1   **Growth enhancements of elevated atmospheric [CO₂] are reduced under drought-like**

2   **conditions in temperate eucalypts**

3

4   **Authors:** Bendall, E. R.[1*], Bedward, M.[1], Boer, M.[2], Clarke, H.[1,2], Collins, L.[3,4,5], Leigh, A.[6],

5   Bradstock, R. A.[1]

6

7   [1]University of Wollongong, Centre for Environmental Risk Management of Bushfires,

8   Northfields Avenue, Wollongong, New South Wales, Australia 2522

9   [2]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, New

10   South Wales

11   [3]La Trobe University, Department of Ecology, Environment & Evolution, Bundoora, Victoria,

12   3086

13   [4]Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water

14   and Planning, Heidelberg, Victoria, 3084

15   [5]Current address: Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada,

16   506 Burnside Road West, Victoria BC V8Z 1M5, Canada

17   [6]University of Technology Sydney, School of Life Sciences, Broadway, New South Wales

18

19   ***Corresponding author:** Eli R. Bendall, email: eli.r.bendall@gmail.com, phone: +61 431 683

20   944, address: 18 Morven Road, Leura, NSW, Australia, 2780

21

37 **Author contributions:**

38 *Design of the research:* E. Bendall (22.5%); R. Bradstock (22.5%); A. Leigh (22.5%); L.

39 Collins (22.5%) M. Boer (10%)

40 *Performance of the research:* E. Bendall (90%); R. Bradstock (2.5%); A. Leigh (2.5%); L.

41 Collins (2.5%); M. Boer (2.5%)

42 *Data analysis:* E. Bendall (35%); R. Bradstock (20%); L. Collins (10%); M. Bedward (35%)

43 *Interpretation:* E. Bendall (25%); R. Bradstock (25%); A. Leigh (10%); L. Collins (10%) M.

44 Boer (5%); M. Bedward (20%); H. Clarke (5%)

45 *Writing the manuscript:* E. Bendall (50%); R. Bradstock (15%); A. Leigh (10%); L. Collins

46 (15%); M. Boer (2.5%); M. Bedward (5%); H. Clarke (2.5%)

47

48 All authors contributed critically to the draft manuscript and gave final approval for publication

49

50 **Author emails:**

51 Eli Bendall: eli.r.bendall@gmail.com

52 Ross Bradstock: rossb@uow.edu.au

53 Luke Collins: l.collins3@latrobe.edu.au

54 Andrea Leigh: Andrea.Leigh@uts.edu.au

55 Matthias Boer: M.Boer@westernsydney.edu.au

56 Michael Bedward: mbedward@uow.edu.au

57 Hamish Clarke: hamishc@uow.edu.au

58

59 All data and code used to produce the results in the manuscript are available in the GitHub

60 repository: https://github.com/erb418/EB.Ch4.scripts

61

1 **Abstract**

2 • Elevated atmospheric $[CO_2]$ ('eCO_2') may alter species composition within

3   vegetation types by favouring growth of some species over others.

4   However, other related changes in climate conditions, such as increased

5   frequency and severity of drought, may reduce eCO_2 fertilisation effects

6   on plant growth. For many species it is not known if responses will reflect

7   variability in trait adaptations due to environment.

8 • We grew seedlings of nine species of eucalypts indicative of three regional

9   vegetation types (representing a mesic–xeric ecosystem gradient) under

10   two CO_2 concentrations (400 parts per million; 640 ppm, i.e. eCO_2) and

11   two watering regimes (well-watered; drought-like conditions).

12 • Elevated CO_2 increased biomass accumulation but drought reduced this

13   effect, with mesic species experiencing larger relative reductions. Elevated

14   CO_2 increased the size of storage organs used during resprouting, in the

15   absence of drought. Typical drought responses, such as increased leaf

16   mass per unit area and root mass ratio, were more pronounced in xeric

17   species and were reduced under eCO_2.

18 • Seedling growth and resprouting may be enhanced by eCO_2, suggesting

19   continued dominance of resprouting species in disturbance-prone

20   ecosystems, although severe drought is likely to offset eCO_2 fertilisation.

21   Xeric species may cope with drought more effectively under eCO_2 than

22   mesic species due to resource acquisition and storage traits that are more

23   responsive.

24

25 **Keywords:** climate change, biomass, temperate forest, drought, elevated CO_2,

26 eucalypt, tree seedling, vegetation type

27

28 **Introduction**

29 Atmospheric $[CO_2]$ is now higher than at any time during at least the last 800,000

30 years and anthropogenic activities are the main cause of increasing $[CO_2]$ and

31 associated climate change (IPCC 2021). Future increases in climatic extremes

32 such as drought are projected to have substantial consequences for forested

33 ecosystems (Liu *et al.* 2019). Elevated CO_2 is hypothesised to lead, directly, to

changes in ecosystem structure and function by favouring some plant taxa over others (Bond 2000; Macinnis-Ng *et al.* 2011; Buitenwerf *et al.* 2012). However, there is still uncertainty around the interactive effects of eCO_2 and changes in climate, e.g. antagonistic effects may limit eCO_2 effects on plants (Duursma *et al.* 2011; Franks *et al.* 2013; Duan *et al.* 2014; Zeppel *et al.* 2015; Walker *et al.* 2021). While there has been substantial work regarding $[CO_2]$ effects or drought and temperature effects on contrasting species (Drake *et al.* 2017; Resco de Dios *et al.* 2018; Blackman *et al.* 2019), most work investigating CO_2–climate interactions has focused on just one or a few species, usually those of commercial interest (e.g. Duursma *et al.* 2011; Lewis *et al.* 2013; Duan *et al.* 2018a; Duan *et al.* 2019). Hence, there is a need for experiments to address the effects of eCO_2–climate interactions among contrasting vegetation communities found in natural landscapes, so that predictions can be made about vegetation responses to global change (Ghannoum *et al.* 2010; Franks *et al.* 2013).

Elevated CO_2 has been identified as a key driver of landscape greening and increased woody biomass across a range of ecosystems globally over the past few decades (Andela *et al.* 2013; Donohue *et al.* 2013; Zhu *et al.* 2016). Elevated CO_2 may increase the growth of woody plants via the direct enhancement of photosynthesis in C_3 species (i.e. CO_2 fertilisation; Roden & Ball 1996; Atwell *et al.* 2007; Eamus & Palmer 2007) or indirectly by increasing plant water use efficiency (Polley *et al.* 1997). Many studies investigating the effects of eCO_2 show strong positive responses such as significant increases in growth rate (Hovenden & Williams 2010) and biomass (e.g. 41–108%, Roden & Ball 1996; Poorter & Nagel 2000; Atwell *et al.* 2007, Walker *et al.* 2021). Enhanced growth of seedlings and saplings under eCO_2 may lead to faster establishment and increase the chances of plants reaching maturity, thereby facilitating population growth (Bond 2000). Increased allocation of non-structural carbohydrates (NSC) is a key physiological response to eCO_2 (Du *et al.* 2020). Non-structural carbohydrates are utilised by plants to grow new foliage following disturbance such as drought or fire (Hoffmann 2000). Elevated CO_2 may accelerate investment in NSC storage organs such as lignotubers (woody mass at the base of the stem containing growth buds) and coarse roots (structural roots >2 mm diameter, Zhang & Wang 2015), increasing the capacity of young plants to draw on reserves

2

67 depleted after disturbance-related damage (Hoffman *et al.* 2000; Bond & Midgley

68 2012).

69   Increases in drought and fire have been linked with elevated plant

70 mortality and demographic shifts in forests around the globe (Allen *et al.* 2010;

71 Brando *et al.* 2014; Cobb *et al.* 2017; Fairman, Bennett & Nitschke 2019). It is

72 predicted that climate change and associated changes to disturbance regimes may

73 lead to the conversion of forest to non-forest biomes (Bowman *et al.* 2013).

74 Forests typically considered resilient to change, such as resprouter-type eucalypt

75 forests, may be vulnerable to severe drought, e.g. through loss of canopy cover

76 and increased mortality (Matusick *et al.* 2013). Plants have a range of

77 physiological mechanisms and traits that enable them to cope with drought, with

78 species from more xeric environments likely to have more highly developed

79 drought adaptations than species from more mesic environments (Merchant *et al.*

80 2006; Merchant *et al.* 2007). Adaptation to xeric environments include increased

81 root to shoot mass ratio (RMR) to maximise water uptake while decreasing water

82 loss (Brunner *et al.* 2015) and increased leaf mass per unit area (LMA) to

83 conserve resources and reduce wilting (Poorter *et al.* 2009). Low-LMA species

84 are generally associated with faster growth and resource acquisition (e.g. higher

85 productivity, mesic environments), while high-LMA species are generally

86 associated with more conservative growth and persistence (e.g. lower

87 productivity, xeric environments; Poorter *et al.* 2009). Elevated CO_2 may alleviate

88 drought stress by allowing sufficient gas exchange to continue during drought via

89 reduced stomatal conductance and increased water use efficiency (Atwell *et al.*

90 2007; Lewis *et al.* 2013). Whereas eCO_2 may increase leaf water potential in

91 some species (Atwell *et al.* 2007), water limitation can also increase LMA (Roden

92 & Ball 1996), assisting survival during drought through limiting transpirational

93 water loss. The response of different vegetation types to the fertilisation effect of

94 eCO_2 in conjunction with detrimental effects of drought remains uncertain, with

95 variable results evident across a range of biomes (Duan *et al.* 2014; Souza *et al.*

96 2019).

97   In Australia, eucalypts (the sub-genera *Corymbia*, *Angophora* and

98 *Eucalyptus*) dominate most fire-prone forest and woodland communities (Nicolle

99 2006). Eucalypts inhabit a diverse range of climates (e.g. semi-arid, moist, alpine,

100 Keith 2004), have diverse physiological responses to eCO_2 and drought (Merchant

101   *et al.* 2006; Merchant *et al.* 2007), well-developed storage organs used for post-

102   disturbance resprouting (Burrows 2013) and are highly resilient to major

103   structural changes under extreme disturbance regimes (Collins 2020). Most

104   eucalypts are 'resprouters', able to produce new foliage from the canopy or main

105   stem via epicormic buds beneath the bark and/or from the base of the stem via

106   below-ground lignotuber buds (Nicolle 2006; Burrows 2013). Plants such as

107   eucalypts typically inhabit fire-prone environment and seedlings must capture and

108   store resources in order to survive drought and fire (Lawes & Clarke 2011;

109   Burrows 2013; Pausas *et al.* 2018), as juvenile stems are vulnerable to mortality

110   until other resistance traits such as tall canopies and thick bark are developed later

111   in life (Prior, Murphy & Russell-Smith 2009; Clarke *et al.* 2013; Nolan *et al.*

112   2020).

113   Eucalypts from xeric communities more effectively maintain osmotic

114   balance (Merchant *et al.* 2006) and higher stomatal conductance under water-

115   stress than mesic eucalypts (Ngugi *et al.* 2004). Thus, such species may be able to

116   more effectively take advantage of eCO_2 under drought conditions by maintaining

117   higher relative growth rates. Elevated CO_2 may facilitate greater allocation of

118   non-structural carbohydrates to storage organs such as lignotubers and roots,

119   which can be utilised to grow new foliage following disturbance (Hoffman *et al.*

120   2000). Plants with larger lignotubers are more likely to successfully resprout

121   (Walters, Bell & Read 2005; Wigley, Cramer & Bond 2009; Borzak, Potts &

122   O'Reilly-Wapstra 2016). Thus, understanding changes in biomass, resource

123   acquisition and storage traits to eCO_2 among species from a range of

124   environments and the degree to which these responses are modified by drought-

125   like conditions, is important to gain insights into potential future changes across a

126   range of eucalypt-dominated plant communities.

127   This study investigated the responses of seedlings of nine common

128   *Eucalyptus* species when grown under two levels of [CO_2] (elevated versus

129   ambient) in combination with two levels of moisture availability (well-watered

130   versus drought-like conditions). To gain insight into community-level responses

131   to future climate change, we compared indicative species of several widespread,

132   contrasting southeastern Australian vegetation types: wet sclerophyll forest

133   (WSF), a mesic type; dry sclerophyll forest (DSF), a moderately xeric type; and

134   grassy woodland (GW), a strongly xeric type. Generally, we expected that eCO_2

4

135   would enhance growth of biomass including storage organs (e.g. Hovenden &

136   Williams 2010; Walker *et al.* 2021), that drought would increase LMA and RMR

137   (e.g. Poorter & Nagel 2000; Poorter *et al.* 2009; Brunner *et al.* 2015). We also

138   expected that drought would result in potential reductions in the CO_2 fertilisation

139   effect (e.g. see Duan *et al.* 2013; Duan *et al.* 2018b) and that such reductions may

140   differ between vegetation types, due to inherent variability in drought adaptation

141   (e.g. see Merchant *et al.* 2007; Cernusak *et al.* 2011; Lewis *et al.* 2011).

142   Specifically, we asked whether eCO_2 has a fertilisation effect on the biomass

143   components indicative of successful growth and establishment (e.g. above-

144   ground, below-ground), resource acquisition traits indicative of adaptation to

145   environmental conditions (e.g. LMA, RMR). We also asked whether eCO_2 has a

146   fertilisation effect on the storage capacity of resprouting organs indicative of

147   resilience to disturbance (e.g. lignotuber size), and whether any such fertilisation

148   effect is modified by drought-like conditions at the community-level.

149

150   **Materials and Methods**

151   *Study Area*

152   The vegetation types examined in this study dominate the southeastern portion of

153   New South Wales, Australia (approximate centre = 36°3'10" S; 149°39'4" E). The

154   topography is heterogeneous and consists of coastal plains, undulating hinterland,

155   coastal escarpments and tablelands west of the escarpment. Elevation ranges from

156   sea level to over 1200 m in the mountains and tablelands. Soils are mainly of low

157   to moderate fertility, derived from a range of parent material including sandstone,

158   granite, metasediments and basalt (DPI 2017). Temperature and rainfall vary across

159   the region as function of both altitude and distance from coast. The mean minimum

160   temperature of the coolest month ranges from -3 to 7°C in DSF, -3 to 6°C in WSF

161   and -3 to 1°C in GW. The mean maximum temperature of the warmest month

162   ranges from 21–31°C in DSF, 21–26°C in WSF and 21–28°C in GW. Mean annual

163   precipitation is lower in areas dominated by DSF (886 mm) and GW (892 mm) than

164   in areas dominated by WSF (989 mm, all values derived from BioClim 2022). Dry

165   Sclerophyll Forest tends to dominate drier, nutrient-limited areas where water

166   drains away, whilst WSF tends to dominate moist microclimates (e.g. gullies) and

167   areas of higher rainfall. Grassy Woodland tends to dominate where soil nutrients

168 are higher in coastal rainshadow valleys and on cooler, drier tablelands west of the

169 coastal escarpment (Keith 2004). Fire regimes in DSF and WSF communities

170 consists of a combination of mixed severity wildfires and low to moderate severity

171 prescribed burns, whilst in GW fires tend to be low to moderate severity grass or

172 litter fires (NPWS 2004; Bradstock *et al.* 2010; Murphy *et al.* 2013; Collins *et al.*

173 2021). Typical fire intervals range between 5–20 years in DSF and 20–100 years in

174 WSF and GW (Murphy *et al.* 2013). The data and R scripts used to generate the

175 climatic envelope of the study region and vegetation types are provided online in a

176 data repository (https://github.com/erb418/EB.Ch4.scripts).

177

178 *Experimental design*

179 Indicative species of the three widespread southeastern Australian forest types

180 (Keith 2004) were chosen for the experiment, with *Eucalyptus viminalis* Labill.,

181 *Eucalyptus fastigata* H.Deane & Maiden and *Corymbia maculata* K.D.Hill &

182 L.A.S.Johnson representing WSF; *Eucalyptus sieberi* F.Muell, *Eucalyptus*

183 *pilularis* Sm. and *Corymbia gummifera* K.D.Hill & L.A.S.Johnson representing

184 DSF; and *Eucalyptus melliodora* A.Cunn ex Schauer, *Eucalyptus blakelyi* Maiden

185 and *Eucalyptus bridgesiana* R.T.Baker representing GW. Each species chosen

186 was common and widespread within their respective vegetation types and capable

187 of epicormic resprouting (see Brooker & Kleinig 1999; Boland et al. 2006).

188 Seedlings were raised as standard tube stock by Greening Australia (Western

189 Sydney University, Hawkesbury Campus) from wild-collected seed acquired from

190 the coast, ranges and tablelands of southeastern Australia. Seedlings were initially

191 grown in low-light conditions (poly tunnel/shade house) under ambient [CO_2]

192 (aCO_2, i.e. 400 ppm) and well-watered conditions for three months commencing

193 18 July 2017. Following this establishment period, seedlings were transplanted

194 into PVC pots (diameter of 150 mm, height of 400 mm), each of which contained

195 10 kg of free-draining alluvial topsoil, with drainage holes to allow water free

196 passage through the pots and plastic mesh to prevent soil loss through drainage

197 holes.

198   The experiment was conducted over 18 weeks (28 October 2016 to 9

199 March 2017) during the regional growing-season at Western Sydney University,

200 Richmond NSW (33°36'40" S; 150°44'26.5"E). Twelve seedlings from each

species were assigned to each of four adjacent sun-lit, climate-controlled

glasshouse chambers (width 3.0 m × length 5.0 m × height 3.5 m each). Daily air

temperature in the chambers was customised to suit the 30-year growing season

average of the study region, changing four times over a 24 hour period to simulate

a daily cycle, and ranging from a minimum of 15°C to a maximum of 25°C

(Aspinwall *et al.* 2019). Two chambers were set at aCO_2 level (400 ppm), while

two chambers were set at eCO_2 level (640 ppm), the latter representing a projected

moderate 2100 climate change scenario, i.e. between Representative

Concentration Pathways 4.5 and 6 (IPCC 2021). Seedlings were given a single

dose of slow-release native fertiliser (Osmocote ®) when initially transplanted to

the pots and watered to field capacity every two to three days to provide two

months of optimal growth conditions prior to imposing drought-like conditions.

The CO_2 treatments began immediately after seedlings were transplanted into the

pots and placed in the glasshouse. Throughout the experiment, plants were rotated

between and within chambers fortnightly to minimise chamber-related effects on

plant growth. $[CO_2]$ was changed with each rotation so that plants remained in the

designated treatment as they moved to a new chamber.

Drought treatment

At 75 days after planting, water limitation was imposed on half of the plants

within each species (n = 24), by reducing water supply by half to simulate

drought-like conditions. Four pots were randomly selected for each species (n =

48 in total) and weighed in the morning (between 08:00–10:00) every 2–4 days to

measure water loss between glasshouse visits. In the well-watered treatment

plants were re-watered to field capacity regardless of species or vegetation type,

while in the water-limited treatment plants received an amount of water equal to

50% of total weight lost between each measurement, thereby incrementally

reducing available water until the onset of wilting. After the first instance of

wilting, water-limited plants were maintained slightly above the threshold of

wilting for the duration of the experiment. Plants in the well-watered treatment

were re-watered to field capacity every 3–4 days. Measurements of pre-dawn leaf

water potential (Ψ_{pd}) were carried out twice a week over four weeks to determine

plant water status and ensure that plants in the water-limited treatment were

234   water-stressed. Water-use efficiency can be variable among eucalypts in a

235   glasshouse setting, particularly where both mesic and xeric species are used

236   (Lewis *et al.* 2013; Kelly *et al.* 2016; Zhou, Medlyn & Prentice 2016). Hence,

237   three individuals of each species in each treatment group within each glasshouse

238   chamber were selected for Ψ_{pd} measurements, with different individuals used on

239   each occasion to minimise the effects of leaf excision on plant health. Ψ_{pd} was

240   measured using a pressure-chamber (Scholander-type, PMS Instruments,

241   Corvallis, Oregon). See Supporting Information Fig. **S1** for Ψ_{pd} monitoring data.

242

243   *Harvest*

244   Plant height was measured with a long ruler from the soil surface to the leading

245   edge of the uppermost canopy leaf. The longest axis of the canopy was measured

246   along with the perpendicular axis, which was then calculated as an ellipse as a

247   proxy for projected crown area. Watering stopped for all plants (dry-down) 10

248   days prior to harvest (Chick 2016). At 133 days after planting, all plants were

249   clipped at 50 mm above the soil surface and shoot biomass was weighed, bagged

250   and placed in an oven to dry for a minimum of 72 hours at 70°C, before dry

251   weight was recorded. Leaf area was measured using a LI-COR leaf area meter

252   (LI-3100C, Lincoln, Nebraska). Finally, all soil was removed by tipping pots

253   upside down and using pressurised water to loosen the soil. Large 3 mm sieves

254   were used to collect root material. Once bulk soil was removed, plant material

255   was gently washed to remove residual soil before fresh biomass was recorded.

256   Lignotuber presence was recorded and roots separated from lignotubers. Roots

257   and lignotubers were weighed and lignotuber dimensions recorded before all plant

258   material was bagged and placed in an oven to dry for a minimum of 72 hours at

259   70°C, before dry weight was recorded.

260

261   *Data analysis*

262   We compared plant responses under each of the 12 treatment combinations (3

263   vegetation types X 2 levels of CO_2 X 2 watering regimes) by fitting a Bayesian

264   cell means model for each measured attribute. This is equivalent to fitting a

265   conventional 3-way analysis of variance, in that the same main effects and

266 interactions are being modelled. However, it has the advantage that estimates of
267 the difference in response between treatment combinations can be quantified by
268 directly querying the fitted model without the need to perform additional post-hoc
269 procedures. The Bayesian approach also naturally allows for minor differences in
270 replication between treatment combinations as this is reflected in the bounds of
271 the model estimates.

272   Community-level responses (i.e. DSF, WSF, GW) were of primary
273 interest, thus data for each species was pooled within each vegetation type for
274 analyses. However, additional modelling of species-specific responses suggested
275 that the majority of species within each vegetation type responded similarly (see
276 Fig. **1,2,3** for species modelling). The measured attributes consisted of three
277 biomass components (total; above-ground; below-ground), four resource
278 acquisition traits (plant height; crown area; leaf mass per unit area; root to shoot
279 mass ratio); and two biomass components associated with storage (lignotuber
280 biomass; coarse root biomass, i.e. structural roots >2 mm diameter). Cell means
281 models were fitted using Markov Chain Monte Carlo (MCMC) as implemented in
282 the 'rjags' package for R version 3.5.0 (Plummer *et al.* 2019; R Core Team 2020).
283 Each model considered 12 cells, representing all combinations CO_2 level,
284 watering treatment and vegetation type. All measured attributes other than RMR
285 were modelled as Gamma-distributed variables, with cell means based on vague
286 Normal prior distributions. The right-tailed nature of the Gamma distribution
287 sometimes resulted in the mean lying some distance from the mode, toward the
288 tail of the distribution. Variances were allowed to vary between cells and were
289 based on a uniform distribution. The RMR measure was modelled as Beta-
290 distributed (see Niekerk *et al.* 2019) using a parameterisation based on cell mean
291 and dispersion, with means drawn from a t-distribution to help account for outlier
292 values within some cells. For each model, we sampled three Markov chains, each
293 consisting of 10,000 model iterations. We assessed model convergence using the
294 Gelman-Rubin diagnostic (Gelman & Rubin 1992) and checked for acceptable
295 levels of serial autocorrelation. Separate Markov chains for each model were then
296 combined into a matrix of samples from the joint posterior distribution of model
297 parameters, which we subsequently used to derive predictions for the value of
298 each measured attribute within each treatment (Kruschke 2015; Suzuki 2019).

299   For each vegetation type, we quantified the extent to which drought-like

300   conditions modified the effects of eCO_2 on each measured attribute using a two-

301   step difference calculation: (i) the posterior sample of values for the attribute in

302   the aCO_2 treatment were subtracted from those in the eCO_2 treatment, generating

303   a distribution of CO_2 fertilisation magnitudes (performed separately for the values

304   corresponding to well-watered and drought-like conditions); (ii) the set of

305   magnitudes for well-watered conditions was subtracted from the set for drought-

306   like conditions, resulting in a distribution of drought-reduction values. Credible

307   intervals were calculated as highest posterior density intervals (HPDI), in order to

308   display the central 50% of model predictions and lower/upper 95% bounds of

309   model predictions. The data and R scripts used to generate the results are provided

310   online in a data repository (https://github.com/erb418/EB.Ch4.scripts) and

311   secondary results summaries can be found in Supporting Information **Table S1–**

312   **S10**.

313
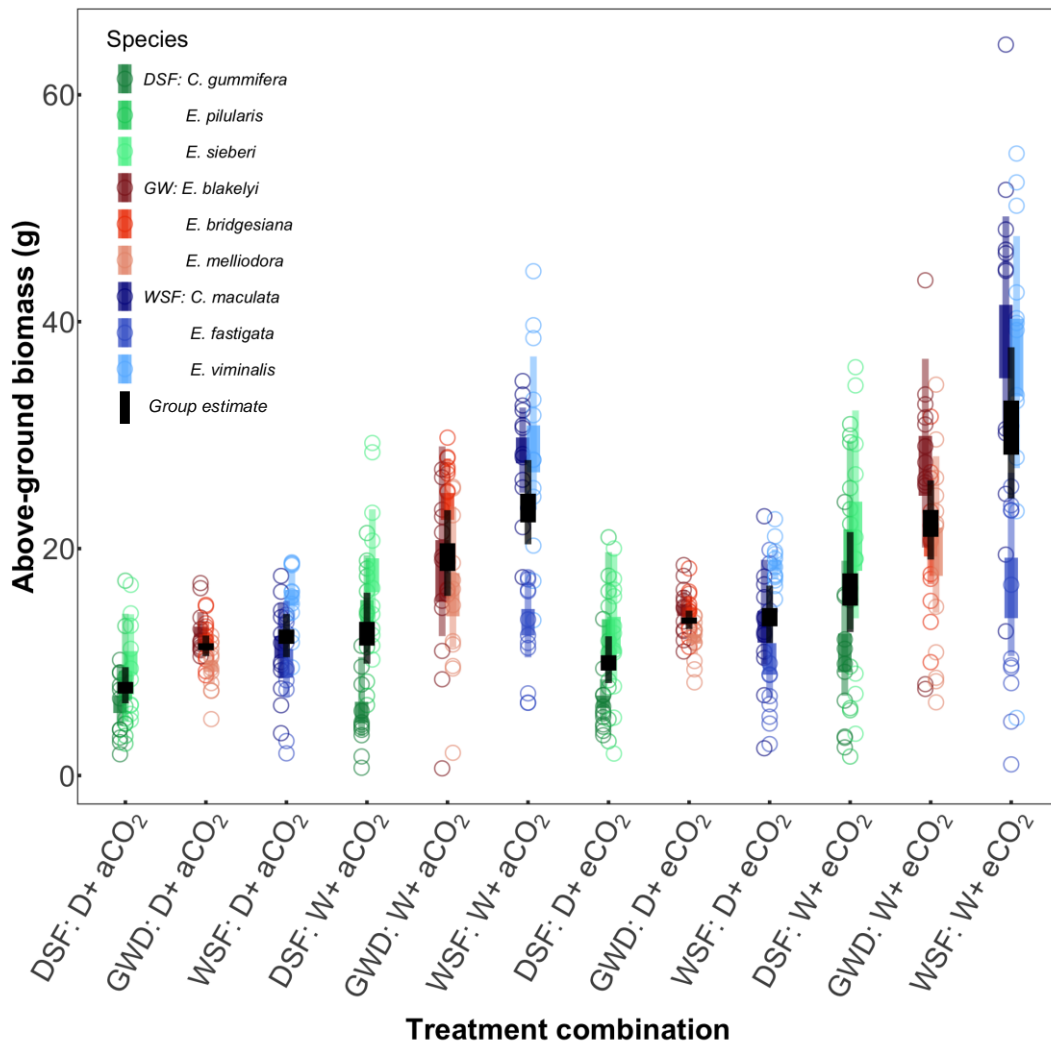
314   **Results**

315   *Biomass: species-level*

316   We analysed species-specific responses to eCO_2 and drought-like conditions to

317   investigate how variability at the community-level was influenced by species, in

318   order to confirm the appropriateness of our experimental design (Fig. **1,2,3**). The

319   modelling approach was similar to that described in the *Data Analysis* section but

320   with adjusted model parameters to account for species-level responses. The

321   majority of species responded similar within each vegetation type, with the

322   exception of one species in both DSF (*C. gummifera*) and WSF (*E. fastigata*), which

323   did not respond as strongly as the other species within their respective vegetation

324   types.
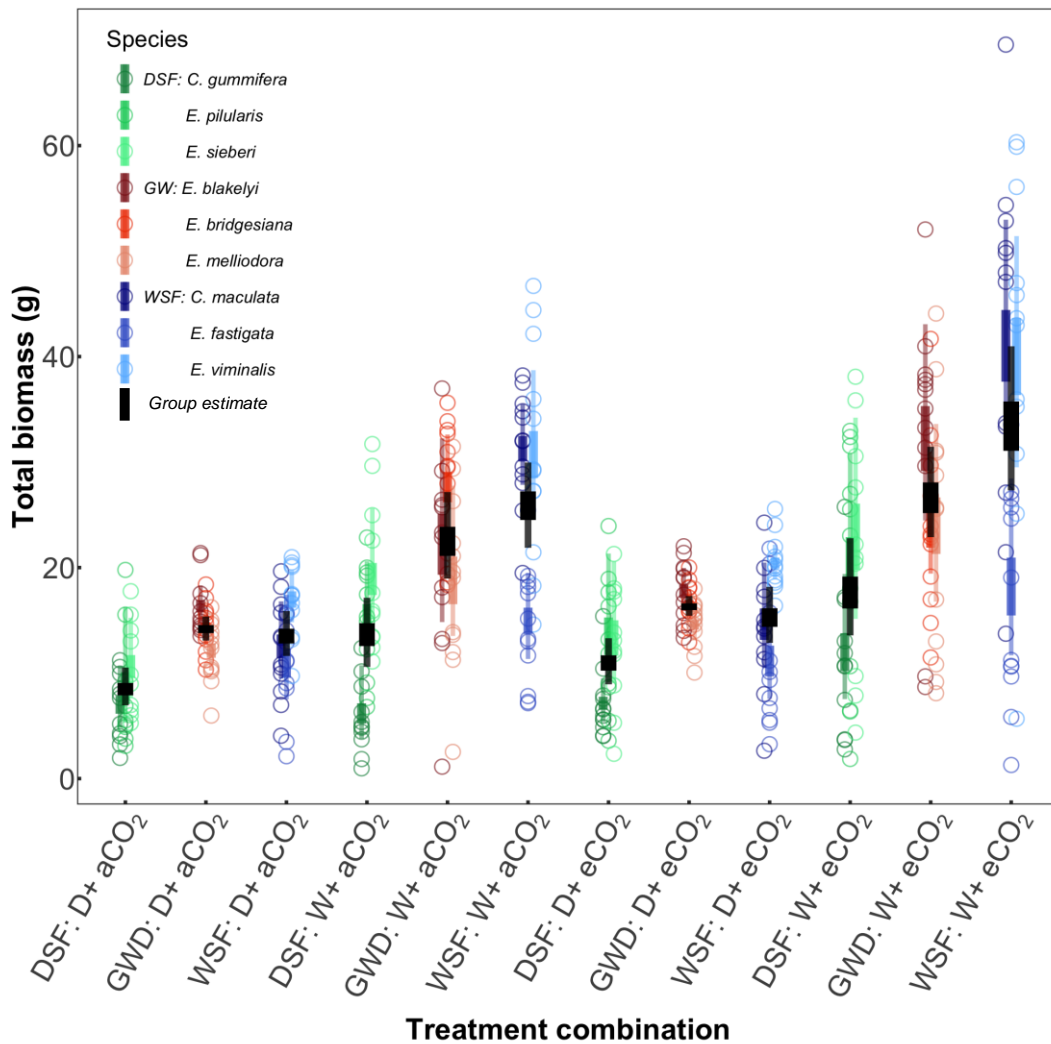
Fig 1. Observed (points) and predicted (box and whiskers) total biomass for plants subjected to four combinations of CO_2 and watering treatments (elevated CO_2 + well-watered = eCO_2 + W; ambient CO_2 + well-watered = aCO_2 + W; elevated CO_2 + drought = eCO_2 + D; ambient CO_2 + drought = aCO_2 + D; bottom x-axis) in a glasshouse experiment consisting of nine eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF; dry sclerophyll forest = DSF; grassy woodland = GW). Coloured points are raw data and colours correspond to species within each vegetation type; black shaded boxes represent 50% credible intervals at the group-level and black shaded whiskers represent 95% intervals at the group-level, independent of the species-level responses. Coloured shaded boxes represent 50% credible intervals at the species-level and coloured shaded whiskers represent 95% intervals at the species-level, independent of the group-level response.

Fig 2. Observed (points) and predicted (box and whiskers) above-ground biomass for plants subjected to four combinations of CO_2 and watering treatments (elevated CO_2 + well-watered = eCO_2 + W; ambient CO_2 + well-watered = aCO_2 + W; elevated CO_2 + drought = eCO_2 + D; ambient CO_2 + drought = aCO_2 + D; bottom x-axis) in a glasshouse experiment consisting of nine eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF; dry sclerophyll forest = DSF; grassy woodland = GW). Coloured points are raw data and colours correspond to species within each vegetation type; black shaded boxes represent 50% credible intervals at the group-level and black shaded whiskers represent 95% intervals at the group-level, independent of the species-level responses. Coloured shaded boxes represent 50% credible intervals at the species-level and coloured shaded whiskers represent 95% intervals at the species-level, independent of the group-level response.

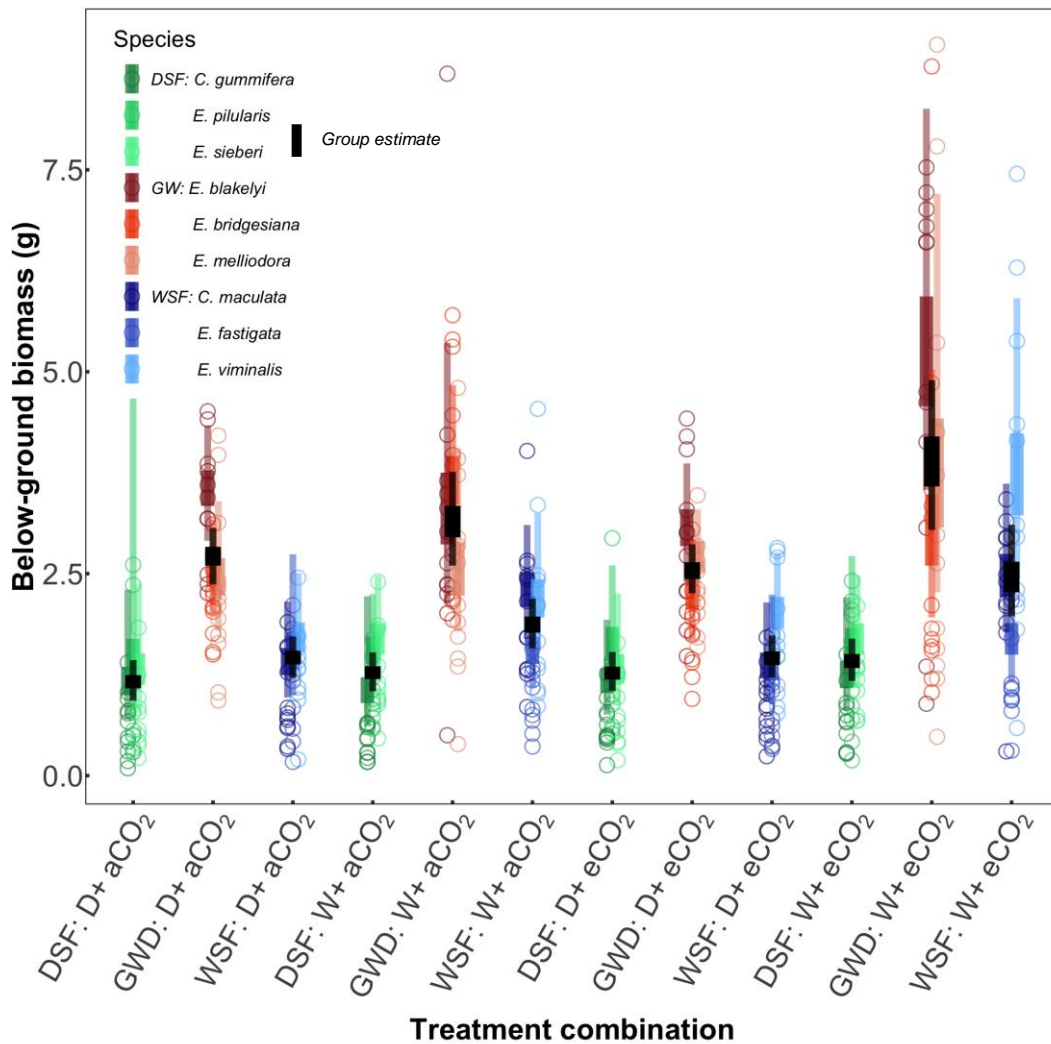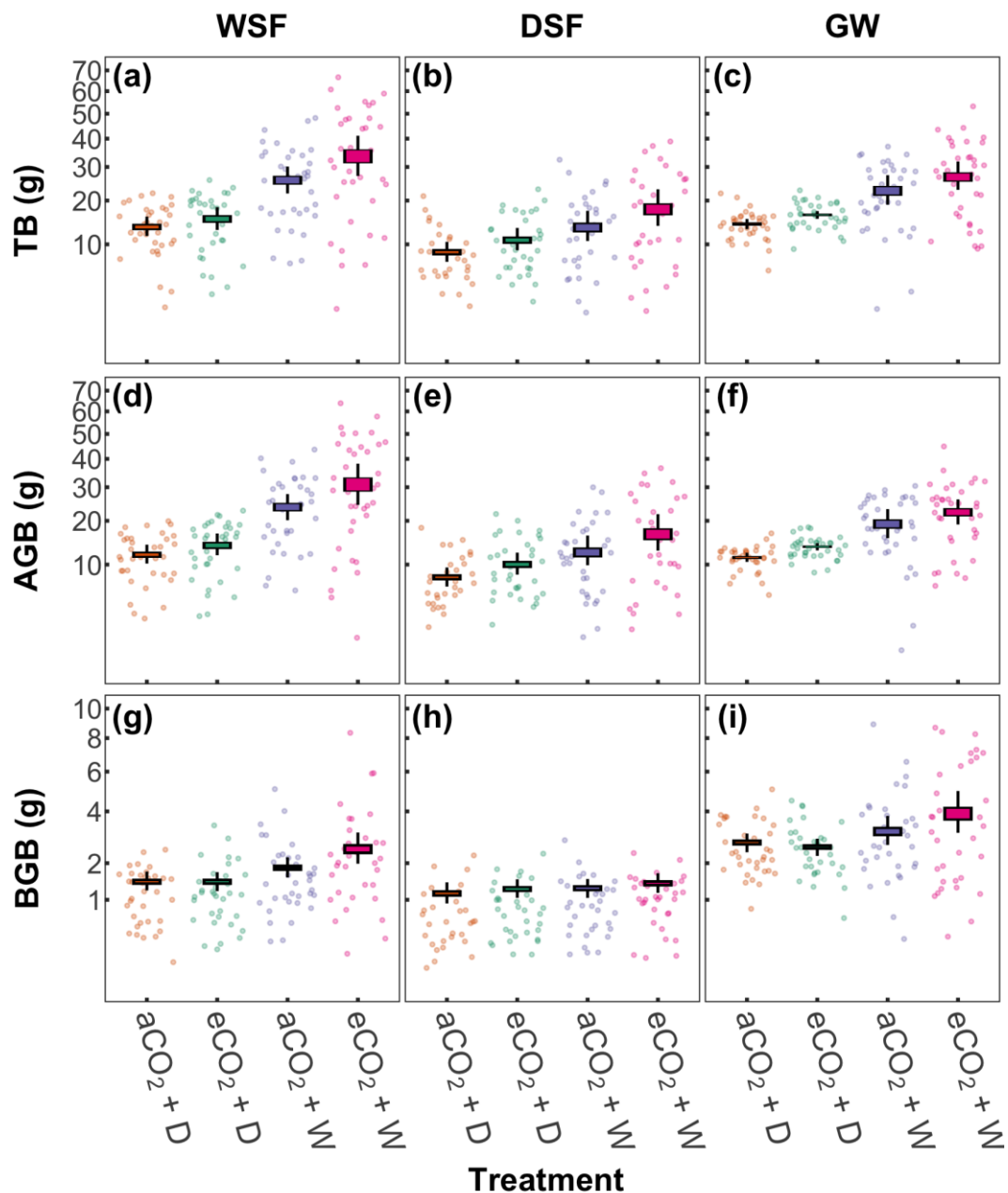**Fig 3.** Observed (points) and predicted (box and whiskers) below-ground biomass for plants subjected to four combinations of CO_2 and watering treatments (elevated CO_2 + well-watered = eCO_2 + W; ambient CO_2 + well-watered = aCO_2 + W; elevated CO_2 + drought = eCO_2 + D; ambient CO_2 + drought = aCO_2 + D; bottom x-axis) in a glasshouse experiment consisting of nine eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF; dry sclerophyll forest = DSF; grassy woodland = GW). Coloured points are raw data and colours correspond to species within each vegetation type; black shaded boxes represent 50% credible intervals at the group-level and black shaded whiskers represent 95% intervals at the group-level, independent of the species-level responses. Coloured shaded boxes represent 50% credible intervals at the species-level and coloured shaded whiskers represent 95% intervals at the species-level, independent of the group-level response.

13

Biomass: community-level

368 For all vegetation types, total biomass (Fig. **4a–c**) was highest under well-watered

369 + eCO$_2$ ('W + eCO$_2$'), followed by well-watered + aCO$_2$ ('W + aCO$_2$') then

370 drought-like conditions + eCO$_2$ ('D + eCO$_2$'). Total biomass was lowest under

371 drought-like conditions + aCO$_2$ ('D + aCO$_2$'; Fig. **4a–c**). Under well-watered

372 conditions, WSF had higher total biomass than both DSF and GW (Fig. **4a–c**).

373 Total biomass values were more similar across the vegetation types under

374 drought-like conditions (Fig. **4a–c**). When the distribution of differences between

375 treatments was calculated, drought-like conditions reduced the eCO$_2$ fertilisation

376 effect on total biomass by 16.38% for WSF, 5.26% for DSF and 4.3% for GW

377 (percentages represent mean values; Fig. **5a–c**). WSF experienced a reduction in

378 total biomass that was four times as large as the reduction experienced by

379 DSF/GW (Fig. **5a–c**), both of which experienced similar reductions (Fig. **5b,c**).

380 Above-ground biomass was consistently larger than below-ground

381 biomass (i.e. >90% of biomass), thus trends and differences followed similar

382 patterns to total biomass (Fig. **4d–f**). For all vegetation types below-ground

383 biomass was highest under W + eCO$_2$ followed by W + aCO$_2$, with eCO$_2$ having

384 negligible effect (mean values: 0.01–0.1 g) in the presence of drought-like

385 conditions, i.e. similar to D + aCO$_2$ (Fig. **4g–i**). Across the treatments GW had

386 consistently higher below-ground biomass than WSF (Fig. **4g,i**) and DSF, which

387 had the lowest (Fig. **4h**). There was little difference (mean values: 1.17–1.42 g)

388 among treatment combinations for DSF (Fig. **4h**). Drought-like conditions

389 reduced the eCO$_2$ fertilisation effect on below-ground biomass by 35.62% for

390 WSF, 1.58% for DSF and 32.52% for GW (Fig. **5g–i**). WSF and GW experienced

391 similarly large reductions in below-ground biomass, while the change was

392 negligible for DSF (Fig. **5g–i**).

Fig 4. Observed (jittered points) and predicted (boxes) total biomass (TB; panels **a–c**), above-ground biomass (AGB; panels **d–f**) and below-ground biomass (BGB; panels **g–i**) for plants subjected to four combinations of CO_2 and watering treatments (elevated CO_2 + well-watered = eCO_2 + W; ambient CO_2 + well-watered = aCO_2 + W; elevated CO_2 + drought = eCO_2 + D; ambient CO_2 + drought = aCO_2 + D; bottom x-axis) in a glasshouse experiment consisting of nine eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF, panels **a,d,g**; dry sclerophyll forest = DSF, panels **b,e,h**; grassy woodland = GW, panels **c,f,i**). Jittered points are raw data and colours correspond to treatment combinations; shaded boxes represent 50% credible intervals and whiskers

15

represent 95% intervals. The y-axis has been rescaled (square root) to ensure all data

points are visible in the plot.
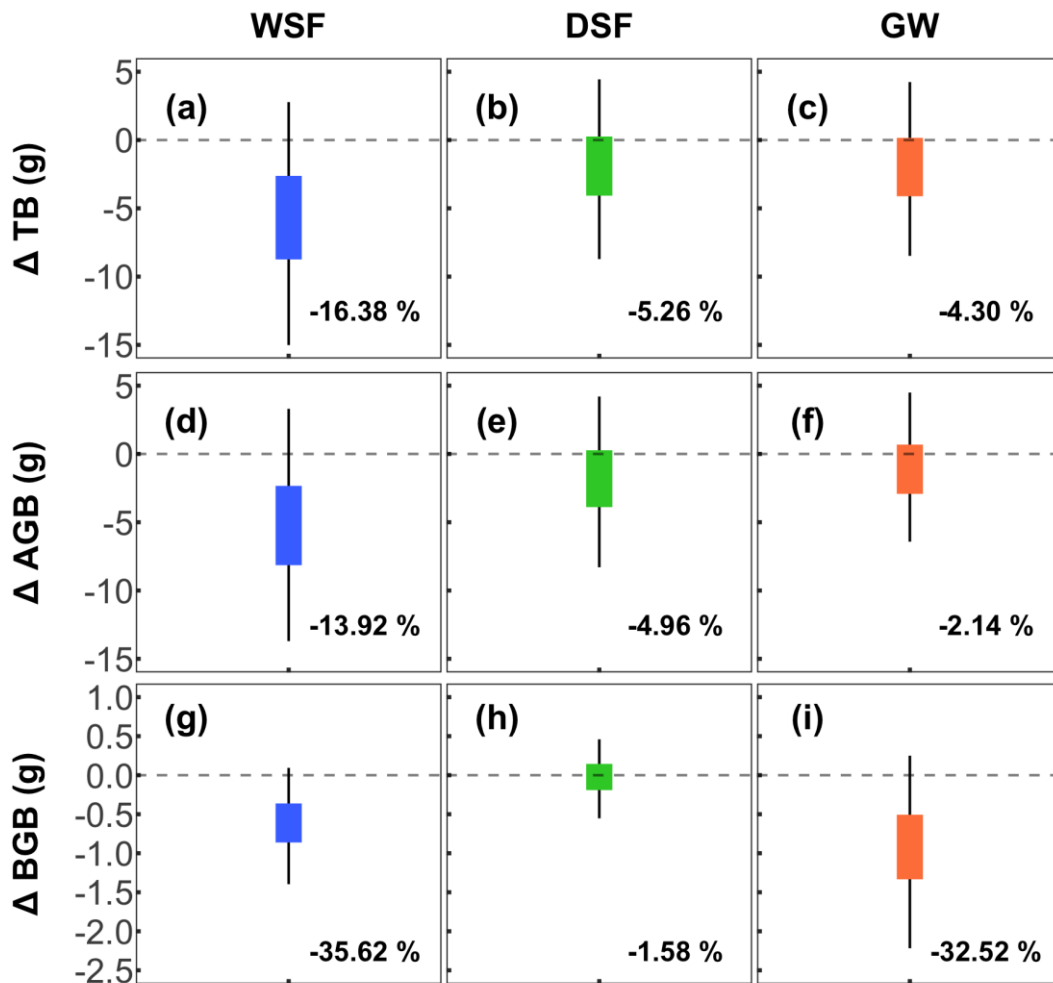
Fig 5. Predicted change (i.e. distribution of differences) in the CO_2 fertilisation effect on total biomass (TB; panels **a–c**), above-ground biomass (AGB; panels **d–f**) and below-ground biomass (BGB; panels **g–i**) under drought versus well-watered conditions in a glasshouse experiment consisting of nine eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF, panels **a,d,g**; dry sclerophyll forest = DSF, panels **b,e,h**; grassy woodland = GW, panels **c,f,i**). Negative values represent a lower, or stronger negative CO_2 fertilisation effect under drought-like compared to well-watered conditions, while positive values represent a greater effect. Colours correspond to vegetation type; shaded boxes represent 50% credible intervals and whiskers represent 95% credible intervals. Annotations indicate mean magnitude of change expressed as percentage. See Methods and Materials for calculation details.

*Resource acquisition traits*

Plant height was greater under well-watered conditions than drought-like conditions for all vegetation types (Fig. **6a–c**). There were only minor differences

between CO_2 treatments within either watering treatment for both WSF and GW
(mean values: 0.75–4.19 g; Fig. **6a,c**). DSF plants grown under eCO_2 were
slightly taller (by 5–8 cm) compared to aCO_2 (Fig. **6b**). Differences in the CO_2
fertilisation effect between drought and well-watered conditions were negligible
(<5% difference in means; Fig. **7a–c**).

Crown area was highest in the well-watered treatment (Fig. **6d–f**) and
lowest in the drought treatment across all vegetation types. WSF consistently had
the largest crown area, while both DSF and GW were similar (Fig. **6d–f**). The
effect of eCO_2 on crown area was negligible (mean values: 0.02–0.18 m^2; Fig. **6d–
f**). Drought-like conditions increased the eCO_2 fertilisation effect on crown area
by 9.16% for WSF, 12.7% for DSF and decreased it by 2.69% for GW (Fig. **7d–
f**), although these changes represented an increase/decrease of <0.1 m^2, e.g.
minimal change in crown area (Fig. **7d–f**).
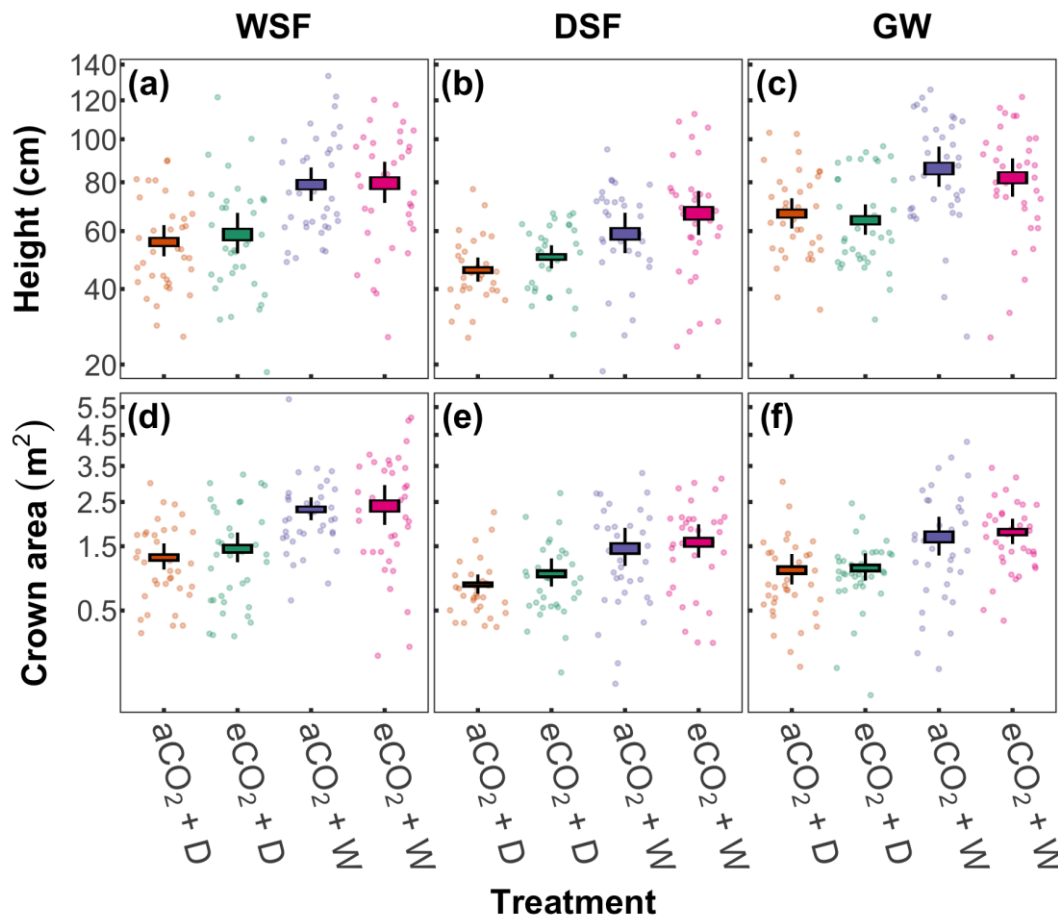
Fig 6. Observed (jittered points) and predicted (boxes) height (panels **a–c**) and crown
area (panels **d–f**) for plants subjected to four combinations of CO_2 and watering
treatments (elevated CO_2 + well-watered = eCO_2 + W; ambient CO_2 + well-watered =
aCO_2 + W; elevated CO_2 + drought = eCO_2 + D; ambient CO_2 + drought = aCO_2 + D;

17

439 bottom x-axis) in a glasshouse experiment consisting of nine eucalypt species grouped

440 into three vegetation types (wet sclerophyll forest = WSF, panels **a,d**; dry sclerophyll

441 forest = DSF, panels **b,e**; grassy woodland = GW, panels **c,f**). Jittered points are raw

442 data and colours correspond to treatment combinations; shaded boxes represent 50%

443 credible intervals and whiskers represent 95% credible intervals. The y-axis has been

444 rescaled (square root) to ensure all data points are visible in the plot.
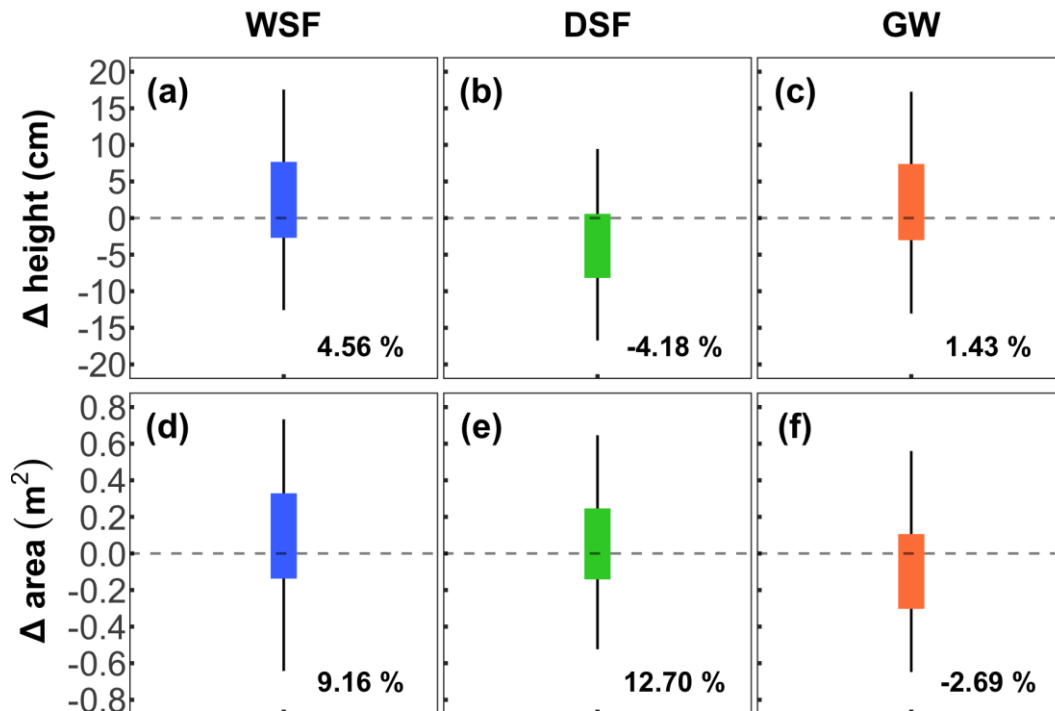
445

446 **Fig 7.** Predicted change (i.e. distribution of differences) in the CO_2 fertilisation effect on

447 plant height (panels **a–c**) and crown area (panels **d–f**) under drought versus well-watered

448 conditions in a glasshouse experiment consisting of nine eucalypt species grouped into

449 three vegetation types (wet sclerophyll forest = WSF, panels **a,d**; dry sclerophyll forest =

450 DSF, panels **b,e**; grassy woodland = GW, panels **c,f**). Negative values represent a lower,

451 or stronger negative CO_2 fertilisation effect under drought-like compared to well-watered

452 conditions, while positive values represent a greater effect. Colours correspond to

453 vegetation type; shaded boxes represent 50% credible intervals and whiskers represent

454 95% credible intervals. Annotations indicate mean magnitude of change expressed as

455 percentage. See Methods and Materials for calculation details.

456

457   For all vegetation types LMA was highest under D + eCO_2 (Fig. **8a–c**).

458 LMA was lowest under W + aCO_2 (Fig. **8a–c**). WSF had lower LMA under

459 drought-like conditions than DSF or GW (Fig. **8a–c**). For all vegetation types

460 LMA was 1–2 mg/cm^2 higher under eCO_2 than aCO_2 (Fig. **8a–c**). LMA response

461   to eCO_2 was reduced by 8.61–9.79% across the vegetation types (Fig. **9a–c**), i.e.

462   all vegetation types experienced similar reductions in LMA.

463   CO_2 or watering treatment had only a minor effect on root mass ratio for

464   both WSF and DSF (e.g. 0.02 difference) where values averaged between 0.08–

465   0.10 (Fig. **8d,e**). For GW, root mass ratio was highest under aCO_2 and around 0.04

466   lower under eCO_2 (Fig. **8f**). Root mass ratio was reduced by eCO_2 by 1.77% for

467   WSF, 0.01% for DSF and 3.58% for GW, i.e. there was a minor change in root

468   mass ratio for DSF and WSF and relatively larger change for GW (Fig. **9d–f**).
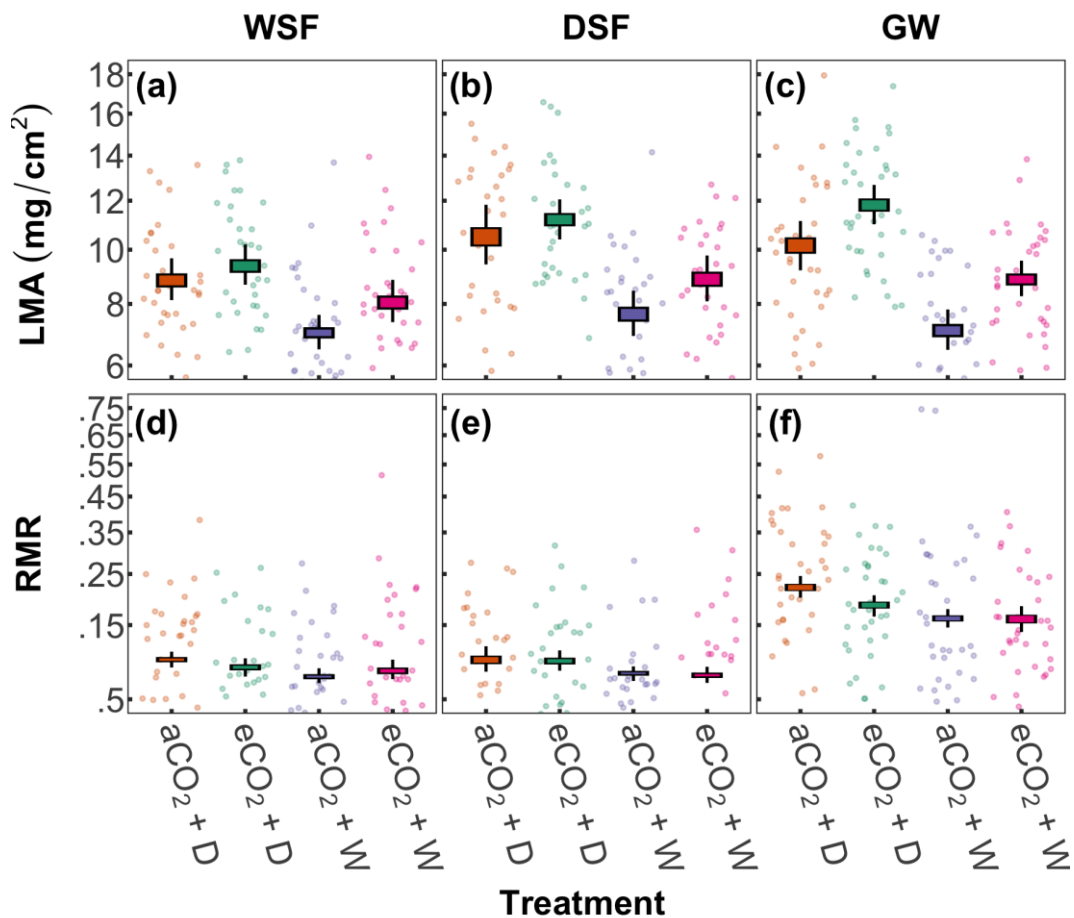
469

470   **Fig 8.** Observed (jittered points) and predicted (boxes) leaf mass per unit area (LMA;

471   panels **a–c**), and root mass ratio (RMR; panels **d–f**) for plants subjected to four

472   combinations of CO_2 and watering treatments (elevated CO_2 + well-watered = eCO_2 + W;

473   ambient CO_2 + well-watered = aCO_2 + W; elevated CO_2 + drought = eCO_2 + D; ambient

474   CO_2 + drought = aCO_2 + D; bottom x-axis) in a glasshouse experiment consisting of nine

475   eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF,

476   panels **a,d**; dry sclerophyll forest = DSF, panels **b,e**; grassy woodland = GW, panels **c,f**).

477   Jittered points are raw data and colours correspond to treatment combinations; shaded

The y-axis has been rescaled (square root) to ensure all data points are visible in the plot.
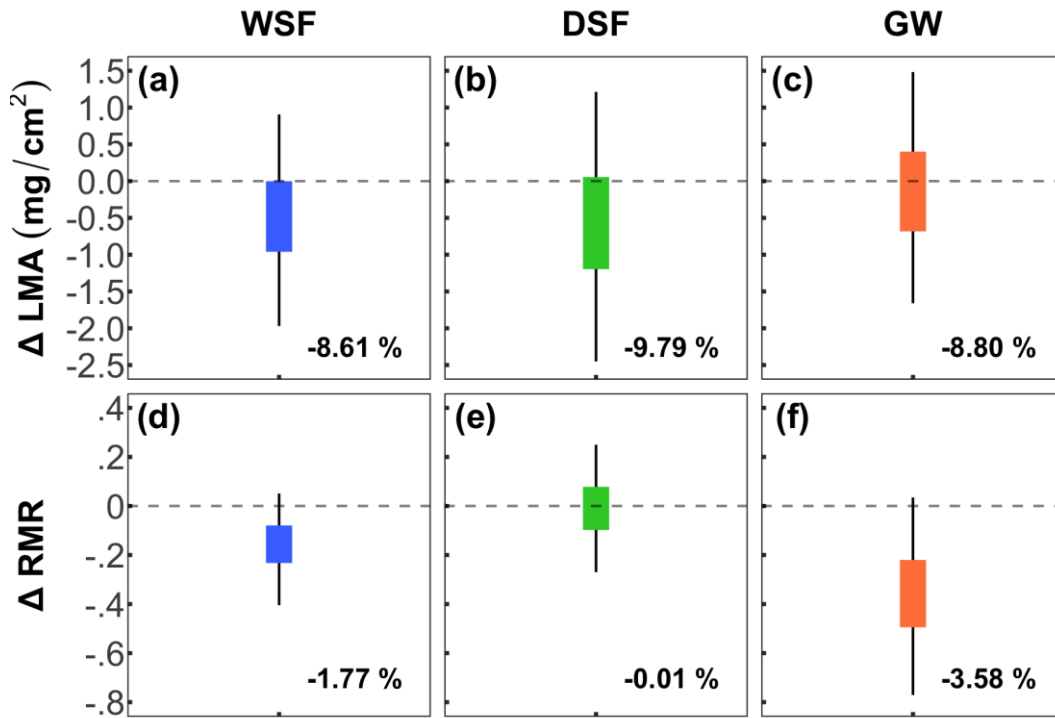
Fig 9. Predicted change (i.e. distribution of differences) in the CO_2 fertilisation effect on leaf mass per unit area (LMA; panels **a–c**) and root mass ratio (RMR; panels **d–f**) under drought versus well-watered conditions in a glasshouse experiment consisting of nine eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF, panels **a,d**; dry sclerophyll forest = DSF, panels **b,e**; grassy woodland = GW, panels **c,f**). Negative values represent a lower, or stronger negative CO_2 fertilisation effect under drought-like compared to well-watered conditions, while positive values represent a greater effect. Colours correspond to vegetation type; shaded boxes represent 50% credible intervals and whiskers represent 95% credible intervals. Annotations indicate mean magnitude of change expressed as percentage. See Methods and Materials for calculation details.

Storage organs

Lignotuber biomass was highest under W + eCO_2 and lowest under D + aCO_2 (Fig. **10a–c**) for all vegetation types. Lignotuber biomass was slightly higher under D + eCO_2 than D + aCO_2 (mean increase: 0.05–0.17 g; Fig. **10a–c**), i.e. eCO_2 had a positive effect on lignotuber biomass regardless of watering treatment. Drought-like conditions reduced the eCO_2 fertilisation effect on lignotuber biomass by 43.29% for WSF, increased it by 22.2% for DSF and decreased it by

500   6.35% for GW (Fig. **11a–c**), i.e. WSF experienced substantially larger reductions

501   in lignotuber biomass than either DSF or GW. For DSF, very wide bounds reflect

502   uncertainty around this result (Fig. **11b**).

503   Coarse-root biomass showed little response to $[CO_2]$ and watering

504   treatment across the vegetation types (e.g. <0.3 g difference; Fig. **10d–f**). Coarse-

505   root biomass was highest for GW and lowest for DSF, while WSF had

506   intermediate coarse-root biomass (Fig. **10d–f**). Drought-like conditions reduced

507   the eCO_2 fertilisation effect on coarse-root biomass by 7.82% for WSF, 4.40% for

508   DSF and 7.09% for GW (Fig. **11d–f**). WSF and GWD experienced slightly larger

509   reductions in coarse-root biomass than DSF (e.g. 2.7–3.4% larger; Fig. **11d–f**).
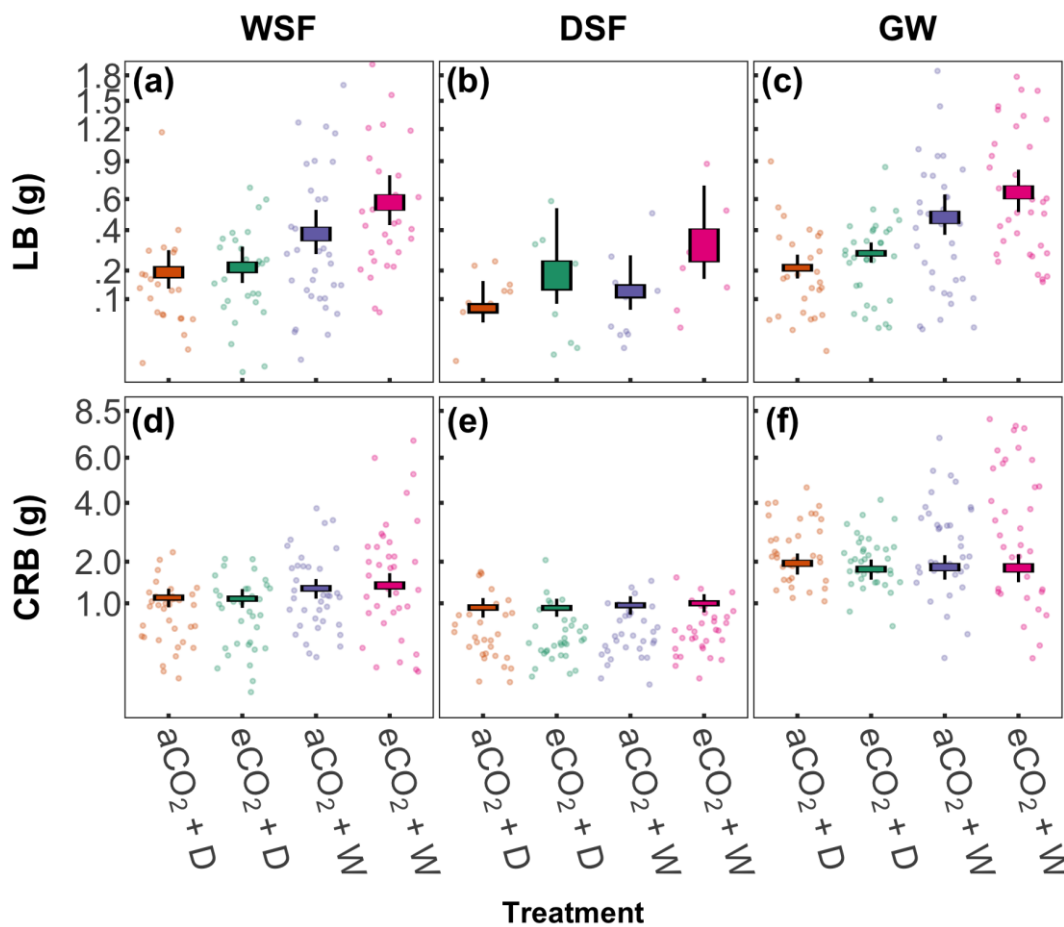
510

511   **Fig 10.** Observed (jittered points) and predicted (boxes) lignotuber biomass (LB; panels

512   **a–c**), and coarse root biomass (CRB; panels **d–f**) for plants subjected to four

513   combinations of CO_2 and watering treatments (elevated CO_2 + well-watered = eCO_2 + W;

514   ambient CO_2 + well-watered = aCO_2 + W; elevated CO_2 + drought = eCO_2 + D; ambient

515   CO_2 + drought = aCO_2 + D; bottom x-axis) in a glasshouse experiment consisting of nine

516   eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF,

517   panels **a,d**; dry sclerophyll forest = DSF, panels **b,e**; grassy woodland = GW, panels **c,f**).

518   Jittered points are raw data and colours correspond to treatment combinations; shaded

boxes represent 50% credible intervals and whiskers represent 95% credible intervals.

520 The y-axis has been rescaled (square root) to ensure all data points are visible in the plot.

521
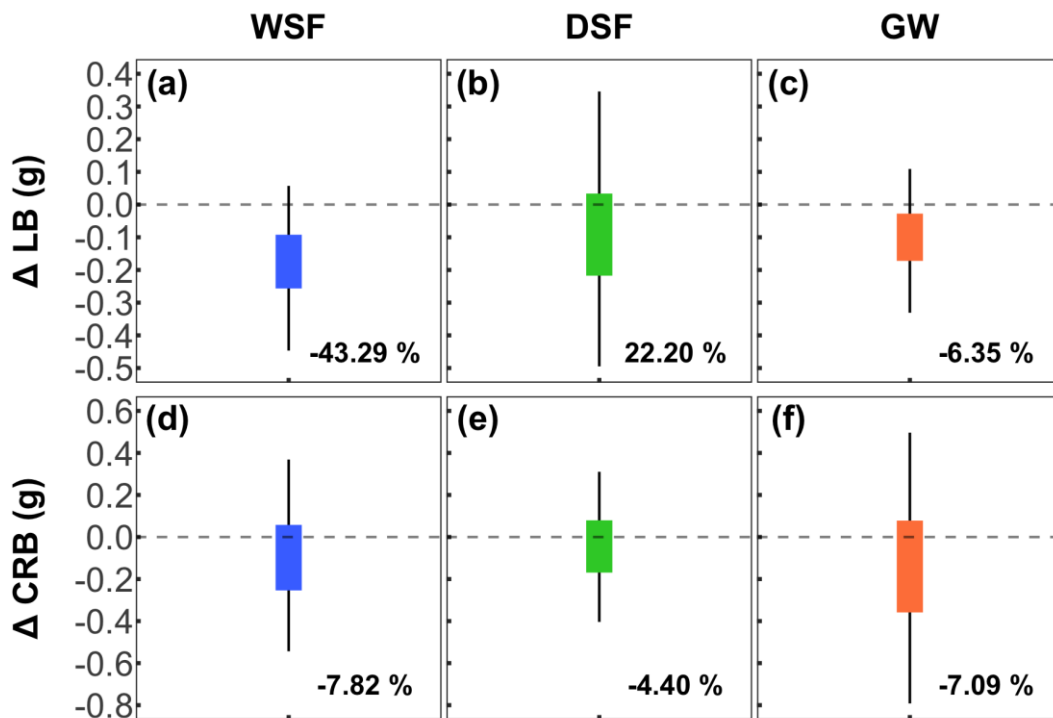
Fig 11. Predicted change (i.e. distribution of differences) in the CO_2 fertilisation effect under drought versus well-watered conditions for lignotuber biomass (LB; panels **a–c**) and coarse-root biomass (CRB; panels **d–f**) in a glasshouse experiment consisting of nine eucalypt species grouped into three vegetation types (wet sclerophyll forest = WSF, panels **a,d**; dry sclerophyll forest = DSF, panels **b,e**; grassy woodland = GW, panels **c,f**). Negative values represent a lower, or stronger negative CO_2 fertilisation effect under drought-like compared to well-watered conditions, while positive values represent a greater effect. Colours correspond to vegetation type; shaded boxes represent 50% credible intervals and whiskers represent 95% credible intervals. Annotations indicate mean magnitude of change expressed as percentage. See Methods and Materials for calculation details.

Discussion

In temperate, eucalypt-dominated vegetation types, the effects of eCO_2 fertilisation on biomass accumulation and storage organs were effectively negated by drought, though some typical drought-stress responses, such as increased LMA and RMR, were reduced under eCO_2. Physical dimensions of eucalypt seedlings, such as height and crown area, were essentially unaffected by eCO_2. In the absence of drought, however, eucalypt species may experience faster seedling growth, establishment and enhanced resprouting capacity due to eCO_2.

Plant biomass

544 When water was not limited, eucalypt seedlings responded to eCO_2 by increasing

545 biomass by more than 30% (Fig. **1,4a–c**), which is comparable to increases found

546 in the majority of global studies on non-eucalypt woody species (e.g. 48%,

547 Poorter & Nagel 2000) and in similar studies of eucalypts (e.g. 41–108%, Roden

548 & Ball 1996; 44–74%, Ghannoum *et al.* 2010). This result suggests there is

549 potential for increased seedling establishment in temperate woody ecosystems in

550 regions or during periods where rainfall is adequate, as has been suggested

551 elsewhere (Ghannoum *et al.* 2010). Seedlings that accumulate biomass more

552 quickly are more likely to escape fire-related mortality by reaching fire-tolerant

553 size-classes (Hoffmann & Solbrig 2003; Clarke *et al.* 2013) and thus transition

554 faster to maturity, supporting the idea that eCO_2 may facilitate woody thickening

555 in temperate woody ecosystems. While some studies have demonstrated that trees

556 in regenerating forests may also increase biomass in response to eCO_2 (e.g. by 20–

557 30%, Norby *et al.* 2001; Kim *et al.* 2019; Walker *et al.* 2019), this enhanced

558 growth is typically reported in the earlier stages of tree growth, with most studies

559 of established mature trees suggesting that eCO_2 has little effect on biomass

560 accumulation (Jiang *et al.* 2020; Walker *et al.* 2021). Competitive interactions

561 with grasses (Manea & Leishman 2015), herbivory (Collins *et al.* 2018a) and

562 nutrient limitation (Norby *et al.* 2010; Ellsworth *et al.* 2017) may limit the

563 potential for increased carbon sequestration in natural ecosystems under eCO_2.

564 In our study, the effect of CO_2 fertilisation on biomass was reduced by

565 drought-like conditions, as found in other studies (Duan *et al.* 2013; Duan *et al.*

566 2018b). We did not find a doubling of biomass under drought-like conditions +

567 eCO_2 as in Atwell *et al.* (2007). Of our nine species, wet sclerophyll species

568 showed the greatest reduction in total, above-ground and below-ground biomass

569 (Fig. **1,2,3,4**), although reductions did occur across all vegetation types. Thus,

570 drought-like conditions placed limitations on growth regardless of species or CO_2

571 level. Relative to the forest species, grassy woodland species invested

572 substantially more resources into roots under drought-like conditions (Fig. **3,4g–**

573 **i**), although the same pattern occurred under well-watered conditions, suggesting

574 that high below-ground biomass investment is typical for grassy woodland

575 systems. Indeed, larger, deeper root systems are characteristic of species adapted

576 to drier climates (Brunner *et al.* 2015).

577 Eucalypts from more mesic environments have been reported to

578 experience reduced biomass accumulation when water is limited (e.g. >80%;

579 Duan *et al.* 2014), with smaller reductions reported in xeric species (e.g. >50%,

580 Susiluoto & Berninger 2007). We found species from wet sclerophyll forest to be

581 relatively more sensitive to drought. For example, the 16.38% reduction in

582 biomass between well-watered and water-stressed wet sclerophyll species was

583 larger than either grassy woodland (4.3%) or dry sclerophyll species (5.26%; Fig.

584 **5**). This suggests that, under drier future climates, trees of wet sclerophyll

585 environments may experience sharper decreases in productivity than those in drier

586 wooded landscapes; for example, through reducing seedling success.

587

588 *Resource acquisition traits*

589 Under climate change, seedling success and ongoing competitive advantage of a

590 given species depends on how resource acquisition is balanced with water

591 conservation, e.g. low-LMA species adapted to high productivity, mesic

592 environments may have greater success under normal rainfall conditions while

593 high-LMA species adapted to lower productivity, xeric environments may have

594 greater success when rainfall declines (Poorter *et al.* 2009). In our study, LMA

595 was highest under drought-like conditions for species of the drier habitats (Fig.

596 **8b–c**), which suggests that such species are more effectively able to cope with

597 drought-like conditions than those of wet sclerophyll forests. This pattern is

598 consistent with trends elsewhere, showing that LMA can vary according to

599 positions along rainfall gradients (Cernusak *et al.* 2011) and eucalypts from xeric

600 environments may have higher LMA than those from mesic environments (Lewis

601 *et al.* 2011). Increasing LMA is a strategy plants employ to conserve resources

602 and reduce wilting (Poorter *et al.* 2009). We found that the LMA increase with

603 eCO_2 was only 8–10% smaller under drought-like conditions compared to well-

604 watered conditions (Fig. **9a–c**), suggesting that eCO_2 may help some species cope

605 with drought (e.g. by developing tougher leaves to reduce water loss).

606 Increasing the proportion of biomass allocated to roots maximises water

607 uptake while limiting water loss (Brunner *et al.* 2015). In this study there was

608   evidence that eCO_2 decreased the root-to-shoot mass ratio under drought

609   conditions, representing a 1–4% ameliorative effect for some species (Fig. **9d–f**).

610   This result was consistent with both general patterns (Poorter & Nagel 2000;

611   Schall *et al.* 2012; Brunner *et al.* 2015) and some studies of eucalypts (e.g. Barton

612   and Montagu 2006; Thomas 2009), though other studies have found little or no

613   difference in RMR under varying watering regimes (Osório *et al.* 1998; Merchant

614   *et al.* 2006; Merchant *et al.* 2007). Our results suggest that eCO_2 fertilisation may

615   reduce drought stress for some species. Root-to-shoot mass ratio was highest for

616   grassy woodland species, around twice that of species in the forest categories.

617   Overall our results were broadly comparable (e.g. ~0.1 for WSF spp., DSF spp.;

618   ~0.2% for GW spp.; Fig. **8d–f**) with global trends in root-to-shoot mass ratio

619   across varying habitats and water availability: e.g. 0.2 at 3000 mm cf. 0.4 at 500

620   mm mean annual rainfall (Brunner *et al.* 2015). The comparatively high LMA and

621   RMR of the more xeric species in our study and the magnitude of increase in

622   these variables due to drought, suggests that these taxa are more capable of

623   withstanding and responding to drought.

624   Changes to plant height due to eCO_2 in our study were generally small

625   (e.g. <5%), with moderate increases in crown area (<12%). Hence, the eCO_2-

626   related biomass gains observed in our study may be due to increases in tissue

627   density, stem diameter, branch number, leaf number and rooting architecture

628   (Atwell *et al.* 2007; Ghannoum *et al.* 2010). This suggests that, for the study

629   species, additional carbon was allocated to biomass and, to some extent, crown

630   area, rather than height.

631

632   *Storage organs*

633   Elevated CO_2 may facilitate greater allocation of non-structural carbohydrates to

634   storage organs such as lignotubers and roots, which resprouting species such as

635   eucalypts utilise following disturbance (Hoffman *et al.* 2000). In our study we

636   found that when sufficient water was available, eCO_2 increased the size of

637   lignotubers by 5–33% for species from wet sclerophyll forests and 21–58% for

638   those native to drier environments (Fig. **10,11a–c**), consistent with results of other

639   glasshouse studies (Hoffman *et al.* 2000; Bond & Midgley 2012). In contrast,

640   Collins *et al.* (2018b) found no effect of eCO_2 on lignotuber growth in eucalypts

641 in a field experiment, probably due to competition with grasses, herbivory and

642 nutrient limitation. Elevated CO_2 may increase the biomass and vigour of

643 resprouting stems and increase the size of coarse roots, which contain resources

644 needed for resprouting (Hoffman *et al.* 2000; Bond & Midgley 2012). The trends

645 in above and below ground biomass (e.g. increased shoot biomass and increased

646 storage capacity under eCO_2) in the study species, described above, may therefore

647 have potential to enhance resprouting capacity as atmospheric CO_2 levels

648 increase. However, our result that drought-like conditions imposed severe

649 restrictions on lignotuber growth for some species and thereby reduced the effect

650 of eCO_2 fertilisation, suggests that enhanced resprouting would be limited to

651 periods of adequate rainfall (Fig. **10,11a–c**). Nonetheless, there remained

652 substantial uncertainty in the results for dry sclerophyll species due to the failure

653 of many plants to produce a lignotuber during the experiment.

654

655 *Future climate and potential ecosystem change*

656 Further rapid and substantial increases in atmospheric [CO_2] are predicted

657 globally, along with increases in global mean air temperature, with changes to

658 rainfall patterns likely to be more diverse and harder to predict (IPCC 2021).

659 Drought has been identified as a factor that may negatively impact resprouting

660 success across many ecosystems, including Australian forests (Rosas *et al.* 2013;

661 Nolan *et al.* 2021). There is also evidence that some eucalypt forests can undergo

662 state-changes, for example a shift toward smaller, multi-stemmed trees, during

663 severe drought conditions (Matusick *et al.* 2016). Climate change-driven increases

664 in fire frequency could potentially result in higher mortality and decreased

665 complexity in resprouting eucalypt woodlands (Fairman *et al.* 2017). One

666 possibility could be that future forested landscapes experience eCO_2-enhanced

667 growth during periods of adequate rainfall, but the coupled effects of more

668 extreme droughts and fires may equate to zero net-change over the long term.

669 Our results indicate that drought offsets the effect of eCO_2 fertilisation on

670 biomass accumulation and lignotuber size in seedlings. Species from drier habitats

671 may have a physiological advantage over those in mesic forests in the seedling

672 phase in a high-CO_2 world where drought pervades landscapes. There may be

673 potential for reduced seedling survival in vulnerable areas within wet sclerophyll

674 forests, e.g. climatically marginal ridgetops, plateaus or ecotones. Species from

675 dry sclerophyll or grassy woodlands that are more effectively able to cope with

676 drought and short-interval fires could potentially encroach into such areas, leading

677 to reductions in the extent of wet sclerophyll forests. However, our study only

678 examined seedlings grown under controlled conditions for a short period of time,

679 so it is not clear how these effects may translate to natural forest ecosystems.

680 Thus, future scenarios of coupled changes to climate and disturbance regime

681 could lead to major shifts in vegetation composition, structure and function,

682 potentially reducing carbon storage within forests, which may accelerate climate

683 change and result in further changes to vegetation.

684

685 **References**

686 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N.,
687 Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H.,
688 Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H.,
689 Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global
690 overview of drought and heat-induced tree mortality reveals emerging
691 climate change risks for forests. *Forest Ecology and Management,* **259,**
692 660-684.
693 Andela, N., Liu, Y.Y., van Dijk, A.I.J.M., de Jeu, R.A.M. & McVicar, T.R. (2013)
694 Global changes in dryland vegetation dynamics (1988-2008) assessed by
695 satellite remote sensing: comparing a new passive microwave vegetation
696 density record with reflective greenness data. *Biogeosciences,* **10,** 6657-
697 6676.
698 Aspinwall, M.J., Pfautsch, S., Tjoelker, M.G., Varhammar, A., Possell, M., Drake,
699 J.E., Reich, P.B., Tissue, D.T., Atkin, O.K., Rymer, P.D., Dennison, S. &
700 Van Sluyter, S.C. (2019) Range size and growth temperature influence
701 Eucalyptus species responses to an experimental heatwave. *Glob Chang*
702 *Biol,* **25,** 1665-1684.
703 Atwell, B.J., Henery, M.L., Rogers, G.S., Seneweera, S.P., Treadwell, M. &
704 Conroy, J.P. (2007) Canopy development and hydraulic function in
705 Eucalyptus tereticornis grown in drought in CO2-enriched atmospheres.
706 *Functional Plant Biology,* **34,** 1137.
707 Barton, C.V.M. & Montagu, K.D. (2006) Effect of spacing and water availability
708 on root:shoot ratio in *Eucalyptus camaldulensis*. *Forest Ecology and*
709 *Management,* **221,** 52-62.
710 BioClim (2022) WorldClim - Global Climate Data.
711 Blackman, C.J., Creek, D., Maier, C., Aspinwall, M.J., Drake, J.E., Pfautsch, S.,
712 O'Grady, A., Delzon, S., Medlyn, B.E., Tissue, D.T. & Choat, B. (2019)
713 Drought response strategies and hydraulic traits contribute to mechanistic
714 understanding of plant dry-down to hydraulic failure. *Tree Physiol,* **39,** 910-
715 924.

716 Boland, D.J., Brooker, M.I.H., Chippendale, N., Hall, N., Hyland, B.P.M., Johnson,
717   R.D., Kleinig, D.A., McDonald, M.W. & Turner, J.D. (2006) *Forest Trees*
718   *of Australia,* Fifth edn. CSIRO Publishing, Collingwood, VIC.
719 Bond, W.J. & Midgley, G.F. (2012) Carbon dioxide and the uneasy interactions of
720   trees and savannah grasses. *Philos Trans R Soc Lond B,* **367,** 607-612.
721 Bond, W.J.a.M., G. F. (2000) A proposed CO_2-controlled mechanism of woody
722   plant invasion in grasslands and savannas. *Glob Chang Biol,* **6,** 865-869.
723 Borzak, C.L., Potts, B.M. & O'Reilly-Wapstra, J.M. (2016) Survival and recovery
724   of *Eucalyptus globulus* seedlings from severe defoliation. *Forest Ecology*
725   *and Management,* **379,** 243-251.
726 Bowman, D.M.J.S., Murphy, B., Boer, M.M., Bradstock, R., Cary, G.J., Cochrane,
727   M.A., Fensham, R.J., Krawchuk, M.A., Price, O.F. & Williams, R.J. (2013)
728   Forest fire management, climate change, and the risk of catastrophic carbon
729   losses. *Frontiers in Ecology and the Environment,* **11,** 66-68.
730 Bradstock, R.A., Hammill, K.A., Collins, L. & Price, O. (2010) Effects of weather,
731   fuel and terrain on fire severity in topographically diverse landscapes of
732   south-eastern Australia. *Landscape Ecology,* **25,** 607-619.
733 Brando, P.M., Balch, J.K., Nepstad, D.C., Morton, D.C., Putz, F.E., Coe, M.T.,
734   Silverio, D., Macedo, M.N., Davidson, E.A., Nobrega, C.C., Alencar, A. &
735   Soares-Filho, B.S. (2014) Abrupt increases in Amazonian tree mortality due
736   to drought-fire interactions. *Proc Natl Acad Sci U S A,* **111,** 6347-6352.
737 Brooker, M.I.H. & Kleinig, D.A. (1999) *Field Guide to Eucalypts of South-eastern*
738   *Australia.* Bloomings Books, Hawthorn VIC.
739 Brunner, I., Herzog, C., Dawes, M.A., Arend, M. & Sperisen, C. (2015) How tree
740   roots respond to drought. *Front Plant Sci,* **6,** 547.
741 Buitenwerf, R., Bond, W.J., Stevens, N. & Trollope, W.S.W. (2012) Increased tree
742   densities in South African savannas: >50 years of data suggests CO_2 as a
743   driver. *Global Change Biology,* **18,** 675-684.
744 Burrows, G.E. (2013) Buds, bushfires and resprouting in the eucalypts. *Australian*
745   *Journal of Botany,* **61,** 331.
746 Cernusak, L.A., Hutley, L.B., Beringer, J., Holtum, J.A.M. & Turner, B.L. (2011)
747   Photosynthetic physiology of eucalypts along a sub-continental rainfall
748   gradient in northern Australia. *Agricultural and Forest Meteorology,* **151,**
749   1462-1470.
750 Chick, M.P. (2016) Fire, environment, and the shrubby understorey of heathy-
751   woodland. Doctor of Philosophy, University of Melbourne.
752 Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E.,
753   Enright, N.J. & Knox, K.J. (2013) Resprouting as a key functional trait: how
754   buds, protection and resources drive persistence after fire. *New Phytol,* **197,**
755   19-35.
756 Cobb, R.C., Ruthrof, K.X., Breshears, D.D., Lloret, F., Aakala, T., Adams, H.D.,
757   Anderegg, W.R.L., Ewers, B.E., Galiano, L., Grünzweig, J.M., Hartmann,
758   H., Huang, C., Klein, T., Kunert, N., Kitzberger, T., Landhäusser, S.M.,
759   Levick, S., Preisler, Y., Suarez, M.L., Trotsiuk, V. & Zeppel, M.J.B. (2017)
760   Ecosystem dynamics and management after forest die-off: a global
761   synthesis with conceptual state-and-transition models. *Ecosphere,* **8,** 1-17.
762 Collins, L. (2020) Eucalypt forests dominated by epicormic resprouters are resilient
763   to repeated canopy fires. *Journal of Ecology,* **00,** 1-15.
764 Collins, L., Boer, M.M., de Dios, V.R., Power, S.A., Bendall, E.R., Hasegawa, S.,
765   Hueso, R.O., Nevado, J.P. & Bradstock, R.A. (2018a) Effects of

competition and herbivory over woody seedling growth in a temperate woodland trump the effects of elevated CO2. *Oecologia,* **187,** 811-823.

Collins, L., Bradstock, R.A., Clarke, H., Clarke, M.F., Nolan, R.H. & Penman, T.D. (2021) The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters,* **16**.

Collins, L., Bradstock, R.A., Resco de Dios, V., Duursma, R.A., Velasco, S. & Boer, M.M. (2018b) Understorey productivity in temperate grassy woodland responds to soil water availability but not to elevated [CO2]. *Glob Chang Biol,* **24,** 2366-2376.

Donohue, R.J., Roderick, M.L., McVicar, T.R. & Farquhar, G.D. (2013) Impact of CO2 fertilization on maximum foliage cover across the globe's warm, arid environments. *Geophysical Research Letters,* **40,** 3031-3035.

DPI, N. (2017) Geoscience Information. pp. Interactive Geological Map of New South Wales. DPI, NSW.

Drake, J.E., Power, S.A., Duursma, R.A., Medlyn, B.E., Aspinwall, M.J., Choat, B., Creek, D., Eamus, D., Maier, C., Pfautsch, S., Smith, R.A., Tjoelker, M.G. & Tissue, D.T. (2017) Stomatal and non-stomatal limitations of photosynthesis for four tree species under drought: A comparison of model formulations. *Agricultural and Forest Meteorology,* **247,** 454-466.

Du, Y., Lu, R., Xia, J. & Martin, A. (2020) Impacts of global environmental change drivers on non-structural carbohydrates in terrestrial plants. *Functional Ecology,* **34,** 1525-1536.

Duan, H., Amthor, J.S., Duursma, R.A., O'Grady, A.P., Choat, B. & Tissue, D.T. (2013) Carbon dynamics of eucalypt seedlings exposed to progressive drought in elevated [CO2] and elevated temperature. *Tree Physiol,* **33,** 779-792.

Duan, H., Chaszar, B., Lewis, J.D., Smith, R.A., Huxman, T.E. & Tissue, D.T. (2018a) CO2 and temperature effects on morphological and physiological traits affecting risk of drought-induced mortality. *Tree Physiol,* **38,** 1138-1151.

Duan, H., Duursma, R.A., Huang, G., Smith, R.A., Choat, B., O'Grady, A.P. & Tissue, D.T. (2014) Elevated [CO2] does not ameliorate the negative effects of elevated temperature on drought-induced mortality in *Eucalyptus radiata* seedlings. *Plant Cell Environ,* **37,** 1598-1613.

Duan, H., Huang, G., Zhou, S. & Tissue, D.T. (2018b) Dry mass production, allocation patterns and water use efficiency of two conifers with different water use strategies under elevated [CO2], warming and drought conditions. *European Journal of Forest Research,* **137,** 605-618.

Duan, H., Ontedhu, J., Milham, P., Lewis, J.D. & Tissue, D.T. (2019) Effects of elevated carbon dioxide and elevated temperature on morphological, physiological and anatomical responses of Eucalyptus tereticornis along a soil phosphorus gradient. *Tree Physiol,* **39,** 1821-1837.

Duursma, R.A., Barton, C.V., Eamus, D., Medlyn, B.E., Ellsworth, D.S., Forster, M.A., Tissue, D.T., Linder, S. & McMurtrie, R.E. (2011) Rooting depth explains [CO2] x drought interaction in *Eucalyptus saligna. Tree Physiol,* **31,** 922-931.

Eamus, D. & Palmer, A.R. (2007) Is climate change a possible explanation for woody thickening in arid and semi-arid regions? *Research Letters in Ecology,* **2007,** 1-5.

816 Ellsworth, David S., Anderson, Ian C., Crous, Kristine Y., Cooke, J., Drake,
817   John E., Gherlenda, Andrew N., Gimeno, Teresa E., Macdonald,
818   Catriona A., Medlyn, Belinda E., Powell, Jeff R., Tjoelker, Mark G. &
819   Reich, Peter B. (2017) Elevated CO_2 does not increase eucalypt forest
820   productivity on a low-phosphorus soil. *Nature Climate Change,* **7,** 279-282.
821 Fairman, T.A., Bennett, L.T. & Nitschke, C.R. (2019) Short-interval wildfires
822   increase likelihood of resprouting failure in fire-tolerant trees. *J Environ*
823   *Manage,* **231,** 59-65.
824 Fairman, T.A., Bennett, L.T., Tupper, S. & Nitschke, C.R. (2017) Frequent
825   wildfires erode tree persistence and alter stand structure and initial
826   composition of a fire-tolerant sub-alpine forest. *Journal of Vegetation*
827   *Science,* **28,** 1151-1165.
828 Franks, P.J., Adams, M.A., Amthor, J.S., Barbour, M.M., Berry, J.A., Ellsworth,
829   D.S., Farquhar, G.D., Ghannoum, O., Lloyd, J., McDowell, N., Norby, R.J.,
830   Tissue, D.T. & von Caemmerer, S. (2013) Sensitivity of plants to changing
831   atmospheric CO_2 concentration: from the geological past to the next
832   century. *New Phytol,* **197,** 1077-1094.
833 Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using
834   multiple sequences. *Statistical Sciences,* **7,** 457-472.
835 Ghannoum, O., Phillips, N.G., Conroy, J.P., Smith, R.A., Attard, R.D., Woodfield,
836   R., Logan, B.A., Lewis, J.D. & Tissue, D.T. (2010) Exposure to
837   preindustrial, current and future atmospheric CO_2 and temperature
838   differentially affects growth and photosynthesis in *Eucalyptus*. *Global*
839   *Change Biology,* **16,** 303-319.
840 Hoffman, W.A., Bazzaz, F.A., Chatterton, N.J., Harrison, P.A. & Jackson, R.B.
841   (2000) Elevated CO_2 enhances resprouting of a tropical savanna tree.
842   *Oecologia,* **123,** 312-317.
843 Hoffmann, W.A., Bazzaz, Fakhri A., Chatterton, Jerry N., Harrison, Phillip A. and
844   Jackson, Robert B (2000) Elevated CO_2 enhances resprouting of a tropical
845   savannah tree. *Oecologia,* **123,** 312-317.
846 Hoffmann, W.A. & Solbrig, O.T. (2003) The role of topkill in the differential
847   response of savanna woody species to fire. *Forest Ecology and*
848   *Management,* **180,** 273-286.
849 Hovenden, M.J. & Williams, A.L. (2010) The impacts of rising CO_2 concentrations
850   on Australian terrestrial species and ecosystems. *Austral Ecology,* **35,** 665-
851   684.
852 IPCC (2021) IPCC, 2021: Climate Change 2021: The Physical Science Basis.
853   Contribution of Working Group I to the Sixth Assessment Report of the
854   Intergovernmental Panel on Climate Change (eds V. Masson-Delmotte, P.
855   Zhai, A. Pirani, C. Connor, C. Péan, S. Berger, N. Caud, Y. Chen, L.
856   Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews,
857   T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu & B. Zhou).
858 Jiang, M., Medlyn, B.E., Drake, J.E., Duursma, R.A., Anderson, I.C., Barton,
859   C.V.M., Boer, M.M., Carrillo, Y., Castañeda-Gómez, L., Collins, L., Crous,
860   K.Y., De Kauwe, M.G., Emmerson, K.M., Facey, S.L., Gherlenda, A.N.,
861   Gimeno, T.E., Hasegawa, S., Johnson, S.N., Macdonald, C.A., Mahmud,
862   K., Moore, B.D., Nazaries, L., Nielsen, U.N., Noh, N.J., Ochoa-Hueso, R.,
863   Pathare, V.S., Pendall, E., Pineiro, J., Powell, J.R., Power, S.A., Reich, P.B.,
864   Renchon, A.A., Riegler, M., Rymer, P., Salomón, R.L., Singh, B.K., Smith,
865   B., Tjoelker, M.G., Walker, J.K.M., Wujeska-Klause, A., Yang, J., Zaehle,

866   S. & Ellsworth, D.S. (2020) The fate of carbon in a mature forest under
867   carbon dioxide enrichment. *Nature,* **580,** 227-231.

868 Keith, D.A. (2004) *Ocean shores to desert dunes: the native vegetation of New*
869   *South Wales and ACT.* Department of Environment and Conservation NSW,
870   Hurstville NSW 2220.

871 Kelly, J.W., Duursma, R.A., Atwell, B.J., Tissue, D.T. & Medlyn, B.E. (2016)
872   Drought x CO2 interactions in trees: a test of the low-intercellular CO2
873   concentration (Ci) mechanism. *New Phytol,* **209,** 1600-1612.

874 Kruschke, J.K. (2015) *Markov Chain Monte Carlo. Doing Bayesian data analysis:*
875   *a tutorial with R, JAGS, and Stan, 2nd edn,* 2 edn. Academic Press,
876   Cambridge.

877 Lawes, M.J. & Clarke, P.J. (2011) Ecology of plant resprouting: populations to
878   community responses in fire-prone ecosystems. *Plant Ecology,* **212,** 1937-
879   1943.

880 Lewis, J.D., Phillips, N.G., Logan, B.A., Hricko, C.R. & Tissue, D.T. (2011) Leaf
881   photosynthesis, respiration and stomatal conductance in six *Eucalyptus*
882   species native to mesic and xeric environments growing in a common
883   garden. *Tree Physiol,* **31,** 997-1006.

884 Lewis, J.D., Smith, R.A., Ghannoum, O., Logan, B.A., Phillips, N.G. & Tissue,
885   D.T. (2013) Industrial-age changes in atmospheric [CO2] and temperature
886   differentially alter responses of faster- and slower-growing *Eucalyptus*
887   seedlings to short-term drought. *Tree Physiol,* **33,** 475-488.

888 Liu, G., Shevliakova, E., Artaxo, P., De Noblet-Ducoudré, N., Houghton, R.,
889   House, J., Kitajima, K., Lennard, C., Popp, A., Sukumar, R. & Verchot, L.
890   (2019) IPCC Special Report: Climate Change and Land. *Chapter 2: Land-*
891   *Climate Interactions* (eds P.Y. Bernier, J.C. Espinoza & S. Semenov), pp.
892   186. IPCC, Geneva, Switzerland.

893 Macinnis-Ng, C., Zeppel, M., Williams, M. & Eamus, D. (2011) Applying a SPA
894   model to examine the impact of climate change on GPP of open woodlands
895   and the potential for woody thickening. *Ecohydrology,* **4,** 379-393.

896 Manea, A. & Leishman, M.R. (2015) Competitive interactions between established
897   grasses and woody plant seedlings under elevated CO(2) levels are mediated
898   by soil water availability. *Oecologia,* **177,** 499-506.

899 Matusick, G., Ruthrof, K., Fontaine, J.B. & Hardy, G.E.S.J. (2016) *Eucalyptus*
900   forest shows low structural resistance and resilience to climate change-type
901   drought. *Journal of Vegetation Science,* **27,** 493-503.

902 Matusick, G., Ruthrof, K.X., Brouwers, N.C., Dell, B. & Hardy, G.S.J. (2013)
903   Sudden forest canopy collapse corresponding with extreme drought and
904   heat in a mediterranean-type eucalypt forest in southwestern Australia.
905   *European Journal of Forest Research,* **132,** 497-510.

906 Merchant, A., Callister, A., Arndt, S., Tausz, M. & Adams, M. (2007) Contrasting
907   physiological responses of six *Eucalyptus* species to water deficit. *Ann Bot,*
908   **100,** 1507-1515.

909 Merchant, A., Tausz, M., Arndt, S.K. & Adams, M.A. (2006) Cyclitols and
910   carbohydrates in leaves and roots of 13 E*ucalyptus* species suggest
911   contrasting physiological responses to water deficit. *Plant Cell Environ,* **29,**
912   2017-2029.

913 Murphy, B.P., Bradstock, R.A., Boer, M.M., Carter, J., Cary, G.J., Cochrane, M.A.,
914   Fensham, R.J., Russell-Smith, J., Williamson, G.J., Bowman, D.M.J.S. &

915 Ladiges, P. (2013) Fire regimes of Australia: a pyrogeographic model
916   system. *Journal of Biogeography,* **40,** 1048-1058.
917 Ngugi, M.R., Hunt, M.A., Doley, D., Ryan, P. & Dart, P. (2004) Selection of
918   species and provenances for low-rainfall areas: physiological responses of
919   *Eucalyptus cloeziana* and *Eucalyptus argophloia* to seasonal conditions in
920   subtropical Queensland. *Forest Ecology and Management,* **193,** 141-156.
921 Nicolle, D. (2006) A classification and census of regenerative strategies in the
922   eucalypts (*Angophora, Corymbia* and *Eucalyptus*—Myrtaceae), with
923   special reference to the obligate seeders. *Australian Journal of Botany,* **54,**
924   391.
925 Niekerk, J.V., Bekker, A. & Arashi, M. (2019) Beta regression in the presence of
926   outliers - A wieldy Bayesian solution. *Stat Methods Med Res,* **28,** 3729-
927   3740.
928 Nolan, R.H., Collins, L., Leigh, A., Ooi, M.K.J., Curran, T.J., Fairman, T.A., Resco
929   de Dios, V. & Bradstock, R. (2021) Limits to post-fire vegetation recovery
930   under climate change. *Plant Cell Environ***,** 1-19.
931 Nolan, R.H., Rahmani, S., Samson, S.A., Simpson-Southward, H.M., Boer, M.M.
932   & Bradstock, R.A. (2020) Bark attributes determine variation in fire
933   resistance in resprouting tree species. *Forest Ecology and Management,*
934   **474,** 118385.
935 Norby, R.J., Todd, D.E., Fults, J. & Johnson, D.W. (2001) Allometric determination
936   of tree growth in a CO2-enriched sweetgum stand. *New Phytol,* **150,** 477-
937   487.
938 Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E. & McMurtrie, R.E. (2010)
939   CO2 enhancement of forest productivity constrained by limited nitrogen
940   availability. *Proc Natl Acad Sci U S A,* **107,** 19368-19373.
941 NPWS (2004) Fire Management Strategy Blue Mountains National Park. pp. 74.
942   New South Wales National Parks and Wildlife Service, NSW, Australia.
943 Osório, J., Osório, M.L., Chaves, M.M. & Pereira, J.S. (1998) Water deficits are
944   more important in delaying growth than in changing patterns of carbon
945   allocation in *Eucalyptus globulus. Tree Physiology,* **18,** 363-373.
946 Pausas, J.G., Lamont, B.B., Paula, S., Appezzato-da-Gloria, B. & Fidelis, A. (2018)
947   Unearthing belowground bud banks in fire-prone ecosystems. *New Phytol,*
948   **217,** 1435-1448.
949 Plummer, M., Stukalov, A. & Denwood, M. (2019) Bayesian Graphical Models
950   using MCMC. pp. Interface to the JAGS MCMC library.
951 Polley, H.W., Mayeux, H.S., Johnson, H.B. & Tischler, C.R. (1997) Viewpoint:
952   atmospheric CO2, soil water, and shrub/grass ratios on rangelands. *Journal*
953   *of Range Management,* **50,** 278-284.
954 Poorter, H. & Nagel, O. (2000) The role of biomass allocation in the growth
955   response of plants to different levels of light, CO2, nutrients and water: a
956   quantitative review. *Australian Journal of Plant Physiology,* **27,** 595-607.
957 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and
958   consequences of variation in leaf mass per area (LMA): a meta-analysis.
959   *New Phytologist,* **182,** 565-588.
960 Prior, L.D., Murphy, B.P. & Russell-Smith, J. (2009) Environmental and
961   demographic correlates of tree recruitment and mortality in north Australian
962   savannas. *Forest Ecology and Management,* **257,** 66-74.

963 Resco de Dios, V., Loik, M., Smith, R. & Tissue, D. (2018) Effects of a Heat Wave
964   on Nocturnal Stomatal Conductance in Eucalyptus camaldulensis. *Forests,*
965   **9**.
966 Roden, J.S. & Ball, M.C. (1996) Growth and photosynthesis of two eucalypt species
967   during high temperature stress under ambient and elevated [CO2] *Glob*
968   *Chang Biol,* **2,** 115-128.
969 Rosas, T., Galiano, L., Ogaya, R., Penuelas, J. & Martinez-Vilalta, J. (2013)
970   Dynamics of non-structural carbohydrates in three Mediterranean woody
971   species following long-term experimental drought. *Front Plant Sci,* **4,** 400.
972 Schall, P., Lödige, C., Beck, M. & Ammer, C. (2012) Biomass allocation to roots
973   and shoots is more sensitive to shade and drought in European beech than
974   in Norway spruce seedlings. *Forest Ecology and Management,* **266,** 246-
975   253.
976 Souza, J.P., Melo, N.M.J., Halfeld, A.D., Vieira, K.I.C. & Rosa, B.L. (2019)
977   Elevated atmospheric CO2 concentration improves water use efficiency and
978   growth of a widespread Cerrado tree species even under soil water deficit.
979   *Acta Botanica Brasilica,* **33,** 425-436.
980 Susiluoto, S. & Berninger, F. (2007) Interactions between morphological and
981   physiological drought responses in *Eucalyptus microtheca. Silva Fennica,*
982   **41**.
983 Suzuki, M. (2019) Bayesian modeling of volatile organic compound emissions
984   from three softwoods in Hokkaido, Japan. *Journal of Wood Science,* **65**.
985 Team, R.C. (2020) R: A language and environment for statistical computing. R
986   Foundation for Statistical Computing, Vienna, Austria.
987 Thomas, D.S. (2009) Survival and growth of drought hardened *Eucalyptus pilularis*
988   Sm. seedlings and vegetative cuttings. *New Forests,* **38,** 245-259.
989 Walker, A.P., De Kauwe, M.G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling,
990   R.F., McMahon, S.M., Medlyn, B.E., Moore, D.J.P., Norby, R.J., Zaehle,
991   S., Anderson-Teixeira, K.J., Battipaglia, G., Brienen, R.J.W., Cabugao,
992   K.G., Cailleret, M., Campbell, E., Canadell, J.G., Ciais, P., Craig, M.E.,
993   Ellsworth, D.S., Farquhar, G.D., Fatichi, S., Fisher, J.B., Frank, D.C.,
994   Graven, H., Gu, L., Haverd, V., Heilman, K., Heimann, M., Hungate, B.A.,
995   Iversen, C.M., Joos, F., Jiang, M., Keenan, T.F., Knauer, J., Korner, C.,
996   Leshyk, V.O., Leuzinger, S., Liu, Y., MacBean, N., Malhi, Y., McVicar,
997   T.R., Penuelas, J., Pongratz, J., Powell, A.S., Riutta, T., Sabot, M.E.B.,
998   Schleucher, J., Sitch, S., Smith, W.K., Sulman, B., Taylor, B., Terrer, C.,
999   Torn, M.S., Treseder, K.K., Trugman, A.T., Trumbore, S.E., van Mantgem,
1000   P.J., Voelker, S.L., Whelan, M.E. & Zuidema, P.A. (2021) Integrating the
1001   evidence for a terrestrial carbon sink caused by increasing atmospheric
1002   CO2. *New Phytol,* **229,** 2413-2445.
1003 Walker, A.P., De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Iversen, C.M., Asao, S.,
1004   Guenet, B., Harper, A., Hickler, T., Hungate, B.A., Jain, A.K., Luo, Y., Lu,
1005   X., Lu, M., Luus, K., Megonigal, J.P., Oren, R., Ryan, E., Shu, S., Talhelm,
1006   A., Wang, Y.P., Warren, J.M., Werner, C., Xia, J., Yang, B., Zak, D.R. &
1007   Norby, R.J. (2019) Decadal biomass increment in early secondary
1008   succession woody ecosystems is increased by CO2 enrichment. *Nat*
1009   *Commun,* **10,** 454.
1010 Walters, J.R., Bell, T.L. & Read, S. (2005) Intra-specific variation in carbohydrate
1011   reserves and sprouting ability in *Eucalyptus obliqua* seedlings. *Australian*
1012   *Journal of Botany,* **53,** 195.

1013 Wigley, B.J., Cramer, M.D. & Bond, W.J. (2009) Sapling survival in a frequently
1014   burnt savanna: mobilisation of carbon reserves in *Acacia karroo*. *Plant*
1015   *Ecology,* **203,** 1-11.
1016 Zeppel, M.J.B., Harrison, S.P., Adams, H.D., Kelley, D.I., Li, G., Tissue, D.T.,
1017   Dawson, T.E., Fensham, R., Medlyn, B.E., Palmer, A., West, A.G. &
1018   McDowell, N.G. (2015) Drought and resprouting plants. *New Phytologist,*
1019   **206,** 583-589.
1020 Zhang, X. & Wang, W. (2015) The decomposition of fine and coarse roots: their
1021   global patterns and controlling factors. *Scientific Reports,* **5**.
1022 Zhou, S.X., Medlyn, B.E. & Prentice, I.C. (2016) Long-term water stress leads to
1023   acclimation of drought sensitivity of photosynthetic capacity in xeric but
1024   not riparian *Eucalyptus* species. *Ann Bot,* **117,** 133-144.
1025 Zhu, Z., Piao, S., Myneni, R.B., Huang, M., Zeng, Z., Canadell, J.G., Ciais, P.,
1026   Sitch, S., Friedlingstein, P., Arneth, A., Cao, C., Cheng, L., Kato, E., Koven,
1027   C., Li, Y., Lian, X., Liu, Y., Liu, R., Mao, J., Pan, Y., Peng, S., Peñuelas,
1028   J., Poulter, B., Pugh, T.A.M., Stocker, B.D., Viovy, N., Wang, X., Wang,
1029   Y., Xiao, Z., Yang, H., Zaehle, S. & Zeng, N. (2016) Greening of the Earth
1030   and its drivers. *Nature Climate Change,* **6,** 791-795.
1031