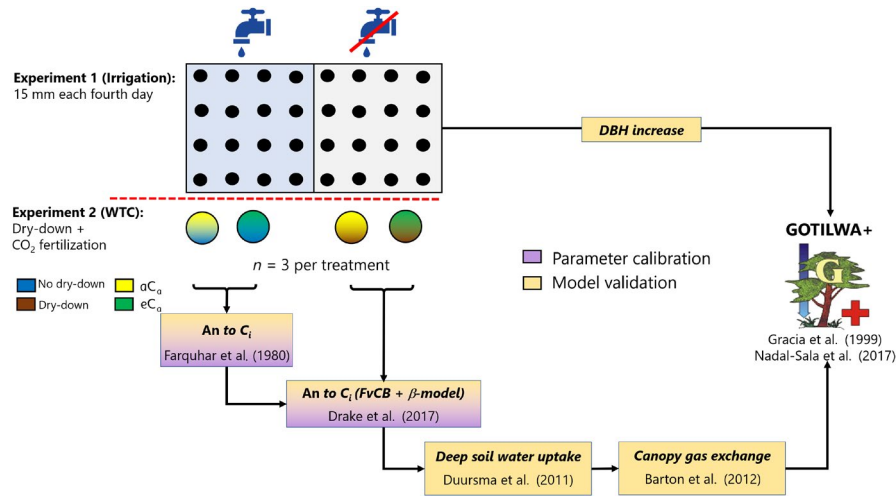


FIGURE 1 Scheme of model calibration validation setup. Experiment 1 is the 10-year long irrigation experiment in the Hawkesbury Forest Experiment plantation of *Eucalyptus saligna* (density = 1000 trees ha⁻¹), and Experiment 2 is the whole-tree chamber (WTC) experiment of *E. saligna* (see details in Barton et al., 2010, 2012; Duursma et al., 2011). The two main references for GOTILWA+ model are provided. Colors in the boxes indicate where calibration (purple color) and validation (tan color) procedures occurred, and the origin for such data or the reference for the model calibrated in such step. aC_a , ambient CO₂ atmospheric concentration (380 $\mu\text{mol mol}^{-1}$); eC_a , elevated CO₂ atmospheric concentration (620 $\mu\text{mol mol}^{-1}$); A_n , net assimilation per unit of leaf area; C_i , CO₂ concentration in the sub-stomatal chamber; DBH, diameter at breast height; FvCB+ β -model, Farquhar, von Caemmerer and Berry photosynthesis model (Farquhar et al., 1980) limited by water availability, when accounting for both the upper soil and deep soil water availability

runs were performed, covering all combinations of environmental change scenarios (Step 7 in Table S2).

2.10 | Data analysis

Data management and statistical analysis were performed using R software, version 3.6.1 (R Development Core Team, 2019). Bayesian model inversions were performed with the “BayesianTools” package (Hartig et al., 2017). GAM analyses were performed with the “mgcv” package (Wood, 2017). For all least-squares regressions, homoscedasticity and normality of the residuals were visually checked, and data were log-transformed when necessary.

3 | RESULTS

3.1 | Model parameterization and validation of leaf gas exchange

Inverse calibration of the Farquhar model captured measured A_n/C_i responses under well-watered conditions (see Supporting Information Notes 1 and Figure S5). Leaf-level photosynthesis decreased with decreasing relative SWC in the upper 50 cm soil layer, S_{up} (Figure 2a). At S_{up} lower than saturation ($S_{up} < 0.7$), the proportion of simulated A_n ($A_{n,sim,S}$) with respect to $A_{n,sim,ref}$ agreed well with observations only as long as water uptake was included from both S_{up} and S_{deep} (Figure 2b). Even under extremely low S_{up} values, observed A_n ($A_{n,obs}$) was reduced only by 55%. The calibrated median α coefficient of 0.45 (Table 1) indicates that, under

well-watered conditions, 55% of the water mobilized by the trees was from the top 50 cm of the soil. S_{deep} proportionally increased in importance as water source for *E. saligna* as S_{up} declined, reproducing observations from two sampling campaigns (Figure 3b). Modeled water uptake below 50 cm contributed about 45% to transpiration when S_{up} was close to saturation, and increased to 80% when S_{up} was almost depleted. Even more, if the dependence on S_{deep} was not accounted for, reductions in photosynthesis due to low water availability were strongly overestimated (Figure 2b). When both soil layers were included, the model reproduced the observations well ($n = 310$, $R^2 = 0.67$, RMSE = 5.05; Figure 3a).

3.2 | Model evaluation of canopy gas exchange and tree growth

D increases strongly affected whole-canopy aboveground net assimilation ($A_{n,tot}$), daily transpiration per unit leaf area (E), and whole-canopy WUE ($WUE = A_{n,tot}/E$). This sensitivity was reproduced by the GOTILWA+ under both aC_a and eC_a conditions (Figure 4). Modeled $A_{n,tot}$ responses to D matched the observed trend in single-tree WTC measurements for both C_a conditions (Figure 4a,d). Also, for both C_a conditions, the highest NCU values were found at a D of 1.1–1.5 kPa, both in the simulations and in observations. After that point $A_{n,tot}$ declined, and even turned negative at very high D (>3 kPa at aC_a and >4 kPa at eC_a), when stomata were likely closed and respiration costs were higher than photosynthetic gains.

Simulations using aC_a compared well with observed transpiration responses to D , although the model slightly underestimated

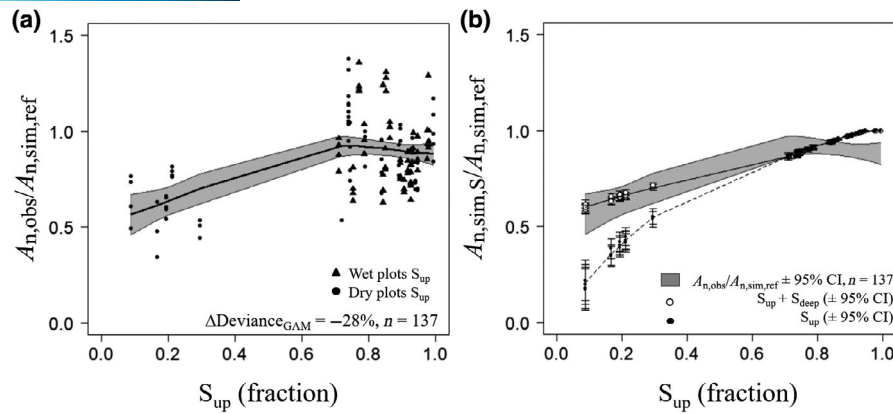


FIGURE 2 Observed (a) and simulated (b) *Eucalyptus saligna* leaf-level net assimilation (A_n) responses to decreases in water availability. (a) Observed A_n ($A_{n,obs}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), normalized by simulated reference A_n under no drought stress ($A_{n,sim,ref}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), as a function of relative soil water content in the in the upper 50 cm soil depth (S_{up}). Fitted 3-df generalized additive models (GAMs; mean \pm 95% CI) are shown (dark gray polygon). Decreases in deviance with respect to the null model are indicated for GAM model. (b) Simulated A_n at observed S_{up} ($A_{n,sim,S}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), normalized by simulated reference A_n under no drought stress ($A_{n,sim,ref}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$), as a function of S_{up} . For each point, 1000 samples of simulated A_n were obtained by posterior distribution sampling, represented as mean \pm 95% CI bars. Two sets of simulated values are shown, one where drought stress is a function of both S_{up} and S_{deep} (white circles), and one where it is a function of only of S_{up} (black dots). Shaded area is the 95% CI of GAM ($A_{n,obs}/A_{n,sim,ref}$ to S_{up}), obtained from panel (a)

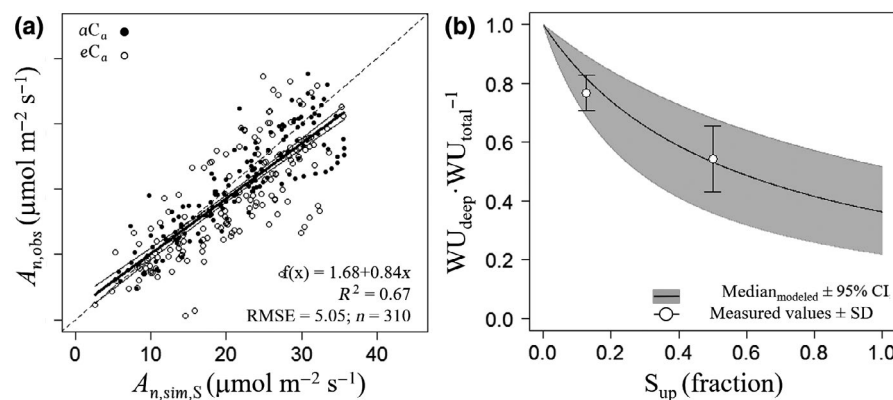


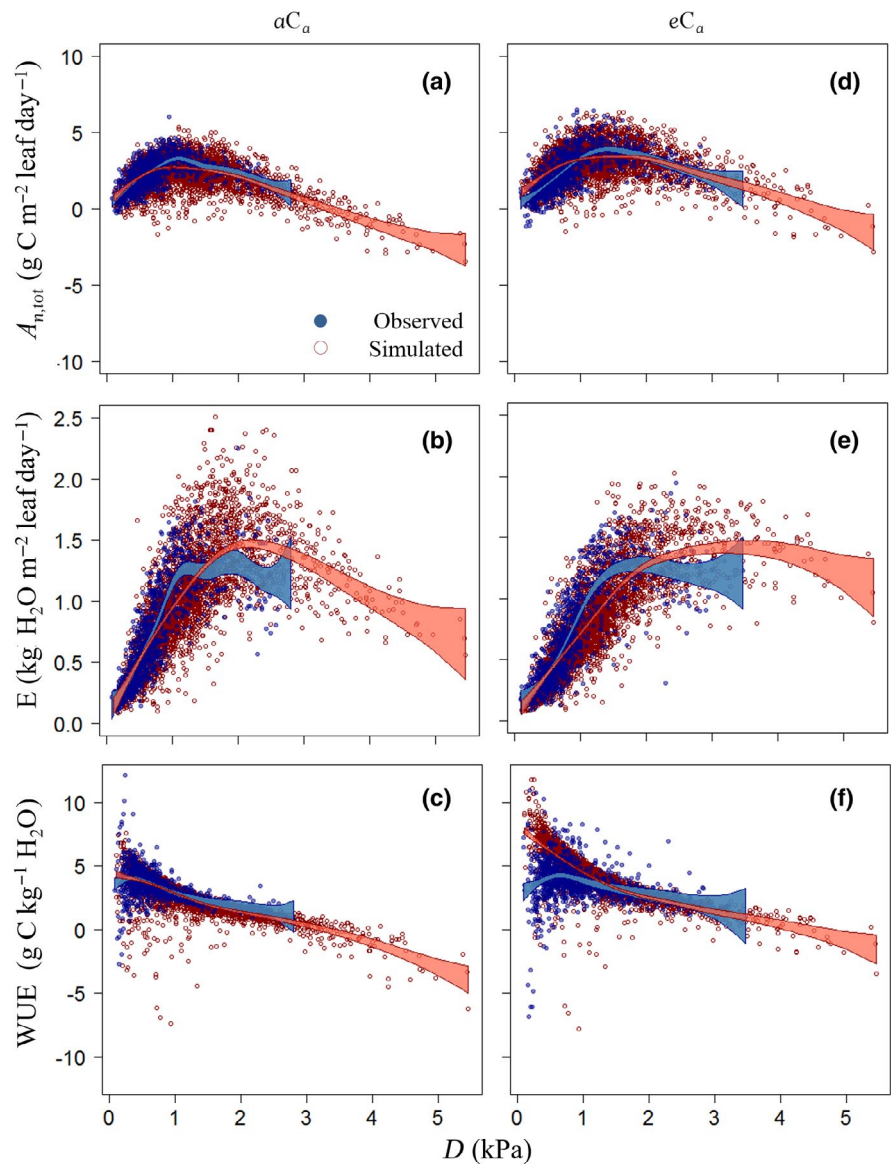
FIGURE 3 Validation of the full leaf model (FvCB+ β) against observations for *Eucalyptus saligna* in Richmond, NSW, Australia. (a) Simulated leaf-level net photosynthesis, A_n under different relative soil water contents in the upper 50 cm soil depth (S_{up}) conditions ($A_{n,sim,S}$ in $\mu\text{mol m}^{-2} \text{s}^{-1}$) is evaluated against measured A_n ($A_{n,obs}$, in $\mu\text{mol m}^{-2} \text{s}^{-1}$), for trees growing under ambient C_a (aC_a , black circles) and elevated C_a conditions (eC_a , open circles). Linear regression (black thick line) \pm 95% CI (black thin lines) are noted. (b) Changes in water source as S_{up} decreases. Modeled ratio of water uptake from below 50 cm soil depth (WU_{deep}) with respect to the total water uptake (WU_{total}), as a function of upper soil water content (S_{up}). It was calculated with the median α coefficient \pm 95% CI (black line \pm gray area) from Table 1. White circles represent measured mean \pm 95% CI ($n = 6$) fraction of $WU_{deep} WU_{total}^{-1}$ below 50 cm during two discrete sampling campaigns, extracted from Duursma et al. (2011, their Figure 7)

the limiting effect of D on E , at high D conditions (Figure 4b,e). At eC_a , the simulated E to D responses were relatively poorly represented, with a modeled peak at 3 kPa, which was 1–1.5 kPa above observed data (Figure 4e). However, for both C_a conditions, the range of E responses to D overlapped observations entirely. While the response of $A_{n,tot}$ to D peaked at $D \sim 1.1$ kPa, after an initial progressive increase, E increased steeply at first, with increasing D up to ~ 2.2 kPa, and then declined slightly. This translated into a decreasing trend of WUE as D increased, with a less steep decrease at eC_a conditions. Observed differences in E responses to increasing D were so slight that they did not result in different WUE responses to D for both eC_a and aC_a when $D > 1$ kPa

(Figure 4c,f), and simulated values were always within the range of the observations.

After running GOTILWA+ under measured climate conditions for 10 years, simulations captured the higher DBH of *E. saligna* trees growing in the irrigated treatment (Figure S6). In the first 2 years of the simulation (2008–2009) GOTILWA+ slightly overestimated DBH under both irrigated and nonirrigated treatments. Such overestimation vanished after the year 2009, when all DBH projections fell within the range of observations. At the end of a 10-year simulation run, an average daily irrigation of 3.75 mm resulted in a 3.48 cm (+14%) larger mean DBH compared to the control plot at the end of year 2017, close to the measured difference of 3.82 cm (+19%) of the irrigated trees.

FIGURE 4 Relationship of daily whole-tree net carbon uptake ($A_{n,tot}$, panel a), transpiration (E , panel b), and water-use efficiency (WUE, panel c) to increasing vapor pressure deficit (D , kPa) are shown for observations of *Eucalyptus saligna* trees growing in irrigated whole-tree chambers (blue dots) and GOTILWA+ outputs (red circles), and at $380 \mu\text{mol mol}^{-1}C_a$ (aC_a) and at $620 \mu\text{mol mol}^{-1}C_a$ (eC_a). In each panel, the colored areas represent the 95% CI interval for the response of that variable to D increases after a generalized additive model analysis with a fixed maximum of 5 df , with observed interval in blue and simulated interval in red. Note that model simulations cover a longer period than observations, and therefore the D distribution vary



3.3 | Model sensitivity to changes in deep soil water availability

Simulated daily $A_{n,tot}$ normalized to $D = 1$ kPa ($A_{n,tot,corr}$) was not different than WTC measurements when S_{up} was below 0.3 (Figure 5a). However, when deep soil water uptake (α) was reduced by 50%, $A_{n,tot,corr}$ was significantly reduced by about 40% of simulated values under ambient climate conditions. Furthermore, simulated $A_{n,tot,corr}$ including a 20% reduction in precipitation was not significantly different from the reference values. Halving α increased the number of days where S_{up} was below 0.3 during the dry season, exemplified for year 2013 (a year with average precipitation) in Figure 5b. Conversely, water savings due to decreased g_s at eC_a reduced the number of days where S_{up} was limiting A_n (Figure S7). Finally, average daily deep soil water uptake from S_{deep} decreased by 44% in the R_α scenario (average 0.6 ± 0.14 mm day⁻¹; Figure 5c) compared to the ambient conditions (1.1 ± 0.23 mm day⁻¹).

3.4 | Sensitivity of modeled canopy gas exchange to environmental drivers

The sensitivity analysis suggests that an increase in C_a of 75% from 400 to 700 $\mu\text{mol mol}^{-1}$ (leaving all other drivers unchanged) increases WUE_L by 55%, driven by a 20% increase in A_n and a 23% reduction in E (Figure 6). Scaling these values to the stand level by accounting for changes in leaf area, the overall change in WUE was very similar (+56%), but was composed of a larger increase in C uptake (33%) and a smaller reduction in E (-15%; Table 2; Figure S8).

Increasing D by 48% (equivalent to a 4°C temperature increase) reduced GPP, while enhancing transpiration, both at the leaf and stand level. As a consequence, both WUE_L and WUE diminished. The stimulating effect of increasing C_a on WUE_L was approximately halved under high D conditions (from +55% to +23%). Similarly, a precipitation reduction by 20% was estimated to lead to a 10% reduction in annual GPP and a 5% reduction in annual E , driven by a shift of water source toward more deep soil

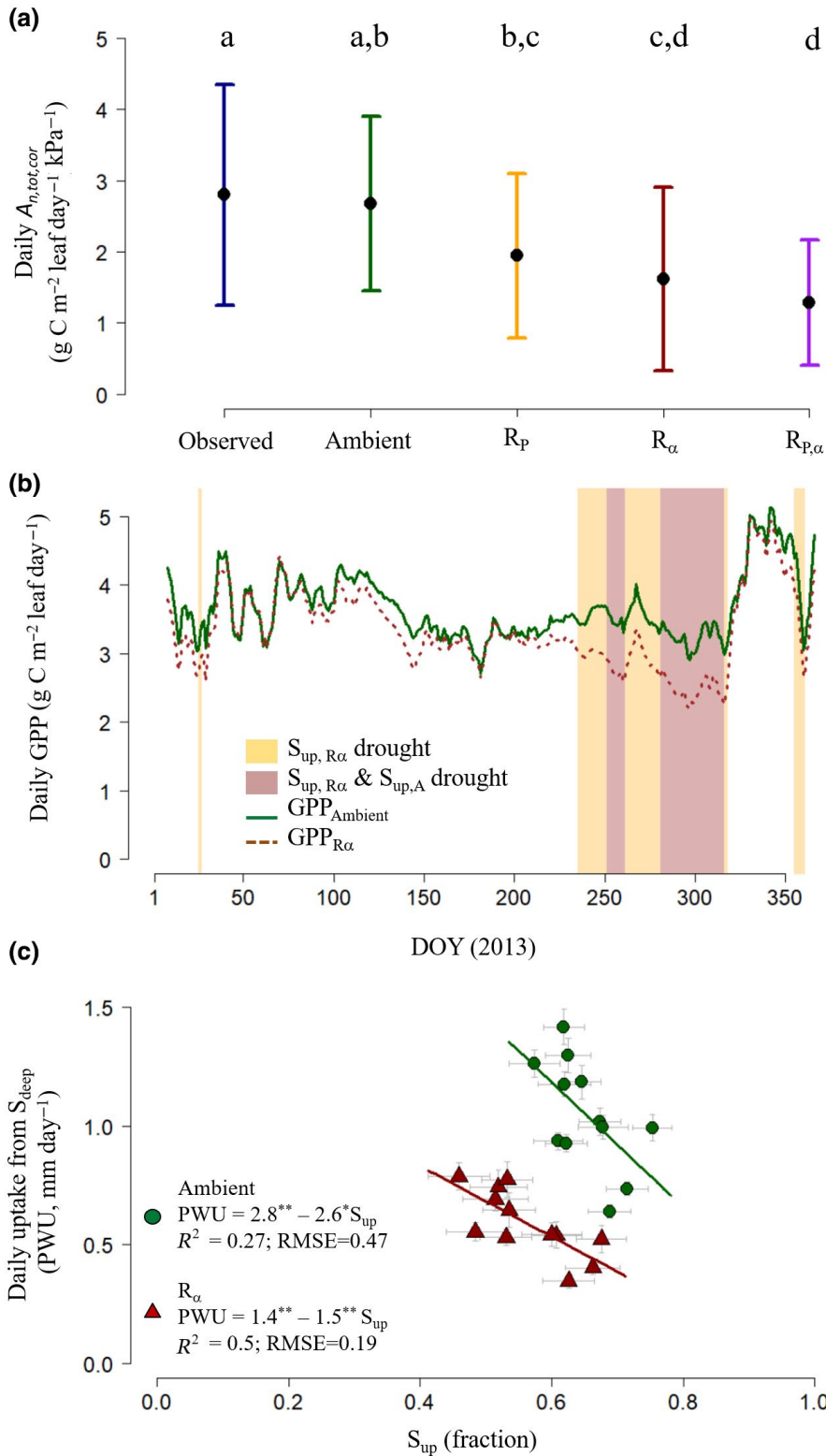


FIGURE 5 Sensitivity of GOTILWA+ model outputs to changes in deep soil water access/uptake (α) for the *Eucalyptus saligna* plantation in Richmond, New South Wales, Australia. (a) Comparison between GOTILWA+ projected whole-tree canopy net carbon uptake corrected at $D = 1$ kPa ($A_{n,tot,corr}$ $g C m^{-2} leaf day^{-1} kPa^{-1}$) under four scenarios: ambient conditions (Ambient), a 20% reduction in precipitation (R_p), a 50% reduction in α (R_α), a 20% reduction in P , and a 50% reduction in α combined ($R_{p,\alpha}$). Both simulations and observations included correspond to the days in which observed relative soil water content in the upper 50 cm of the soil (S_{up}) in whole-tree-chambers under dry-down experiment was below 0.3. Common letters indicate nonsignificant differences after pairwise Mann-Whitney tests ($p < 0.05$). (b) Comparison of 7-day moving averages of daily whole-tree canopy GPP ($g C m^{-2} leaf day^{-1}$) during the 2013 year (a year with average precipitation), for the Ambient and R_α simulations. Shaded area corresponds when $S_{up} < 0.3$, in R_α simulation (orange) and both in R_α and Ambient simulations (red). (c) Relationship between monthly averaged daily water uptake from below 50 cm soil depth (PWU, in $mm day^{-1}$) in relation to S_{up} , for Ambient (green, circles) and R_α (red, triangles) scenarios. Mean monthly values +95% CI are represented, as well as the linear regression for each simulation (* $p < 0.05$; ** $p < 0.01$)

water uptake, and a higher reliance of *E. saligna* on deep water access under more arid conditions. However, the increase in WUE_L to rising C_a was not affected by such reduction in precipitation. Under constant $400 \mu mol mol^{-1} C_a$ conditions, combined increases in D and reductions in P decreased both, A_n and WUE (-10% and -25%, respectively). Considering all three drivers together, above

$C_a = 500 \mu mol mol^{-1}$ GPP fertilization was not fully offset by aridity increases, even under the most extreme scenario ($\Delta D = +48\%$ and $\Delta P = -20\%$; Figure 6).

Canopy transpiration was strongly affected by increases in D , while decreases in precipitation only slightly affected E , due to the ability of this stand to obtain water from deep soil layers. Although

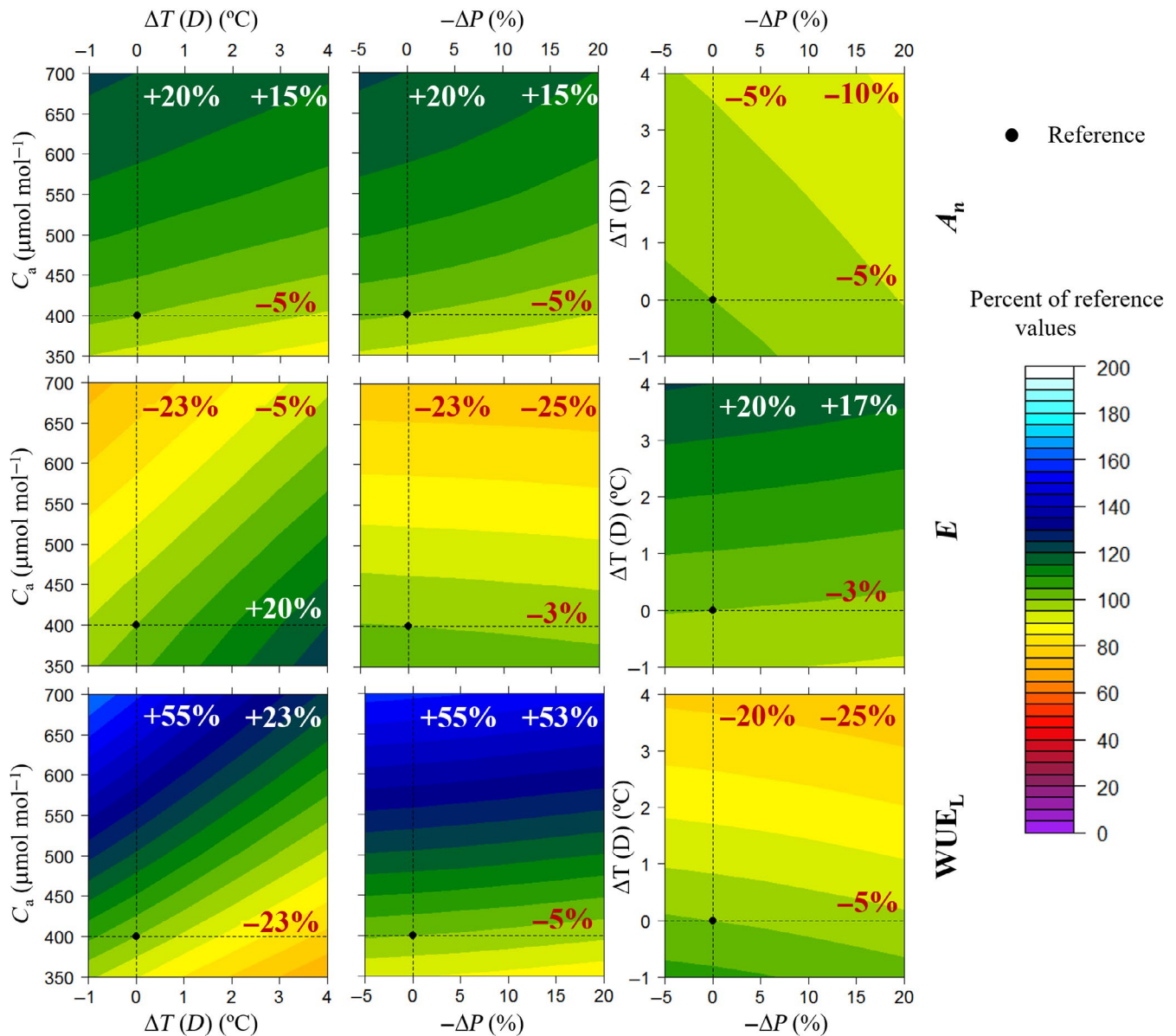


FIGURE 6 Responses of simulated canopy leaf gas exchange—that is, net assimilation (A_n), transpiration per unit of leaf area (E), and water-use efficiency at the leaf level (WUE_L , calculated as A_n/E)—in a *Eucalyptus saligna* plantation to pairwise changes in key environmental drivers with respect to reference conditions (i.e., $C_a = 400 \mu\text{mol mol}^{-1}$, $\Delta T(D) = 0^\circ\text{C}$ and $-\Delta P = 0\%$, black dots, percent = 100%). Percentages depict extreme responses in white (increase) and red (decrease) letters

eC_a alone lowered g_s by 33%, reductions in E were estimated to be about 120 mm year^{-1} (-15%; Table 2). Furthermore, increments in D offset eC_a induced water savings, resulting in similar transpiration rates as under aC_a . When considering all changes together, the annual transpiration was reduced by a mere 23 mm year^{-1} (3% of the reference values).

3.5 | Changes in aboveground biomass related to environmental drivers

Modeled changes in aboveground biomass stock (ABS) were strongly affected by changes in C_a , with a 62% increase in ABS at

$700 \mu\text{mol mol}^{-1}$ relative to aC_a . However, increases in atmospheric evaporative demand and decreases in precipitation reduced this stimulation. For instance, in eC_a , a 20% reduction in precipitation reduced ABS to a 50% increase relative to aC_a . Similarly, a 48% increase in D (equivalent to an anomaly in temperature of $+4^\circ\text{C}$) reduced C_a fertilization to a 48% increase relative to aC_a (Figure 7b; Table 2). In aC_a , $+4^\circ\text{C}$ $\Delta T(D)$ resulted in a 14% reduction in ABS, whereas a 20% reduction in P led to a 13% reduction. The interactive effects of $+4^\circ\text{C}$ $\Delta T(D)$ and -20% ΔP resulted in a reduction of ABS by 27% compared to the control conditions (Figure 7c). When all three environmental drivers were assessed in combination, ABS increased by 35%, which was approximately half of the stimulation when accounting for eC_a alone.

TABLE 2 Simulation outputs for different ecophysiological variables under the three environmental drivers considered (C_a , $\Delta T(D)$, and ΔP), after a simulation of *Eucalyptus saligna* plantation stand growth over 10 years. ABS is the aboveground biomass stock (in $Mg\ ha^{-1}$), GPP is the canopy gross primary productivity (in $Mg\ C\ ha^{-1}\ year^{-1}$), NCU_t is the total forest net carbon uptake ($NCU_t = GPP - Maintenance\ respiration - Growth\ respiration$, $Mg\ C\ ha^{-1}\ year^{-1}$), CUE is the carbon-use efficiency (GPP/ NCU_t , in $g\ C\ g^{-1}\ C$), g_s is the average daytime stomatal conductance during the year (in $mmol\ m^{-2}\ s^{-1}$), LAI is the leaf area index (in $m^2\ m^{-2}$), E is the stand transpiration (in $mm\ year^{-1}$), WUE is the canopy water-use efficiency (GPP/ E) ($g\ C\ kg^{-1}\ H_2O$). All variables but ABS are reported as mean annual values for the 6- to 10-year period. ABS is reported as the final ABS after the 10 simulation years

C_a ($\mu mol\ mol^{-1}$)	$\Delta T(D)$ ($^{\circ}C$)	ΔP (%)	ABS ($Mg\ ha^{-1}$)	GPP ($Mg\ C\ ha^{-1}\ year^{-1}$)	NCU_t ($Mg\ C\ ha^{-1}\ year^{-1}$)	CUE ($g\ C\ g^{-1}\ C$)	g_s ($mmol\ m^{-2}\ s^{-1}$)	LAI ($m^2\ m^{-2}$)	E ($mm\ year^{-1}$)	WUE ($g\ C\ kg^{-1}\ H_2O$)
400	0	0	116	31.3	17.1	0.55	145.7	2.3	789	4.0
		-20	101	28.7	15.3	0.53	133.3	2.2	753	3.8
	4	0	100	28.6	15.2	0.53	117.9	2.2	918	3.1
		-20	85	25.9	13.3	0.51	108.0	2.1	861	3.0
700	0	0	188	41.7	25.8	0.62	98.6	2.5	671	6.2
		-20	172	39.0	23.8	0.61	91.2	2.4	649	6.0
	4	0	174	39.5	24.2	0.61	81.6	2.5	806	4.9
		-20	157	36.5	22.0	0.6	75.8	2.4	766	4.8

4 | DISCUSSION

We investigated *E. saligna* responses to key environmental drivers that are expected to change in the near future. We parameterized and validated the GOTILWA+ model for an *E. saligna* plantation with field observations from two experiments at a site close to its natural distribution. We then used GOTILWA+ to simulate *E. saligna* sensitivities of key ecophysiological processes to changes in vapor pressure deficit (D), precipitation (P), and atmospheric carbon dioxide concentration (C_a), and assuming no nutrient limitation. Our results suggest that young *E. saligna* plantations will increase their C uptake and growth at rising C_a under this assumption. Thus, the CO_2 -fertilizing effect will be halved, but not offset by increasing aridity. We found that the access to the deep water-enriched soil layers will play a key role in this response, as it will ameliorate drought stress in *E. saligna*. Nevertheless, this highlights the sensitivity of *E. saligna* to the future dynamics of deep soil water reservoirs, which are highly uncertain. Furthermore, we found that a 48% increase in D will limit the eC_a fertilization effect on ABS at a similar magnitude as a 20% reduction in precipitation. This emphasizes the role that D increases will play for forest functioning under global warming, and the need to properly capture tree responses to D increments in process-based models.

4.1 | Photosynthesis responses to eC_a

The derived FvCB model parameters, V_{cmax} and J_{max} at $25^{\circ}C$, were similar to the ones reported for *E. saligna* trees growing in a nearby common garden (Heroult et al., 2013). While our $R_{d,25,ref}$ parameters differed from the ones reported by Duursma et al. (2014) likely because we assumed a fixed R_d to V_{cmax} ratio (based on Collatz et al., 1991), the $R_{d,25,ref}$ parameter estimates still fall within the range of $R_{d,20,ref}$ values reported by Crous et al. (2011), when standardized to $25^{\circ}C$. Elevated CO_2 downregulated photosynthetic activity in *E. saligna* such that with each $100\ \mu mol\ mol^{-1}$ increase in CO_2 above ambient CO_2 , there was a 4.5% and 2.5% decrease in $V_{cmax,25,ref}$ and $J_{max,25,ref}$ respectively (Table 1), which is in accordance with previous observations (e.g., Long et al., 2004; Medlyn et al., 1999). Photosynthetic downregulation may occur due to changes in leaf morphology and biochemistry, such as reductions in specific leaf area (SLA), and leaf N and P content (e.g., Ainsworth & Rogers, 2007; Ellsworth et al., 2004; Lewis et al., 2013; Wang et al., 2018). However, we found no differences in N dry weight per unit of leaf area ($g\ m^{-2}\ leaf$) between aC_a and eC_a treatments (see Notes S2 and Table S3). This is similar to observations in the nearby EucFACE experiment (Crous et al., 2019). *E. saligna* trees growing under eC_a presented significantly lower SLA, which has been reported to reduce photosynthetic potential (e.g., De la Riva et al., 2016; Flexas et al., 2008; Sperlich et al., 2015). This might partially explain the downregulation of photosynthesis under eC_a conditions. Also, in the abovementioned study by Crous et al. (2019), leaf phosphorous concentration was additionally limiting photosynthesis in trees

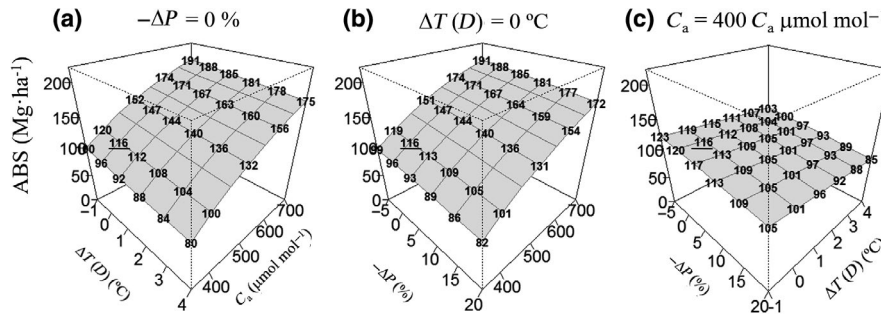


FIGURE 7 Sensitivity of simulated aboveground biomass stock (ABS, in Mg ha^{-1}) in a *Eucalyptus saligna* plantation after 10 years of simulation to pairwise environmental drivers assuming no change in precipitation (a), no change in D driven by temperature increases (b), and constant C_a (c). Underlined variables are simulated ABS under reference conditions (i.e., no increase in D , no reduction in P , and $400 \mu\text{mol mol}^{-1} C_a$)

growing at eC_a conditions. Although leaf P content was not analyzed here, we acknowledge that it might have also played a role in photosynthesis downregulation, providing the low P availability in the soil of the HFE.

4.2 | Mobilizing water from deep soil layers ameliorates drought stress

Declining soil water availability reduced A_n , as expected. However, we found that A_n declined less in response to soil dry-down than that reported previously for *E. saligna*. Thus, Lewis et al. (2013) reported 80% reductions in A_n on potted *E. saligna* seedlings after only 10 days under imposed experimental dry-down. Contrastingly, we found A_n for *E. saligna* in the WTCs to decline during a 4-month-long complete rain exclusion by only about 40% (Figure 2a). This suggests that drought responses were buffered in *E. saligna* growing in the HFE. There, *E. saligna* has been suggested to be highly reliant on deep soil water uptake (Duursma et al., 2011). Our results confirm this observation, especially during autumn, when upper soil layers become dry. The ability of fast-growing eucalypts to obtain water from deep soil layers has already been widely reported (e.g., Calder et al., 1997; Christina et al., 2017; Drake et al., 2018; Laclau et al., 2013; White et al., 2000; Zeppel et al., 2008). In the HFE, the ability to mobilize an average of 1.1 mm day^{-1} from the deep soil water-enriched layers (Figure 5c) clearly explains why a long-lasting dry-down experiment in the WTCs resulted only in moderate reductions of photosynthesis in *E. saligna*.

Beyond this particular eucalypt plantation, our findings suggest that projections from models relying on SWC observations in the upper soil layers will overestimate drought impacts on tree species with the ability to mobilize water from deep soil (e.g., Humphrey et al., 2018; Uddin et al., 2018). Therefore, including the ability of vegetation to access deep soil water reservoirs could improve dynamic global vegetation models (DGVMs) when addressing the interaction of increasing aridity and rising C_a (e.g., Berg et al., 2017; Goulden & Bales, 2019; Humphrey et al., 2018; Medlyn et al., 2016).

Thus far, stand-scale simulation models tend to better describe tree water uptake than DGVMs (e.g., Mu et al., 2021; Ukkola et al., 2016). However, this is generally done at the expense of an exhaustive soil biophysical parameterization and root vertical distribution assumptions (Vereecken et al., 2016). It is challenging for DGVMs to go beyond the stand scale because uncertainties in soil composition, in plant rooting depth and in deep soil water availability increase at larger scales (e.g., Seneviratne et al., 2010; Sitch et al., 2015). Also, unfortunately rooting depth and vertical root distribution are not routinely measured in field experiments, and actual water source partition measurements, such as the ones we used here to validate model projections, are scarcely available. Our study shows that such measurements are necessary to properly account the impacts of drought on tree productivity, and that this could potentially improve the accuracy of simulation models.

4.3 | Sensitivity of GPP and stand biomass to increasing C_a

In the absence of nutrient limitation, eC_a is projected to increase GPP and enhance biomass stock in the HFE plantation. If *E. saligna* can access water from deep soil layers, our projections suggest that an increase in aridity will only partially offset the positive eC_a effect on GPP. Our simulations showed that GPP increased by 16%–33% at $700 \mu\text{mol mol}^{-1} C_a$ depending on the degree of aridity. This increase falls within the range (10%–45% increase) reported for *E. saligna* (e.g., Barton et al., 2012; Ghannoum, Phillips, Conroy, et al., 2010; Ghannoum, Phillips, Sears, et al., 2010; but see Lewis et al., 2013). It also agrees with observations from FACE experiments in early-succession, non-nutrient limited stands, which present similar GPP increases per unit of C_a increase (e.g., Ainsworth & Rogers, 2007; Jiang et al., 2020; Norby & Zak, 2011; Nowak et al., 2004).

Sustainment of increasing forest C stock with rising atmospheric CO_2 will depend on diverse environmental and stand-specific conditions, such as succession stage and nutrient availability (e.g., Ainsworth et al., 2004; McCarthy et al., 2010; Norby et al., 2005;

Norby & Zak, 2011; Terrer et al., 2019; Walker et al., 2019). For young, fast-growing eucalypts, most studies have observed increasing biomass under eC_a . For instance, in a greenhouse experiment with *Eucalyptus radiata* saplings grown for 200 days at $640 \mu\text{mol mol}^{-1}$, biomass increased between 15% and 65% (Duan et al., 2014). Similarly, Ghannoum, Phillips, Sears, et al. (2010) found 33%–44% increases in dry mass of *E. saligna* saplings growing at $650 \mu\text{mol mol}^{-1}$. Also, Quentin et al. (2015) reported a 66% increase in biomass in *Eucalyptus globulus* trees after 15 months growing in tree chambers at HFE. Contrastingly, Ellsworth et al. (2017) reported no biomass increases for a mature stand of *E. tereticornis* at the nearby strongly P-limited EucFACE site. Therefore, our projections of a 35%–62% biomass increase at $700 \mu\text{mol mol}^{-1} \text{CO}_2$ and no nutrient limitations occur in the upper end of observed biomass increases. Other processes not accounted in GOTILWA+, such as changes in carbon allocation (Jiang et al., 2020; Riikonen et al., 2004), changes in leaf turnover rate at eC_a (e.g., Duursma et al., 2016), and physiological and structural acclimation to eC_a (e.g., Sperry et al., 2019), are likely to further limit biomass production stimulation at eC_a .

4.4 | Sensitivity of gas exchange and stand biomass to $C_a \times$ aridity

As D rises, trees reduce stomatal conductance (Creek et al., 2020; Martínez-Vilalta et al., 2014). This limits CO_2 substrate for photosynthesis, and therefore limits primary productivity. Our results suggest that in the HFE stand, this may limit forest productivity to a similar degree as projected reductions in precipitation, which supports previous observations in subhumid regions (e.g., Grossiord et al., 2020; Novick et al., 2016; Sanginés de Cárcer et al., 2018). This further may indicate an overall influence of D on reported variations in GPP responses to eC_a from different FACE experiments (e.g., Medlyn et al., 2015; Walker et al., 2019). Furthermore, properly capturing D limitations on productivity is still challenging in simulation models (e.g., Grossiord et al., 2020; 2021). Hence, responses to rising D are still a major source of uncertainty in forest C uptake projections under global warming. Even more, D itself is affected by transpiration, as vegetation is a major driver of atmospheric humidity over land (e.g., Berg & Sheffield, 2018; Berg et al., 2017; Lemordant et al., 2018). Therefore, changes in forest transpiration due to eC_a and reduced water availability could potentially increase D , hence amplifying drought limitations over forest productivity.

As expected, plants reduced stomatal conductance as C_a increased. This resulted in lower transpiration rates if precipitation and evaporative demands remained unchanged. At $C_a = 700 \mu\text{mol mol}^{-1} g_s$ declined (–32%). However, transpiration was reduced by a mere 15%. The slight increase in leaf area (9%) under eC_a does not account for such differences. Instead, lower g_s led to non-limiting SWC for a longer period, thus reducing the number of days in which *E. saligna* experienced severe drought stress, without severely reducing overall annual stand transpiration. This phenomenon was already observed

by Fatichi et al. (2016) in water-limited ecosystems. It is also in accordance with previous reports, which did not report changes in evapotranspiration fluxes in surrounding eucalypt woodlands growing at eC_a (Gimeno et al., 2016, 2018).

Elevated C_a was found to be the dominant driver of changes in GPP and biomass, while the combined effects of reduced precipitation and increased D halved eC_a fertilization. Intense drought stress has been reported to potentially offset the positive effects of eC_a (e.g., Andresen et al., 2016; Barbata & Penuelas, 2017; Birami et al., 2020; Peters et al., 2018). The positive responses projected in the HFE to combined eC_a and increasing aridity are related to the ability of the eucalypts to access deep soil water reservoirs. Accounting both for productivity gains and water savings, a simulated 55% increase in WUE_L at $C_a = 700 \mu\text{mol mol}^{-1}$ is consistent with previous reports about WUE_L increases with rising CO_2 (e.g., Battipaglia et al., 2013; Eamus, 1991; Keenan et al., 2013; Mastrotheodoros et al., 2017). Interestingly, rising D has been reported to enhance intrinsic WUE (e.g., Ficklin & Novick, 2017; Zhang et al., 2019), but to reduce both WUE_L and WUE (e.g., Grossiord et al., 2020; Jarvis & McNaughton, 1986). Increases in WUE_L in the *E. saligna* saplings growing under eC_a conditions in the HFE have been thoroughly discussed in Barton et al. (2012). WUE_L and WUE are driven by physiological adjustments such as changes in canopy conductance, but also by biophysical drivers such as increases in transpiration per unit of stomatal conductance at increasing D . This is especially true for WUE, as both the residual transpiration due to stomatal leakiness and leaf carbon losses due to reduced photosynthesis under limiting environmental conditions scale with stand leaf area. Accordingly, our results suggest that an increase in D by 48% would reduce the stimulating effect of eC_a on whole-tree WUE to 20%, less than half when considering eC_a alone.

5 | CONCLUSION

A simulation model was used to analyze the potential sensitivity of a *E. saligna* plantation to changes in C_a , D , precipitation, and access to deep soil water reserves. Best-case scenario (i.e., no nutrient limitation) model projections suggest that eC_a will drive *E. saligna* responses to climate change, resulting in an increase in stand GPP and growth. Our results also confirm the importance of accounting together, both, soil and atmospheric aridity increases when projecting climate change impacts on plantations and forests. Thus, a 48% increase in D will limit CO_2 fertilization in a similar magnitude as a 20% reduction in precipitation, under our assumptions. Those two drivers combined are projected to halve the eC_a fertilization effect on GPP, and also reduce WUE gains at the stand scale. The ability of *E. saligna* to access deep soil water reservoirs is projected to mitigate stress from increasing aridity, potentially allowing it to take advantage of eC_a conditions. Nevertheless, we expect *E. saligna* to be increasingly reliant on such deep soil water in the future, linking its persistence to the still uncertain deep soil water reservoir dynamics.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Daniel Nadal-Sala wrote the initial version of the manuscript, designed the research, performed the simulations, and analyzed the data. Belinda E. Medlyn assisted with manuscript writing, research design, and supervised data analysis. Nadine K. Ruehr assisted with manuscript writing and scientific discussion. Craig V. M. Barton, David S. Ellsworth, David T. Tissue, and Mark G. Tjoelker designed the field experiment, collaborated with the manuscript content, collected field data, and helped to design the research. Carles Gracia and Santi Sabaté contributed to research design, and supervised the manuscript content and GOTILWA+ model implementation. All authors contributed to manuscript editing and writing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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