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11 **Early vigour in wheat: could it lead to more severe terminal drought stress under elevated**
12 **atmospheric [CO₂] and semi-arid conditions?**

13

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42 **Abstract**

43 Early vigour in wheat is a trait that has received attention for its benefits reducing evaporation from
44 the soil surface early in the season. However, with the growth enhancement common to crops
45 grown under elevated atmospheric CO₂ concentrations (e[CO₂]), there is a risk that too much early
46 growth might deplete soil water and lead to more severe terminal drought stress in environments
47 where production relies on stored soil water content. If this is the case, the incorporation of such a
48 trait in wheat breeding programs might have unintended negative consequences in the future,
49 especially in dry years. We used selected data from cultivars with proven expression of high and low
50 early vigour from the Australian Grains Free Air CO₂ Enrichment (AGFACE) facility, and
51 complemented this analysis with simulation results from two crop growth models which differ in the
52 modelling of leaf area development and crop water use. Grain yield responses to e[CO₂] were lower
53 in the high early vigour group compared to the low early vigour group, and although these
54 differences were not significant, they were corroborated by simulation model results. However, the
55 simulated lower response with high early vigour lines was not caused by an earlier or greater
56 depletion of soil water under e[CO₂] and the mechanisms responsible appear to be related to an
57 earlier saturation of the radiation intercepted. Whether this is the case in the field needs to be
58 further investigated. In addition, there was some evidence that the timing of the drought stress
59 during crop growth influenced the effect of e[CO₂] regardless of the early vigour trait. There is a
60 need for FACE investigations of the value of traits for drought adaptation to be conducted under

61 more severe drought conditions and variable timing of drought stress, a risky but necessary
62 endeavour.

63

64 Keywords: physiological pre-breeding, climate change adaptation, model intercomparison, *Triticum*
65 *aestivum*, drought adaptive traits.

66

67 Abbreviations: atmospheric carbon dioxide concentration ($[\text{CO}_2]$); elevated atmospheric carbon
68 dioxide concentration ($e[\text{CO}_2]$); environment type (ET); genotype by environment by management
69 interaction (GxExM); harvest index (HI); leaf area index (LAI); specific leaf area (SLA)

70 **Introduction**

71 Atmospheric CO_2 concentrations ($[\text{CO}_2]$) have been increasing from about 280 ppm to more than 400
72 ppm from the pre-industrial era until now. If global greenhouse gas emissions remain at the 2010
73 level, then atmospheric $[\text{CO}_2]$ will reach 550 ppm by 2050 (IPCC, 2014). For C3 crops like wheat, this
74 considerable increase in the substrate of photosynthesis leads to higher growth rates, better water
75 use efficiency and larger yields in the absence of temperature or rainfall changes (Leakey *et al.*,
76 2009). Because $e[\text{CO}_2]$ reduces stomatal conductance, and therefore increases transpiration
77 efficiency, the response to elevated CO_2 ($e[\text{CO}_2]$) has often been reported to be greater under
78 conditions of water stress and/or in semi-arid environments (Fitzgerald *et al.*, 2016; Leakey *et al.*,
79 2009; Gifford 1979). However, there are also recent reports that seem to indicate the contrary (Gray
80 *et al.*, 2016) or that there are no consistent differences (van der Kooi *et al.*, 2016), leading some to
81 suggest the response to $e[\text{CO}_2]$ might depend on the timing of the drought experienced by the crop
82 (Bourgault *et al.*, 2017). The relationships between timing and extent of drought and trade-offs
83 between biomass stimulation and leaf level water use efficiency gains have been shown to be
84 especially important in highly variable, semi-arid or Mediterranean field conditions (Tausz-Posch *et*
85 *al.*, 2019).

86

87 Early vigour, defined as a larger leaf area early in the season, is a trait that has recently received
88 attention for its benefits under Mediterranean environments where intermittent, low rainfall
89 conditions prevail (Rebetzke and Richards, 1999). The greater cover reduces evaporation from the
90 soil surface and this water is then available for transpiration. Early vigour in wheat is associated with
91 greater early root development, greater early nitrogen uptake and higher photosynthetic nitrogen
92 use efficiency (Pang *et al.*, 2014), and appears to be partially achieved through a larger specific leaf
93 area (SLA) early in the development of the plant (Rebetzke *et al.*, 2004). Multi-regional field trials
94 have shown that the value of the trait is more important in areas that receive frequent small rainfall

95 events during the growing season, but is not as useful in areas that depend on stored soil water
96 (Wilson *et al.*, 2015).
97
98 If crop traits affect the response to $e[\text{CO}_2]$ in crops, it might be possible to take advantage of rising
99 atmospheric $[\text{CO}_2]$ by selecting for greater responsiveness in crop breeding programmes either
100 directly or by selecting traits that are associated with a greater response (Ainsworth *et al.*, 2008;
101 Ziska *et al.*, 2012; Tausz *et al.*, 2013). On the other hand, there could also be drought adaptive traits
102 that, by modifying growth patterns in time, might negatively impact the response to $e[\text{CO}_2]$
103 (Bourgault *et al.*, 2013). Considering crop breeding takes 10-20 years to release cultivars, it is
104 important to evaluate future environmental conditions, such as increased $[\text{CO}_2]$ on their relative
105 performance. On the one hand, larger leaf area early in crop development leads to greater
106 photosynthesis and lower evaporation from the soil surface. It is possible therefore that early vigour
107 lines might benefit more than low vigour lines from the effects of $e[\text{CO}_2]$, as they may carry an early
108 benefit in both carbon gain and increased transpiration efficiency throughout the season. On the
109 other hand, depending on the result of the competing effects of increased transpiration efficiency
110 and lower evaporation compared to the higher water use of the larger leaf area development, too
111 much growth early in the season could deplete the soil profile of water before grain filling. In
112 environments where crops depend on stored water, this would lead to severe terminal drought
113 stress (Nuttall *et al.*, 2012), analogue to the “haying-off” phenomenon observed in response to
114 excess early N fertilizer application (van Herwaarden *et al.*, 1998). This could therefore negate some
115 of the benefits from $e[\text{CO}_2]$ under terminal drought but not under well-watered conditions or more
116 moderate types of drought. We would thus expect that the benefits of this trait and its impact on
117 the response to $e[\text{CO}_2]$ might depend on the seasonal pattern of water availability.
118
119 Crop simulation models are particularly useful to investigate genotype by environment (GxE)
120 interactions that are difficult to test experimentally and for climate scenarios that are not yet
121 realised. Field and controlled environment experiments testing pairs of lines differing in traits such
122 as tillering propensity, early vigour or water soluble carbohydrate accumulation in wheat have rarely
123 been able to detect genotypic differences in the response to $e[\text{CO}_2]$ (Bourgault *et al.*, 2013; Tausz-
124 Posch *et al.*, 2015). This trait by $[\text{CO}_2]$ interaction, if it exists, may be masked by large GxE variability
125 related to environmental factors other than changes in $[\text{CO}_2]$ and by background genetic differences
126 not related to the trait being evaluated. This makes the occurrence of Type II statistical errors highly
127 likely where true differences are not detected as significant. While this risk can be minimised by
128 more elaborate and expensive experimental designs, complementing field data with simulation

129 results can help explore GxE or, in this case, Gx[CO₂]xE interactions and can offer additional insights
130 regarding likely interactive mechanisms between physiological traits and environmental factors,
131 information that is useful to breeders. They can also deliver information about variables that are not
132 typically observed and highlight further research questions to evaluate in the field. However,
133 comparison against measured data is still fundamental to validate findings and improve crop models
134 (Boote and Sinclair, 2006; Fischer, 2011).

135

136 Because drought as an environmental factor can have vastly different effects on crop growth based
137 on its timing and intensity, more refined analyses of the E component of the GxE interaction might
138 be needed. For example, Chenu *et al.* (2013) clustered wheat growing seasons for various locations
139 across Australia into four environment types (ET) based on the ratio of crop water demand met by
140 the soil water supply. The four environment types described four different drought patterns: no
141 stress or negligible stress (ET1), moderate water stress post-anthesis (ET2), moderate to severe
142 water stress beginning before anthesis but relieved during grain filling (ET3), or that continued
143 through to maturity as a severe terminal drought (ET4). Because of the various feedback
144 mechanisms between crop growth and the environment, such characterisation is more useful in
145 exploring GxE interactions than aggregated meteorological data to understand the response to
146 stressful conditions and evaluate the usefulness of adaptive traits (Chenu *et al.*, 2013).

147

148 The objective of this study was to evaluate the response to e[CO₂] of wheat lines that differed in
149 early vigour under semi-arid conditions, and whether this was influenced by seasonal patterns of
150 water availability. Specifically, we hypothesised that the greater increase in leaf area development in
151 high early vigour lines grown under e[CO₂] would lead to more water use pre-anthesis and
152 subsequently greater drought stress post-anthesis, therefore reducing the grain yield response to
153 e[CO₂], but only in severe terminal stress conditions of ET3 and ET4 environments as characterised
154 by Chenu *et al.* (2013). In order to do this, we identified a subset of lines grown in the Australian
155 Grains Free Air CO₂ Enrichment (AGFACE) research programme which included lines with proven
156 expression of high and low early vigour, and compare their response to e[CO₂]. We also extracted
157 from the experimental data variables needed to modify early leaf area development and model the
158 early vigour trait in two crop models: APSIM and SIMPLACE. We were then able to compare the
159 simulated response to e[CO₂] between high and low early vigour lines, but also to investigate the
160 water use dynamics between the two groups. We were thus able to answer the following questions:

161

1. Do simulations give us similar responses to e[CO₂] than the experimental data?

162

2. Does the response to e[CO₂] depend on the type of drought experienced by the crop?

163 3. Does e[CO₂] lead to more severe terminal drought stress in high vigour lines?
164 The experimental and simulation results showed that the response to e[CO₂] of high early vigour
165 lines was indeed lower, but greater water use pre-anthesis under e[CO₂] was not associated with the
166 early vigour trait. Therefore, we further asked:

167 4. How else could we explain the lower response to e[CO₂] in high early vigour lines?
168

169 **Materials and Methods**

170 *AGFACE Experiment*

171 The Australian Grains Free Air CO₂ Enrichment (AGFACE) facility was located near Horsham, Victoria
172 (36°45'07"S 142°06'52"E, 127 m above sea level). Long term average (based on 1981-2010 period)
173 annual rainfall is 435 mm, with approximately 320 mm falling during the winter growing season
174 (from May to November inclusively). Average maximum and minimum temperatures are 17.6°C and
175 5.3°C respectively during the season, with July being the coldest month (Bureau of Meteorology,
176 2016). Elevated CO₂ levels (target 550 mmol mol⁻¹ air) were maintained during daylight hours by
177 injecting pure CO₂ into the air on the upwind side from horizontal stainless-steel tubes so the gas
178 would be carried across the ring. Concentrations were maintained within 90% target (495-605 mmol
179 mol⁻¹ air) for 93-98% of the time. More details on the site and the CO₂ exposure equipment are given
180 in Mollah *et al.* (2009). Details about the general management of the experiment are also given in
181 O'Leary *et al.* (2015) and Fitzgerald *et al.* (2016).
182

183 The experimental design was a randomized complete block split-split-plot design with 4 ambient and
184 4 elevated CO₂ octagonal wheat plots organised in blocks each containing one ambient (a[CO₂]) and
185 one e[CO₂] main plot. In each year, a plus/minus supplemental irrigation treatment was usually
186 nested within each main plot, except in 2007 when time of sowing was nested as sub-plots, and
187 supplemental irrigation treatments were on separate main plots. There were two or more cultivars
188 grown inside each sub-plot. More details are available on the design and treatments in O'Leary *et al.*
189 (2015) and Fitzgerald *et al.* (2016) for 2007 to 2009, from Tausz-Posch *et al.* (2012, 2013, 2015) for
190 2009 to 2010 and in Houshmandhar *et al.* (2015) for 2013.
191

192 Initial soil water data was obtained from field samples collected before sowing in each main plot
193 using a hydraulic soil corer and the gravimetric method at 0-10, 10-20 and in 20 cm increments
194 thereafter up to 1.2 to 1.8 m depending on the year. These samples were averaged over the entire
195 site from 2007 to 2010 as main plots were moved, whereas from 2011 to 2013, these were averaged
196 over irrigation treatments as the main plots were rotated with field pea plots that were also subject

197 to a plus/minus supplemental irrigation treatment. Bulk density was calculated for each layer based
 198 on the site average and assumed constant throughout the experiment. Initial soil mineral nitrate
 199 concentrations were also obtained from field samples at depths of 0-10, 10-20, 20-60 cm on
 200 separate samples and averaged over the entire site in each year.

201
 202 Destructive harvests were performed at the first node stage, anthesis and maturity (DC31, DC65 and
 203 DC90 according to the scale by Zadoks *et al.* (1974); see Table 1 for dates) on pre-determined areas
 204 of 50 to 75 cm in length (depending on year and sampling) across 4 rows excluding edge rows (from
 205 2007 to 2009) or 5 rows including edge rows (from 2010-2013). The inclusion of edge rows is a
 206 source of increased experimental error, both in terms of increased variability and overestimation of
 207 treatment means (Rebetzke *et al.*, 2013), but we assumed that DC31 data, the calculated specific
 208 leaf area data, and mean biomass and yield responses to e[CO₂] were not affected. At DC31 and
 209 DC65, a subsample was taken from the biomass sample and separated into green leaves, dead
 210 leaves, stems and heads (if applicable), and leaf area was determined on this subsample (LI-3100C or
 211 LI-3000C with conveyor belt, LI-COR Biosciences, Lincoln, NE, USA). Leaf area of the quadrat
 212 harvested was extrapolated based on the ratio of the subsample biomass to the total quadrat
 213 biomass, and leaf area index (LAI) was calculated by dividing this by the quadrat area. Specific leaf
 214 area (SLA) was calculated by dividing the subsample leaf area by the subsample green leaf biomass.
 215 At DC90, samples were dried at 40 or 70°C depending on the year, but biomass and grain yield were
 216 calculated and presented on a 0% water content basis. Sampling dates are given for each cultivar
 217 and each year in Table 1.

218
 219

220 Table 1: Cultivars selected from AGFACE 2007-2013 with planting date, date of first node
 221 development (DC31), anthesis (DC65) and final harvest (DC90) samplings.

222

Cultivar	Vigour classification (see Figure 1)	Planting date	Stem elongation (DC31) sampling date	Anthesis (DC65) sampling date	Final harvest (DC90) sampling date
2007					
Janz	Low	18 Jun	6 Sept	29 Oct	12 Dec
Yitpi	Reference	18 Jun	6 Sept	29 Oct	12 Dec
2008					

Janz	Low	4 Jun	20 Aug	20 Oct	8 Dec
Yitpi	Reference	4 Jun	20 Aug	20 Oct	8 Dec
2009					
Hartog	High	23 Jun	2 Sept	27 Oct	4 Dec
Janz	Low	23 Jun	2 Sept	27 Oct	4 Dec
Yitpi	Reference	23 Jun	2 Sept	27 Oct	4 Dec
2010					
Hartog	High	27 May	5 Aug	18 Oct	9 Dec
Janz	Low	27 May	5 Aug	18 Oct	9 Dec
Yitpi	Reference	27 May	5 Aug	22 Oct	9 Dec
2011					
Janz	Low	25 May	1 Aug	12 Oct	5 Dec
SB062	High	25 May	1 Aug	12 Oct	5 Dec
SsrT65	Low	25 May	1 Aug	7 Oct	5 Dec
Yitpi	Reference	25 May	1 Aug	17 Oct	5 Dec
2012					
Janz	Low	30 May	15 Aug	18 Oct	5 Dec
SB062	High	30 May	15 Aug	15 Oct	5 Dec
SsrT65	Low	30 May	7 Aug	8 Oct	5 Dec
Yitpi	Reference	30 May	15 Aug	18 Oct	5 Dec
2013					
Bolac	Low	29 May	13 Aug	21 Oct	6 Dec
Spitfire	High	29 May	13 Aug	8 Oct	2 Dec
Yitpi	Reference	29 May	13 Aug	16 Oct	6 Dec

223

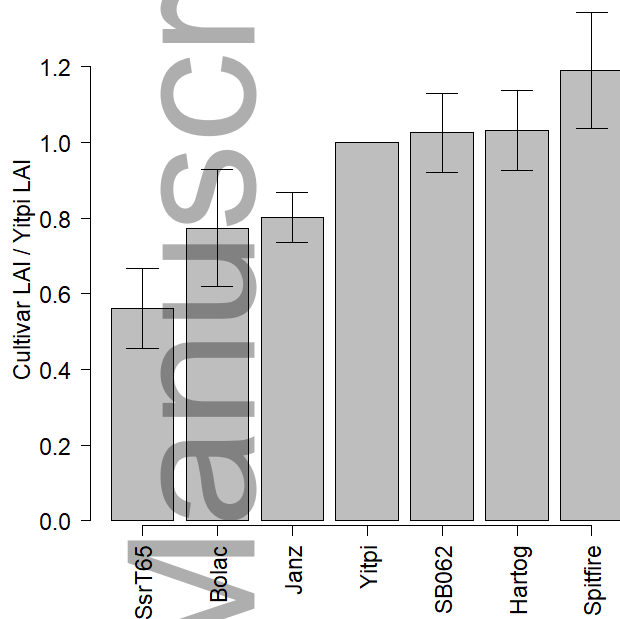
224

225 We restricted our analysis to include the reference cultivar “Yitpi” which was grown in every year
 226 from 2007 to 2013, as well as three cultivars which expressed high early vigour and three cultivars
 227 with low early vigour, based on LAI data collected at DC31 in AGFACE. In order to remove the effect
 228 of the year on LAI, we calculated the ratio of each cultivar LAI to the reference cultivar “Yitpi” under
 229 a[CO₂] for each year, and averaged this ratio across years if the cultivar was grown in more than one
 230 year (Figure 1). Efforts were made to select cultivar combinations that would span as many years as
 231 possible in the experimental data. The list of selected cultivars and years in which they were grown is

232 given in Table 1. The normalized LAI (or ratio to reference cultivar “Yitpi”) at DC31 was found to be
233 significantly different between the two groups ($p < 0.001$).

234

235 Figure 1: Ranking of cultivars for early vigour based on comparison with reference cultivar Yitpi leaf
236 area index (LAI) at the first node stage (DC31) in AGFACE 2007-2013 based on subsequent grouping
237 into low (< 1), and high (> 1) early vigour groups. Bars represent the average ratio of the cultivar leaf
238 area index (LAI) to Yitpi LAI across the years grown and are presented \pm standard errors.



239

240

241 *Statistical Analyses*

242 Given the design was slightly different across years, analyses were conducted separately for each
243 year with ASREML-R 3 (Butler *et al.*, 2009; R Core Team, 2017). The effects of $[CO_2]$, plus/minus
244 supplemental irrigation, and early vigour groups (or cultivars) were treated as fixed and Wald tests
245 were performed. Blocks, main plot number (nested within blocks), subplot number (nested within
246 plots) and sub-subplot number (nested within subplots) were considered random effects. Predicted
247 means were obtained for leaf area index at DC31 with the complete data set and used to select
248 cultivars that expressed high and low early vigour, as described above. Analyses of the response to
249 $e[CO_2]$ were performed using early vigour groups or cultivars depending on the question being
250 investigated.

251

252 *Simulation models*

253 APSIM-Wheat

254 The Agricultural Production Systems Simulator (APSIM version 7.8) is a modular modelling
255 simulation framework that employs a daily time step and has been extensively tested for wheat in
256 Australian conditions. APSIM modules consist of plant, soil and management modules that simulate
257 crop growth, soil water and nitrogen dynamics and various management controls (Holzworth *et al.*,
258 2014).

259
260 Growth is conceptualised as biomass accumulation from radiation intercepted, limited by water
261 deficit (if any) and modified by elevated [CO₂] (if applicable) and stress factors such as temperature
262 and nitrogen deficiency. The [CO₂] factor is calculated from the atmospheric CO₂ concentration and
263 temperature as published in Reyenga *et al.*, (1999). This growth is partitioned into roots, stems,
264 leaves and reproductive structures according to plant developmental stage. Wheat phenology is
265 based on thermal time accumulation for each of 11 predefined stages of development and modified
266 for cultivar-specific differences with photoperiod sensitivity and vernalisation sensitivity parameters.
267 Plant organ biomass and leaf area are initialised at emergence. The default value of the initial leaf
268 area is set at 200 mm² plant⁻¹. The daily increase in carbon-limited leaf area is calculated from the
269 increase in leaf dry weight and maximum specific leaf area which varies from 27000 to 22000 mm² g⁻¹
270 depending on leaf area index. The actual daily increase in leaf area is the minimum between the
271 carbon-limited leaf area and the stressed leaf area, which is a function of the potential increase in
272 leaf number and leaf size and modified by stress factors related to nitrogen deficiency and soil water
273 deficit effects on canopy expansion. Crop water demand is modelled as a function of the potential
274 daily biomass accumulation divided by the transpiration efficiency, which in turn is a function of the
275 average daylight vapour pressure deficit (VPD) and [CO₂], but capped at a factor of 1.5 of the
276 Priestly-Taylor potential evapotranspiration (E_o). The [CO₂] factor is calculated from a linear function
277 and is approximately 1.05 at 400 ppm, and 1.21 at 550 ppm. The VPD is estimated using daily
278 maximum and minimum temperatures according to Tanner and Sinclair (1983). The crop water
279 supply (or potential soil water uptake) is based on the approach by Monteith (1986) as the sum of
280 potential root water uptake from each profile layer where the rate of water extraction is determined
281 by the KL factor which varies by layer with crop species and soil type (Zheng *et al.*, 2015).

282 283 SIMPLACE

284 The SIMPLACE modeling framework (Gaiser *et al.*, 2013) was used to bring together the
285 aboveground growth and development aspects of the Lintul-5 crop growth model (Wolf, 2012), the
286 SlimWater3 water balance model based on SLIM (Addiscott and Whitmore, 1991), and modified to
287 use evaporation and crop water extraction functions from the FAO-56 ETo manual (Allen *et al.*,

288 1998), a heat stress reduction function (Gabaldón-Leal *et al.*, 2016) and a canopy temperature model
289 (Webber *et al.*, 2016). The resulting model configuration, SIMPLACE<Lintul5, SlimWater3, CanopyT,
290 HeatStressHourly> is further referred to as SIMPLACE.

291

292 In SIMPLACE, intercepted photosynthetically active radiation is converted to crop biomass by
293 multiplication with radiation use efficiency (RUE), which varies with phenological stage, mean
294 temperature, water and nutrient stress as well as atmospheric CO₂ concentration. At 400 ppm, the
295 [CO₂] factor is approximately 1.04 and 1.18 at 550 ppm. Daily biomass production is allocated to
296 roots, leaves, stems and grain yield with water stress increasing partitioning to roots. Phenological
297 development rates are driven by 24-hour mean temperatures, photoperiod and vernalization
298 requirements. Leaf area growth is initially exponential and later governed by the product of biomass
299 expansion and specific leaf area, which can vary with the phenological stage. Water stress is
300 conceptualized as the ratio of actual transpiration to potential transpiration, which is estimated as
301 the product of a reference crop evapotranspiration and the transpiration crop coefficient following
302 the FAO-56 dual crop coefficient methodology (Allen *et al.*, 1998). This is denoted TRANRF in
303 SIMPLACE outputs. Transpiration is also reduced linearly by 0.336% per ppm as ambient CO₂
304 concentrations increases (Zhao *et al.*, 2015). Daily crop water use is calculated as the minimum of
305 crop available water in the soil and potential transpiration.

306

307 *Cultivar-specific calibration*

308 In APSIM, cultivar values were available to determine time to anthesis and time to maturity for all
309 but two genotypes (SsrT65 and SB062). SsrT65 was given values of Silverstar based on its genetic
310 background and previous observations of similar phenology within AGFACE and elsewhere
311 (Bourgault *et al.*, 2013; Mitchell *et al.*, 2012). SB062 was given values identical to Yitpi based again
312 on observed values within AGFACE. In addition, the cultivar Bolac had additional parameters
313 associated with thermal time to flower initiation, flowering and grain filling. These were set to the
314 base cultivar values for a better fit with the experimental data. The values for the other genotypes
315 were checked against experimental data and deemed acceptable without modifications (Table 2;
316 Figure S1). The APSIM model was run without further calibration apart from modifications to
317 parameters to define the early vigour groups (see below). In SIMPLACE, thermal time to anthesis and
318 thermal time from anthesis to maturity were estimated from the experimental data (provided in
319 Table 2; see also Figure S1). The default values for biomass partitioning were also checked against
320 experimental data and deemed acceptable without modifications.

321

322 Table 2: Crop model phenological parameters for the cultivars used in this study.

	APSIM		SIMPLACE/Lintul5	
	photo_sens*	vern_sens*	TSUM1**	TSUM2**
Yitpi	3.0	1.5	850	750
Janz	2.2	2.9	800	750
SsrT65	1.5	1.5	750	750
Bolac	3.1	3.1	925	750
Hartog	3.0	1.5	850	750
SB062	3.0	1.5	850	750
Spitfire	3.0	1.5	850	750

323 * photo_sens and vern_sens are parameters in the APSIM wheat module that relate to photoperiod
 324 and vernalisation sensitivity, respectively. These modify thermal time parameters to extend or
 325 contract thermal time in early phases of crop development.

326 ** TSUM1 and TSUM2 in SIMPLACE-Lintul5 specify the thermal time requirements from emergence
 327 to anthesis and from anthesis to maturity, respectively, and are modified by both a response to
 328 photoperiod and a small vernalisation response.

329

330 *Modification of early leaf area development and vigour groups*

331 Early vigour was modified in APSIM by modifying the relationship between SLA and LAI. To obtain
 332 regression coefficients of the maximum SLA as a function of LAI as observed in AGFACE and compare
 333 this to APSIM model parameters, we fitted boundary lines on experimental data with quantile
 334 regression estimate of 0.95 using the “quantreg” package in R (Koenker, 2017). SIMPLACE uses SLA
 335 values as a function of crop development and these were therefore modified according to
 336 approximations of experimental data from AGFACE (Table 3). SLA values used by SIMPLACE are for
 337 newly expanded leaves and therefore some calibration was needed to arrive at the integrated SLA
 338 value at DC65. The differences in SLA at the DC31 and DC65 growth stages were in general well
 339 simulated by APSIM and SIMPLACE with the modifications we imposed (Figure S2). The modification
 340 of this one parameter in the models was sufficient to bring about the changes in leaf area index at
 341 DC31 and at DC65 that we observed in the experimental data (Figures S3 and S4).

342

343

344 Table 3: Specific Leaf Area (SLA, in $\text{cm}^2 \text{g}^{-1}$) differences between early vigour groups from selected cultivars in AGFACE (2007-2013) and translation of values
 345 into model inputs.

Cultivar/Group	APSIM		SIMPLACE										
	Calculated slope and intercept for 95 percentile of SLA ($\text{cm}^2 \text{g}^{-1}$) as a function of LAI	max SLA	SLA ($\text{cm}^2 \text{g}^{-1}$) at DC31	SLA ($\text{cm}^2 \text{g}^{-1}$) at DC65	SLATB (in $\text{m}^2 \text{g}^{-1}$)								
High vigour group	300 – 7x	<table border="1"> <tr> <th>LAI</th> <th>Max SLA ($\text{mm}^2 \text{g}^{-1}$)</th> </tr> <tr> <td>0.0</td> <td>30000</td> </tr> <tr> <td>5.0</td> <td>26000</td> </tr> </table>	LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)	0.0	30000	5.0	26000	224 ± 14	174 ± 12	DVS	SLA	
LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)												
0.0	30000												
5.0	26000												
					0.0	0.022							
					0.4	0.022							
					1.0	0.016							
					2.0	0.016							
Low vigour group	250 – 5x	<table border="1"> <tr> <th>LAI</th> <th>Max SLA ($\text{mm}^2 \text{g}^{-1}$)</th> </tr> <tr> <td>0.0</td> <td>25000</td> </tr> <tr> <td>5.0</td> <td>22000</td> </tr> </table>	LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)	0.0	25000	5.0	22000	191 ± 14	152 ± 12	DVS	SLA	
LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)												
0.0	25000												
5.0	22000												
					0.0	0.018							
					0.4	0.018							
					1.0	0.011							
					2.0	0.011							
Yitpi	256 – 5x	<table border="1"> <tr> <th>LAI</th> <th>Max SLA ($\text{mm}^2 \text{g}^{-1}$)</th> </tr> <tr> <td>0.0</td> <td>27000</td> </tr> <tr> <td>5.0</td> <td>22000</td> </tr> </table>	LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)	0.0	27000	5.0	22000	196 ± 14	155 ± 12	DVS	SLA	
LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)												
0.0	27000												
5.0	22000												
					0.0	0.019							
					0.4	0.019							
					1.0	0.012							

		(Default values)			2.0	0.012	
					(Default values)		

346

347 In APSIM, the maximum SLA parameter value is a function of the LAI, whereas in SIMPLACE, the SLA value (within the SLATB parameter) is a function of the
348 developmental stage (DVS), which varies from 0 to 2 (maturity), with 1 being anthesis.

349 *Simulation of AGFACE results*

350 Simulations were performed with all seven cultivars in the seven years investigated (2007-2013)
351 using weather data obtained on-site (MEA Premium Weather Station, Measurement Engineering
352 Australia, Magill, SA, Australia). Soil parameters related to the soil water lower limit, drained upper
353 limit and saturated water content, as well as other soil parameters necessary for running the two
354 models were taken from O'Leary *et al.* (2015) (Table S1). Four treatments were simulated
355 (plus/minus supplemental irrigation, a[CO₂]/e[CO₂] treatments) using the experimental planting
356 dates (Table 1), initial soil water content (Table S2), nitrate content (Table S3), and supplemental
357 irrigation water used in AGFACE (Table S4). For comparisons with experimental data, only
358 simulations with the cultivars grown in specific years were used. In addition, for DC31 data,
359 comparisons were conducted based on the date of sampling rather than the simulated growth stage.
360 To explore differences in simulated water use, all combinations were used to provide a balanced
361 comparison between high and low early vigour lines.

362

363 *Environmental characterisation*

364 In APSIM, for each simulation, the proportion of the crop water demand satisfied by the soil water
365 supply was calculated as a daily water stress index. This value was constrained between 0 and 1
366 where 1 represents 100% of the water demand satisfied by the available soil water content. The
367 daily water stress index value was aggregated over periods of 100°Cd (thermal time) centred at
368 anthesis, as presented in Chenu *et al.* (2013). Classification of each year by irrigation treatment by
369 [CO₂] by cultivar combination into an environment type was done by minimising the sums of squared
370 differences between the aggregated water stress index curve for each simulation and the water
371 stress index curves of the four environment types from Chenu *et al.* (2013)(Figure 2).

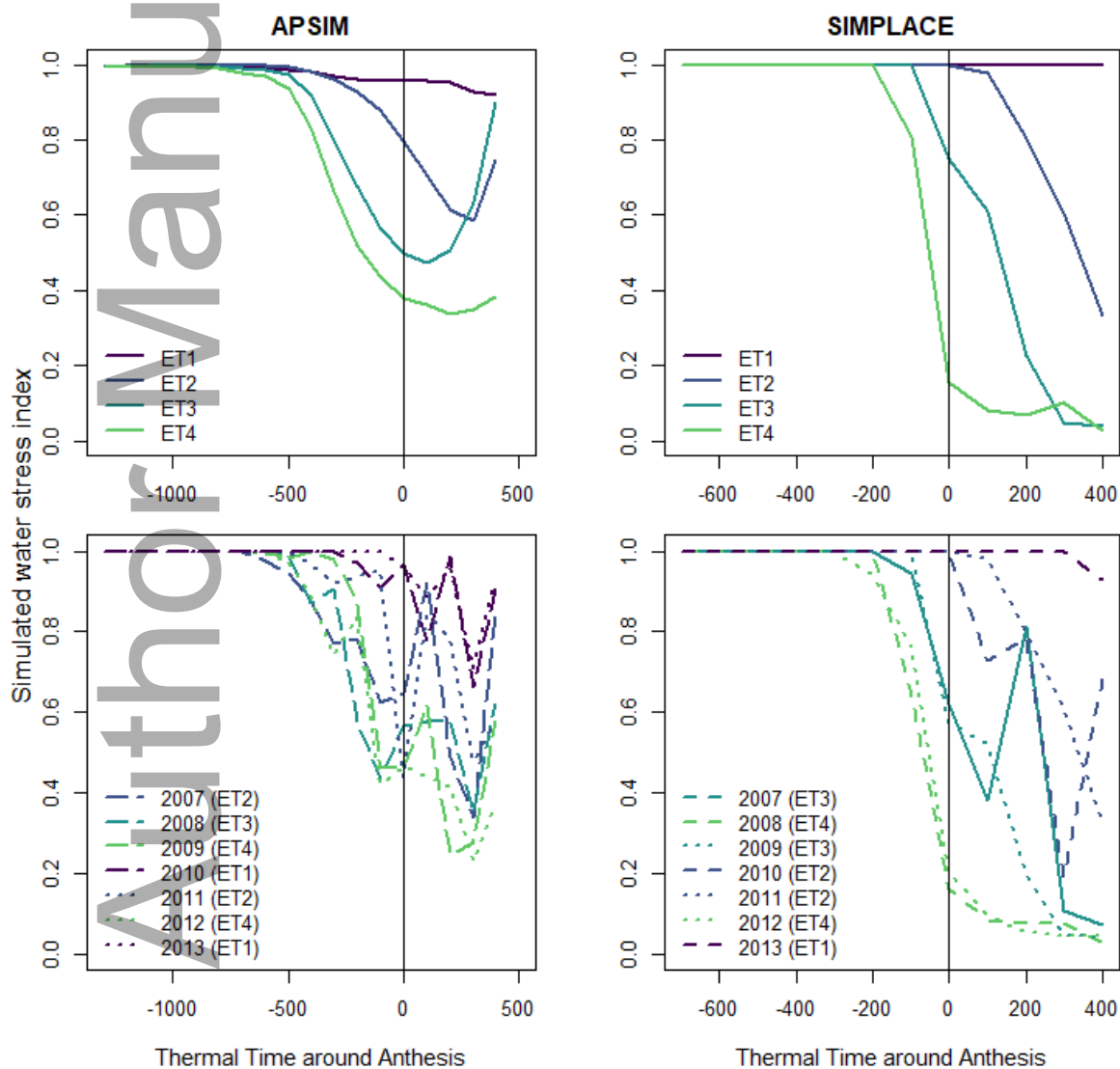
372

373 In SIMPLACE, the parameter TRANRF, which represents the ratio of actual transpiration to potential
374 transpiration, was similarly aggregated over 100°Cd and centred at anthesis. Since environmental
375 type curves were not easily transferable between the two models, we used the partitioning
376 clustering function *pam* from the *cluster* package in R (R Core Team, 2017) to define four
377 environmental types (adapted from Chenu *et al.*, 2013) based on the full set of simulations (i.e.
378 combinations of 7 cultivars, 7 years, a[CO₂]/e[CO₂] and plus/minus supplemental irrigation for a total
379 of 198 simulations). The results of the environment type clustering for both models (including curves
380 reproduced from Chenu *et al.*, 2013) are presented in Figure 2 (top row). Examples of the
381 environmental characterisation based on the reference cultivar Yitpi under a[CO₂] and rainfed
382 conditions are also presented (Figure 2; bottom row).

383

384

385 Figure 2: Environmental characterisation from modelling outputs. Top row refers to clusters
386 identifying environmental types, while bottom row shows patterns of simulated water stress for the
387 reference cultivar Yitpi under ambient [CO₂] and rainfed conditions. This water stress index was
388 calculated in APSIM (left) from the ratio of the soil water supply to crop water demand (with an
389 upper bound of 1), while the water stress index in SIMPLACE (right) is the ratio of actual
390 transpiration to potential transpiration (TRANRF parameter). A water stress index of 1 represents no
391 stress, while a value of 0 represents a situation where no soil water is available to the crop. Daily
392 ratios were aggregated over periods of 100°Cd thermal time centred at anthesis. The top left panel is
393 taken from Chenu *et al.*, 2013.



394

395

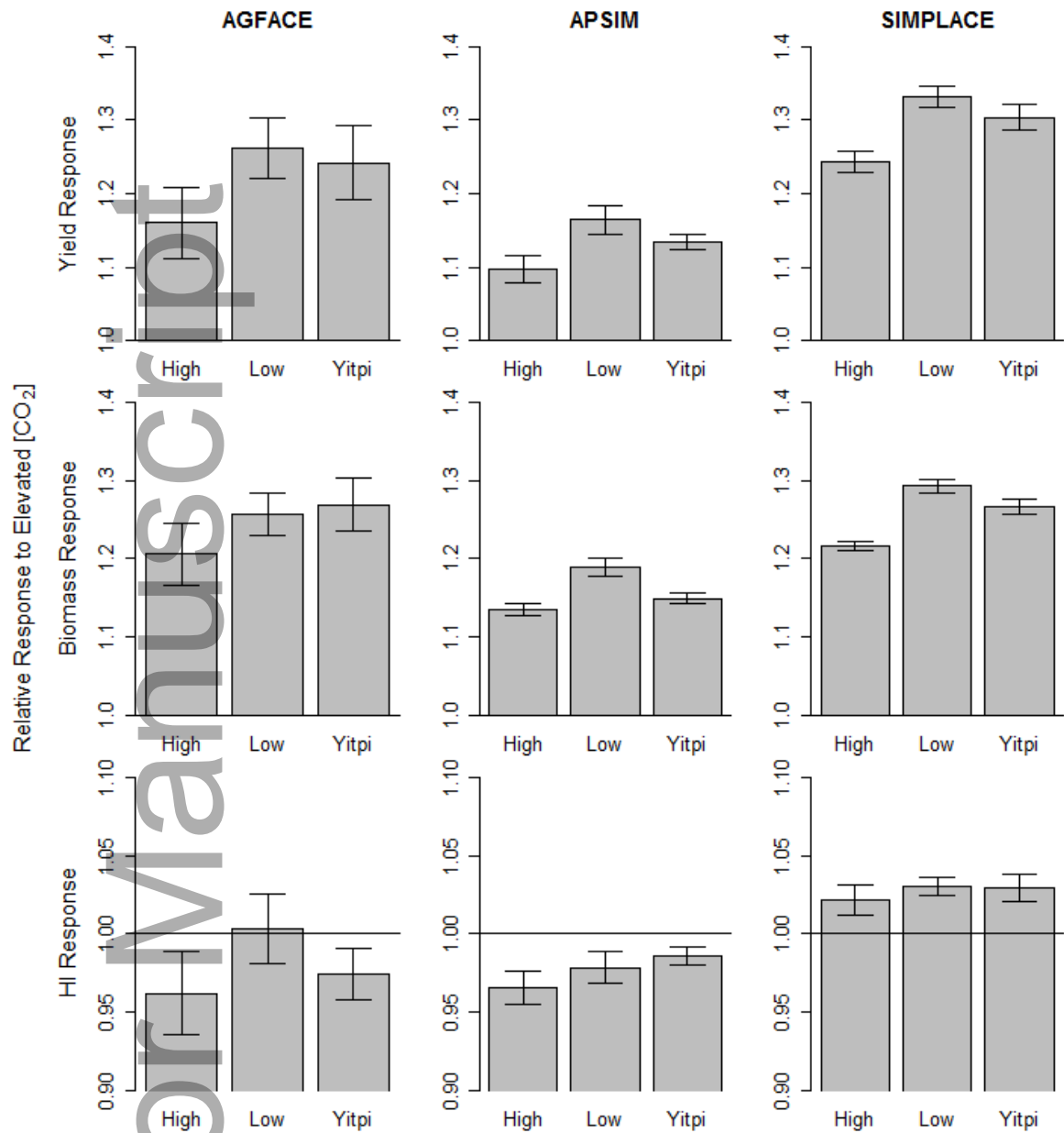
396 **Results**

397 *Do model simulations give us similar responses to e[CO₂] than the experimental data?*

398 Experimental results suggested that early vigour decreased the average grain yield response to
399 e[CO₂] with high early vigour lines showing a 16% mean increase compared to 26% increase for low
400 early vigour lines, although vigour group effects on the response were not statistically significant
401 (p=0.2879; Figure 3). The biomass response at maturity was similar to the grain yield response,
402 although with slightly higher mean values: 30% versus 39% for high and low early vigour lines,
403 respectively (p=0.4375; Figure 3). For the harvest index (HI), there is a small non-significant decrease
404 of 4% for high early vigour lines, but no change in low vigour lines (p=0.1644; Figure 3). Simulated
405 results from both APSIM and SIMPLACE showed similar trends to the experimental data. In APSIM,
406 the response to e[CO₂] was 10 and 16% for grain yield, and 13 and 19% for biomass at maturity for
407 high and low vigour, respectively. Results from SIMPLACE showed slightly higher values but similar
408 differences: 24 and 33% for grain yield, 22 and 29% for biomass at maturity (Figure 3). Although
409 SIMPLACE generally showed a slight increase in HI as a response to e[CO₂], rather than the slight
410 decrease observed in the experimental data and in APSIM simulation results, both models simulated
411 the small differences in the response of HI between high and low early vigour lines accurately (Figure
412 3).

413

414 Figure 3: Responses to elevated [CO₂] according to early vigour group (high, low, and the cultivar
415 Yitpi as reference) for yield, above-ground biomass at maturity (DC90) and harvest index (HI) in the
416 Australian Grains Free Air CO₂ Enrichment (AGFACE) facility in 2007-2013 (experimental data) and as
417 simulated by APSIM and SIMPLACE. Results presented are response means ± standard error of
418 means.



419
420

421 *Does the response to e[CO₂] depend on the type of drought experienced by the crop?*

422 As mentioned previously, the clustering of environment types was slightly different between the two
423 models (Figure 2), and therefore the environmental characterization also varied between the two
424 models. In general, however, both models followed the same trends, with SIMPLACE indicating more
425 stress than APSIM in 29 instances out of 84 year-cultivar-irrigation-[CO₂] combinations (Table 4).

426 Using the ET characterization from APSIM (under a[CO₂]), the experimental response to e[CO₂] for
427 grain yield and biomass at maturity was smaller in the most severe terminal stress conditions (ET4;
428 Figure 4, top left). This was not significant with the response in grain yield (p=0.1485), but was
429 significant with the biomass response (p=0.0296). The vigour group by ET interactions for these two

430 parameters were not statistically significant, but according to APSIM, the low stress environment
431 types ET1 and ET2 represented the large majority of instances, while ET3 and ET4 were only
432 experienced by Yitpi or high vigour lines (Table 4). Therefore, there were no experimental data for
433 low vigour lines in ET3 and ET4 to compare to high early vigour lines in these same environments. By
434 contrast, the ET characterization of experimental data with SIMPLACE did show instances of low
435 early vigour lines experiencing ET3 and ET4 environment types in the experimental data set (Table
436 4). However, the responses to e[CO₂] in grain yield and final biomass showed no differences
437 between the environment types (Figure 4 top right; p=0.9710 and p=0.7992 respectively). Similarly,
438 there were no early vigour group by ET interactions, so there were no significant differences in
439 response between high and low vigour lines in the more stressful environments.

440

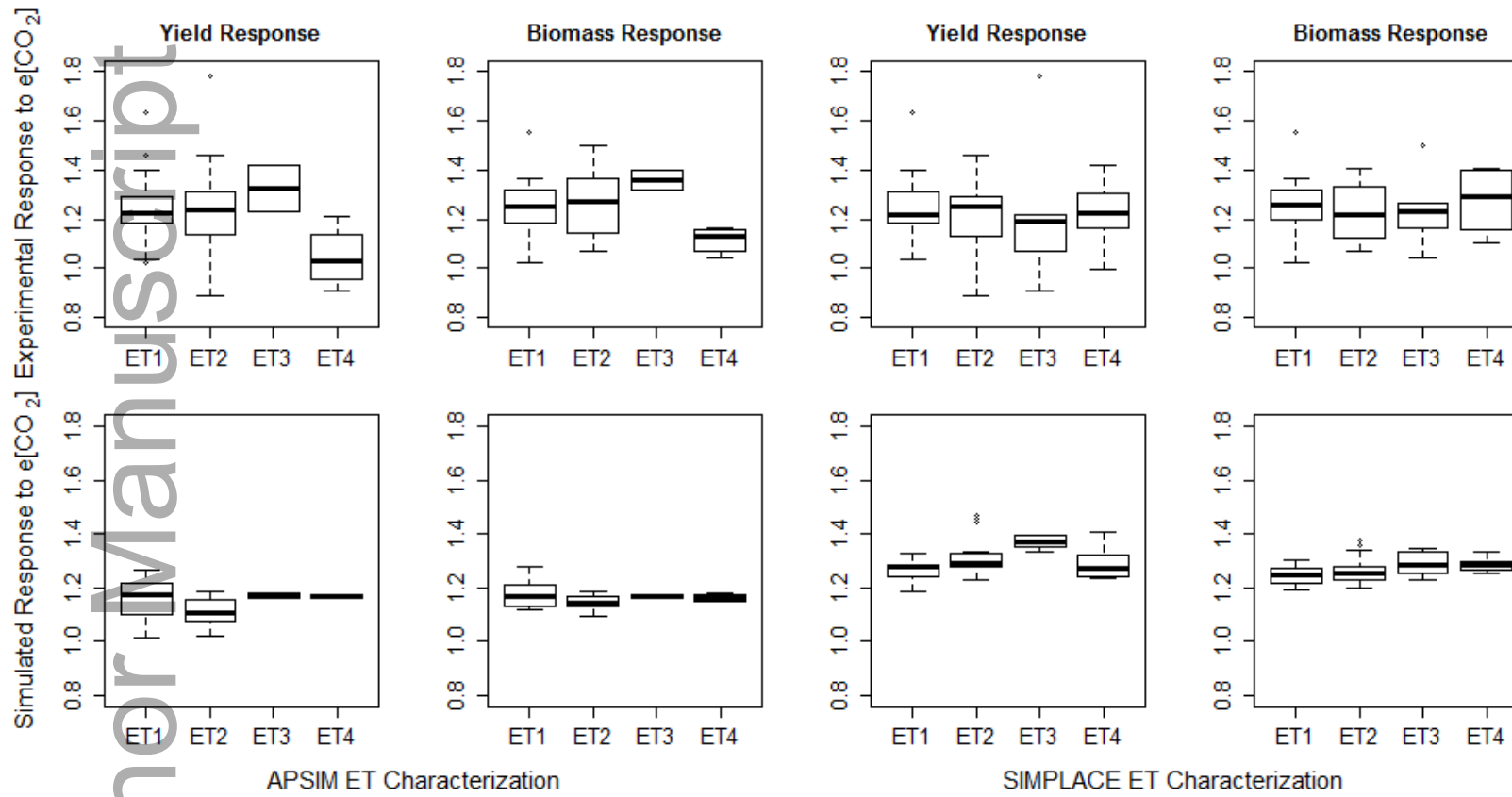
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441 Table 4: Environmental characterisation of AGFACE experimental data with APSIM and SIMPLACE simulations outputs, according to methodology by Chenu
 442 *et al.* (2013). The four environment types describe four different drought patterns: no stress or negligible stress (ET1), moderate water stress post-anthesis
 443 (ET2), moderate to severe water stress beginning before anthesis but relieved during grain filling (ET3), or that continued through to maturity as a severe
 444 terminal drought (ET4).

		APSIM Outputs				SIMPLACE Outputs			
		Rainfed		Supplemental		Rainfed		Supplemental	
Year	Cultivar	a[CO ₂]	e [CO ₂]	a[CO ₂]	e [CO ₂]	a[CO ₂]	e [CO ₂]	a[CO ₂]	e [CO ₂]
2007	Janz	ET2	ET2	ET2	ET2	ET2	ET2	ET2	ET2
	Yitpi	ET2	ET3	ET2	ET2	ET3	ET3	ET2	ET2
2008	Janz	ET2	ET2	ET2	ET2	ET4	ET4	ET3	ET3
	Yitpi	ET3	ET3	ET3	ET3	ET4	ET4	ET4	ET4
2009	Hartog	ET4	ET4	ET2	ET3	ET3	ET3	ET2	ET2
	Janz	ET2	ET2	ET2	ET2	ET3	ET3	ET2	ET2
	Yitpi	ET4	ET4	ET2	ET2	ET3	ET3	ET2	ET2
2010	Hartog	ET2	ET2	ET1	ET1	ET2	ET2	ET1	ET1
	Janz	ET1	ET1	ET1	ET1	ET2	ET2	ET1	ET1
	Yitpi	ET1	ET1	ET1	ET1	ET2	ET2	ET1	ET1
2011	Janz	ET2	ET2	ET1	ET1	ET2	ET2	ET1	ET1
	SB062	ET2	ET2	ET2	ET1	ET2	ET2	ET1	ET1
	SsrT65	ET1	ET1	ET1	ET1	ET1	ET1	ET1	ET1
	Yitpi	ET2	ET2	ET1	ET1	ET2	ET2	ET1	ET1

2012	Janz	ET2	ET2	ET1	ET2	ET4	ET3	ET2	ET2
	SB062	ET4	ET4	ET2	ET2	ET4	ET4	ET2	ET2
	SsrT65	ET1	ET1	ET1	ET1	ET3	ET3	ET1	ET1
	Yitpi	ET4	ET4	ET2	ET2	ET4	ET4	ET2	ET2
2013	Bolac	ET1	ET1	ET1	ET1	ET2	ET2	ET2	ET2
	Spitfire	ET1	ET1	ET1	ET1	ET1	ET1	ET1	ET1
	Yitpi	ET1	ET1	ET1	ET1	ET1	ET1	ET1	ET1

445 Figure 4: Experimental (top row) and simulated (bottom row) responses to elevated [CO₂] according to environment type (ET) for grain yield and above-
 446 ground biomass at maturity (DC90) in the Australian Grains Free Air CO₂ Enrichment (AGFACE) facility in 2007-2013 (experimental data) and as simulated by
 447 APSIM and SIMPLACE (with their respective ET characterization). Results are presented as boxplots, with the central line as the median, and the edges of
 448 the box as first and third quartiles.



450 The lower experimental response under ET4 with the APSIM ET characterization was not captured in
451 simulated yield results (Figure 4 bottom row). Using the full set of simulations (i.e. all 7 cultivars in all
452 7 years, with a[CO₂]/e[CO₂], and plus/minus supplemental irrigation (196 instances)), we were able
453 to simulate ET3 and ET4 environments experienced by low vigour lines (mostly with the longer-
454 season cultivar Bolac). Simulated yield and biomass accumulation at maturity with APSIM did not
455 show the lower response in ET4 (Figures S5 and S6 for yield and biomass response respectively)
456 observed in the experimental data. On the other hand, in this balanced set of simulated data, both
457 models simulated larger responses for low vigour lines compared to high vigour lines under ET1 and
458 ET2 environments (Figures S5 and S6). Differences in response were quite consistent between the
459 two models, despite using distinct clustering analyses.

460

461 *Does e[CO₂] lead to more severe terminal drought stress in high early vigour lines?*

462 Simulation results with both models suggested that in most cases, the savings from greater
463 transpiration efficiency and lower soil evaporation were more than enough to compensate for the
464 greater transpiration from the larger leaf area, so that pre-anthesis water use was generally lower
465 under e[CO₂]. When pre-anthesis water use was greater under e[CO₂], this was not necessarily
466 associated with high early vigour lines or with greater water stress post-anthesis. In APSIM, the only
467 instances (14 out of 98) when e[CO₂] led to greater water use pre-anthesis compared to growth at
468 a[CO₂] involved low vigour lines (Janz and SsrT65). This led to greater water stress post-anthesis in
469 the majority of cases (10/14 instances), but considering these all occurred in ET1 and ET2
470 environments, the stress was not important. For high vigour lines, e[CO₂] consistently led to more
471 soil water availability in the profile at anthesis: although transpiration pre-anthesis was consistently
472 greater with e[CO₂] due to the greater leaf area index, water savings from the lower soil surface
473 evaporation and greater transpiration efficiency were more than enough to compensate. In
474 SIMPLACE, pre-anthesis water use was greater in 16 instances in all vigour groups, but only 5 of
475 these led to greater post-anthesis water stress: one with a low vigour line (Janz), one with Yitpi and
476 three with high vigour lines (Hartog, SB062 and Spitfire). All these instances were characterized with
477 SIMPLACE as ET4 environment types. This could indicate a greater propensity, in some cases, for
478 e[CO₂] conditions to exacerbate drought stress in dry years, but the grain yield response to e[CO₂]
479 did not seem affected (Figure 4).

480

481 *How else could we explain the lower response to e[CO₂] in high early vigour lines?*

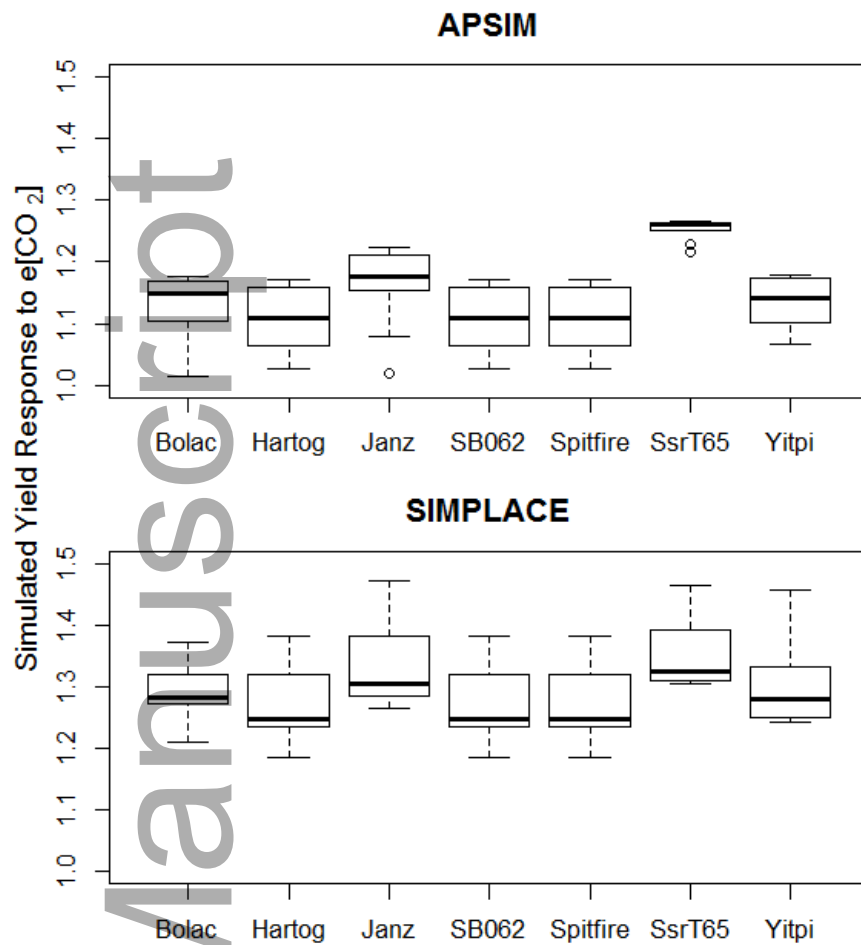
482 Cultivar differences in simulations for this study were limited to phenology and early vigour. Out of
483 the three selected low vigour cultivars in this study, SsrT65 and Janz are shorter-season than Yitpi

484 and high vigour lines, and phenology could therefore be a confounding factor: pre-anthesis and post-
485 anthesis drought stress would occur under different conditions in the same season depending on
486 when anthesis occurs. Based on the comparison between the three low vigour lines SsrT65, Janz and
487 Bolac (which only differed in phenology in the models), time to anthesis did have a substantial effect
488 on the simulated response to $e[\text{CO}_2]$ (Figure 5). Both models were consistent in showing a higher
489 response with a shorter time to anthesis. The comparison between high vigour lines and Yitpi (which
490 all have the same phenology) confirmed that early vigour also reduced the response to $e[\text{CO}_2]$. In
491 addition, the cultivar Bolac is a low vigour long-season cultivar which showed a larger grain yield
492 response than high vigour lines despite its long phenology. Clearly, both traits have effects on the
493 response to $e[\text{CO}_2]$ according to simulated results.

494

495 Figure 5: Simulated Responses to elevated $[\text{CO}_2]$ according to cultivars for grain yield in the
496 Australian Grains Free Air CO_2 Enrichment (AGFACE) facility in 2007-2013, including 7 cultivars across
497 7 years, plus/minus supplemental irrigation (therefore including combinations that did not occur
498 experimentally, but providing a balanced data set). Results are presented as boxplots, with the
499 central line as the median, and the edges of the box as first and third quartiles.

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500
501

502 We hypothesised high early vigour lines under e[CO₂] would respond with a greater increase in leaf
 503 area early in their development, which would lead to more water use pre-anthesis and greater
 504 drought stress post-anthesis, which would reduce the grain yield response to e[CO₂]. Models showed
 505 that a greater response in leaf area led to a greater increase in pre-anthesis water use and this led to
 506 more post-anthesis water stress with e[CO₂] in APSIM, but not in SIMPLACE (Figure S7). More post-
 507 anthesis water stress with e[CO₂] led to larger grain yield responses with APSIM, but smaller yield
 508 responses in SIMPLACE (Figure S8). In addition, models showed that low vigour lines, and not high
 509 vigour lines, responded with a larger pre-anthesis leaf area stimulation (Figure S7) and larger
 510 increases in radiation intercepted, and this was positively, rather than negatively, correlated with
 511 the grain yield response (Figure S8). The pre-anthesis response in radiation intercepted explained
 512 63% of the response in grain yield in APSIM and 50% in SIMPLACE. The simulated higher grain yield
 513 responses in low vigour lines in ET1 and ET2 environments (Figures S5 and S6) further suggested a
 514 larger potential for growth increases in these lines under favourable conditions. This is consistent

515 with a scenario where high vigour lines closed the canopy earlier in the crop development compared
516 to low vigour lines and radiation becomes saturated and limiting growth.

517

518 **Discussion**

519 We hypothesised there might be a three-way interaction between vigour, [CO₂] and water
520 availability post-anthesis, with high vigour lines under e[CO₂] being more prone to deplete soil water
521 before grain filling, which would negate some of the benefits of e[CO₂]. Experimental data from
522 AGFACE with a subset of cultivars with proven expression of high and low early vigour suggested a
523 lower response from high early vigour lines but was not statistically significant. While simulations
524 with both APSIM and SIMPLACE also suggested high vigour lines responded less to e[CO₂] than low
525 vigour lines, this did not appear to be directly related to the scenario envisaged in our hypothesis.
526 Instead, pre-anthesis growth stimulation, and in particular larger increases in radiation intercepted
527 in low early vigour lines, explained differences in grain yield responses. The importance of radiation
528 intercepted as illustrated by the models is in sharp contrast with the current literature: among
529 environmental factors hypothesized to influence the response to e[CO₂], the scientific focus has
530 rather been on investigating water and nutrient availabilities, sometimes with varying temperatures
531 (see for example recent reviews by Kimball, 2016; Tausz-Posch *et al.*, 2019; van der Kooi *et al.*, 2016)
532 while differences in radiation intercepted are not typically among the primary factors being
533 considered. A notable connection, however, is the work by Shimono (2011; and Shimono *et al.* 2014,
534 2019) who suggested using the response to low density planting (in rice) as a surrogate for grain
535 yield response to e[CO₂], although they also argue that the two responses would likely occur through
536 different physiological mechanisms (Shimono *et al.*, 2019). To properly test the effect of radiation
537 intercepted on the response to e[CO₂] in an experimental setting, data on the rate of canopy
538 development and timing of canopy closure in addition to daily radiation would need to be collected.

539

540 The experimental yield and biomass response to e[CO₂], when characterized by drought type with
541 APSIM, suggested that the response increased slightly with moderate water stress (in ET2 and ET3
542 environments), but decreased sharply in severe terminal drought stress (ET4 environment). These
543 results are consistent with the study of Gray *et al.* (2016) with 8-year of soybean experimentation,
544 which showed that severe drought led to a complete lack of response to e[CO₂]. This might also
545 explain why the response to e[CO₂] is more variable with water stress as shown in a recent meta-
546 analysis by van de Kooi *et al.* (2016). This study highlighted a gap in knowledge of the response to
547 e[CO₂] under severe water stress scenarios. While the environmental characterisation with APSIM
548 showed a tendency towards a lower response in the strongest terminal stress environment (ET4)

549 with the experimental data (Figure 4), we still do not have many replicates of each ETs even with 7
550 years of data. In fact, by adding vigour as an additional factor, we are completely missing
551 representations of low early vigour lines in ET3 and ET4 seasons, partly because of confounding
552 effects of short phenology in 2 of the 3 low early vigour lines. While advanced statistical models such
553 as mixed models used here can handle some missing data (Smith *et al.*, 2005), the absence of
554 treatment combinations limits our confidence in results. In particular, the environmental
555 characterization with SIMPLACE did not lead to the same pattern of effects on the response (Figure
556 4), which might be partially explained by some cultivar-season combinations being characterized
557 differently based on the model used. However, the clustering analysis for SIMPLACE was also based
558 on a much smaller data set than the APSIM clustering.

559

560 The lack of response to $e[CO_2]$ under severe water stress as reported here and by Gray *et al.*, (2016)
561 suggests there are still real gaps in knowledge about interactions between $[CO_2]$ and water stress
562 above and beyond the relationships with primary productivity and stomatal conductance. As
563 simulated responses did not show this pattern, such knowledge has not been incorporated in
564 simulation models. For example, Gray *et al.* (2016) showed that soybean plants grown under $e[CO_2]$
565 were more responsive to water stress than those grown under $a[CO_2]$, showing a lower stomatal
566 conductance for the same leaf-level ABA concentration. Whether, or to what extent, this might also
567 be true for wheat has not been investigated. In addition, Tausz-Posch *et al.* (2013) observed that
568 differences in stomatal conductance in wheat depended on the time of day or the measurement
569 day, so there may be other factors that interact with $[CO_2]$ on an hourly or minute scale that are not
570 captured in the single TE modifier used by models. Other research pointed out differences in the
571 root-to-shoot ratio under $e[CO_2]$: for example, Pandey *et al.* (2018) showed increased partitioning to
572 roots with $e[CO_2]$ and low phosphorus conditions for hydroponically grown wheat plants. These
573 findings remain to be confirmed in field settings. Nie *et al.* (2013) in a meta-analysis with heavy
574 reliance on perennial systems showed $e[CO_2]$ not only led to increased root-to-shoot ratio, but also
575 increased proportion of roots at depth and increased proportion of fine roots. Such effects of $e[CO_2]$,
576 if also present in wheat, would modify the ratios of water demand and water supply in the models,
577 and therefore the water stress indices from simulation models, potentially leading to different
578 environmental characterisations under $e[CO_2]$ and/or better relationships between water stress
579 indices and the grain response to $e[CO_2]$.

580

581 The simulation of leaf area curves assumes a bell-shaped growth, peaking shortly before anthesis,
582 and simulation of early vigour therefore leads to a larger maximum leaf area. However, there are

583 indications that in some populations bred for high early vigour this might not be the case: for
584 example, Bourgault *et al.* (2013) demonstrated high early vigour lines had a greater leaf area for the
585 first three leaves, but had fewer leaves, so their leaf area at anthesis was less than for the low early
586 vigour parent. If we were to explore this in greater detail with such lines, the simulation of leaf area
587 would need to be conceptualized in more detail and possibly with less reliance on SLA, which is
588 assumed by models to be either fixed for a specific growth stage (SIMPLACE) or vary with LAI
589 (APSIM), even though we know it is also sensitive to environmental factors and therefore a source of
590 uncertainty in these models (Tardieu *et al.*, 1999; Setiyono *et al.*, 2008).

591
592 Then, how confident are we about the partitioning of ET into soil evaporation and transpiration in
593 models? Although the LAI was increased approximately 30% with e[CO₂], cumulative differences
594 between ambient and e[CO₂] simulations in both evaporation and transpiration were below 9 and 16
595 mm respectively. While it is expected that the higher transpiration demand from a greater LAI under
596 e[CO₂] might be offset by savings through improved transpiration efficiency, are such small
597 differences realistic for differences in soil evaporation? The time period during which differences in
598 soil evaporation between high and low vigour lines is arguably quite short, and usually lies during the
599 time of the year for which potential ET is low. Then perhaps the value of the early vigour trait in
600 reducing evaporation might be secondary to other benefits, such as a more vigorous root system,
601 which would allow for quicker uptake of soil water and nutrients early in the season (Palta *et al.*,
602 2011).

603
604 Finally, increasing atmospheric [CO₂] will also cause increasing temperatures in most regions of the
605 world. The net effect of the water savings from e[CO₂] combined with the advanced crop
606 development and higher water use from higher chronic temperatures and/or the effects of potential
607 heat waves during grain filling with regards to biomass development and grain yield are highly
608 uncertain. Although the inclusion of this fourth factor is not possible with this study, a proper
609 assessment of the implications of genetic traits for climate change adaptation would require the
610 evaluation of several scenarios in regards to temperature pattern changes. Previous research has
611 shown that considering temperature and [CO₂] effects separately resulted in very different findings
612 compared to studies where the effects were combined, in particular with regards to crop water
613 requirement and heat stress (Zhao *et al.*, 2015).

614

615 **Conclusion**

616 Experimental data from AGFACE gave some indications that lines expressing high early vigour might
617 respond less to $e[\text{CO}_2]$ than low vigour lines. Although the effect was not found to be statistically
618 significant in the experimental data, two crop growth models supported this notion. We had
619 hypothesized these observations could be explained by that high early vigour lines depleting
620 available soil water earlier in the season when grown under $e[\text{CO}_2]$, and thus suffering from more
621 severe terminal drought stress. Environmental characterizations of the seasonal pattern of drought
622 stress in the experimental data and patterns of water use in the simulations however did not
623 support this hypothesis. Rather, both simulation models suggested early canopy closure in high early
624 vigour lines would limit the potential for increased growth and yield, especially in more favourable
625 environments. Under less favourable conditions, the timing of the drought stress appears to
626 influence the effect of $e[\text{CO}_2]$. This study highlighted the need to resolve whether there are
627 differences in the response to $e[\text{CO}_2]$ under drought types that differ in intensity and timing.

628

629 **Acknowledgements**

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641

642 The authors declare no conflict of interest.

643

644 The data that support the findings of this study are available from the corresponding author upon
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647

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Table 1: Cultivars selected from AGFACE 2007-2013 with planting date, date of first node development (DC31), anthesis (DC65) and final harvest (DC90) samplings.

Cultivar	Vigour classification (see Figure 1)	Planting date	Stem elongation (DC31) sampling date	Anthesis (DC65) sampling date	Final harvest (DC90) sampling date
2007					
Janz	Low	18 Jun	6 Sept	29 Oct	12 Dec
Yitpi	Reference	18 Jun	6 Sept	29 Oct	12 Dec
2008					
Janz	Low	4 Jun	20 Aug	20 Oct	8 Dec
Yitpi	Reference	4 Jun	20 Aug	20 Oct	8 Dec
2009					
Hartog	High	23 Jun	2 Sept	27 Oct	4 Dec
Janz	Low	23 Jun	2 Sept	27 Oct	4 Dec
Yitpi	Reference	23 Jun	2 Sept	27 Oct	4 Dec
2010					
Hartog	High	27 May	5 Aug	18 Oct	9 Dec
Janz	Low	27 May	5 Aug	18 Oct	9 Dec
Yitpi	Reference	27 May	5 Aug	22 Oct	9 Dec
2011					
Janz	Low	25 May	1 Aug	12 Oct	5 Dec
SB062	High	25 May	1 Aug	12 Oct	5 Dec
SsrT65	Low	25 May	1 Aug	7 Oct	5 Dec
Yitpi	Reference	25 May	1 Aug	17 Oct	5 Dec
2012					
Janz	Low	30 May	15 Aug	18 Oct	5 Dec
SB062	High	30 May	15 Aug	15 Oct	5 Dec
SsrT65	Low	30 May	7 Aug	8 Oct	5 Dec
Yitpi	Reference	30 May	15 Aug	18 Oct	5 Dec

2013					
Bolac	Low	29 May	13 Aug	21 Oct	6 Dec
Spitfire	High	29 May	13 Aug	8 Oct	2 Dec
Yitpi	Reference	29 May	13 Aug	16 Oct	6 Dec

Table 2: Crop model phenological parameters for the cultivars used in this study.

	APSIM		SIMPLACE/Lintul5	
	photo_sens*	vern_sens*	TSUM1**	TSUM2**
Yitpi	3.0	1.5	850	750
Janz	2.2	2.9	800	750
SsrT65	1.5	1.5	750	750
Bolac	3.1	3.1	925	750
Hartog	3.0	1.5	850	750
SB062	3.0	1.5	850	750
Spitfire	3.0	1.5	850	750

* photo_sens and vern_sens are parameters in the APSIM wheat module that relate to photoperiod and vernalisation sensitivity, respectively. These modify thermal time parameters to extend or contract thermal time in early phases of crop development.

** TSUM1 and TSUM2 in SIMPLACE-Lintul5 specify the thermal time requirements from emergence to anthesis and from anthesis to maturity, respectively, and are modified by both a response to photoperiod and a small vernalisation response.

Table 3: Specific Leaf Area (SLA, in $\text{cm}^2 \text{g}^{-1}$) differences between early vigour groups from selected cultivars in AGFACE (2007-2013) and translation of values into model inputs.

Cultivar/Group	APSIM		SIMPLACE					
	Calculated slope and intercept for 95 percentile of SLA ($\text{cm}^2 \text{g}^{-1}$) as a function of LAI	max SLA	SLA ($\text{cm}^2 \text{g}^{-1}$) at DC31	SLA ($\text{cm}^2 \text{g}^{-1}$) at DC65	SLATB (in $\text{m}^2 \text{g}^{-1}$)			
High vigour group	300 – 7x	LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)	224 ± 14	174 ± 12	DVS	SLA	
		0.0	30000			0.0	0.022	
		5.0	26000			0.4	0.022	
						1.0	0.016	
				2.0	0.016			
Low vigour group	250 – 5x	LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)	191 ± 14	152 ± 12	DVS	SLA	
		0.0	25000			0.0	0.018	
		5.0	22000			0.4	0.018	
						1.0	0.011	
				2.0	0.011			
Yitpi	256 – 5x	LAI	Max SLA ($\text{mm}^2 \text{g}^{-1}$)	196 ± 14	155 ± 12	DVS	SLA	
		0.0	27000			0.0	0.019	
		5.0	22000			0.4	0.019	
						1.0	0.012	
				2.0	0.012			

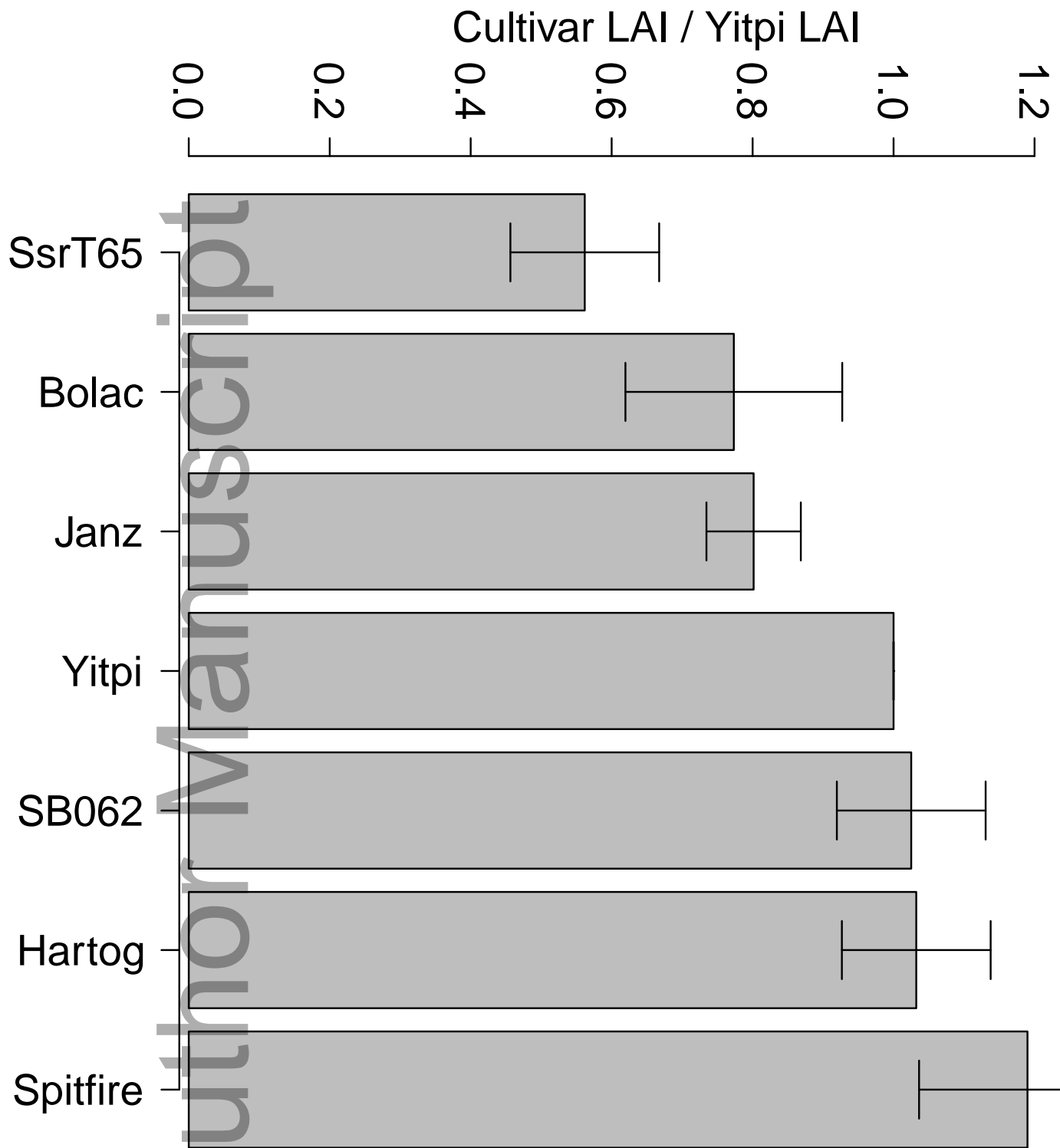
					(Default values)
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In APSIM, the maximum SLA parameter value is a function of the LAI, whereas in SIMPLACE, the SLA value (within the SLATB parameter) is a function of the developmental stage (DVS), which varies from 0 to 2 (maturity), with 1 being anthesis.

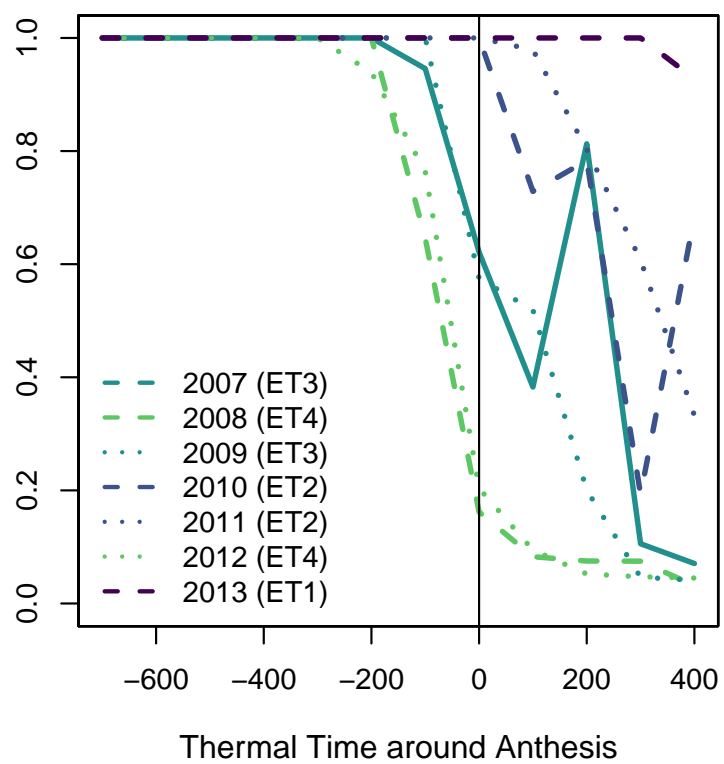
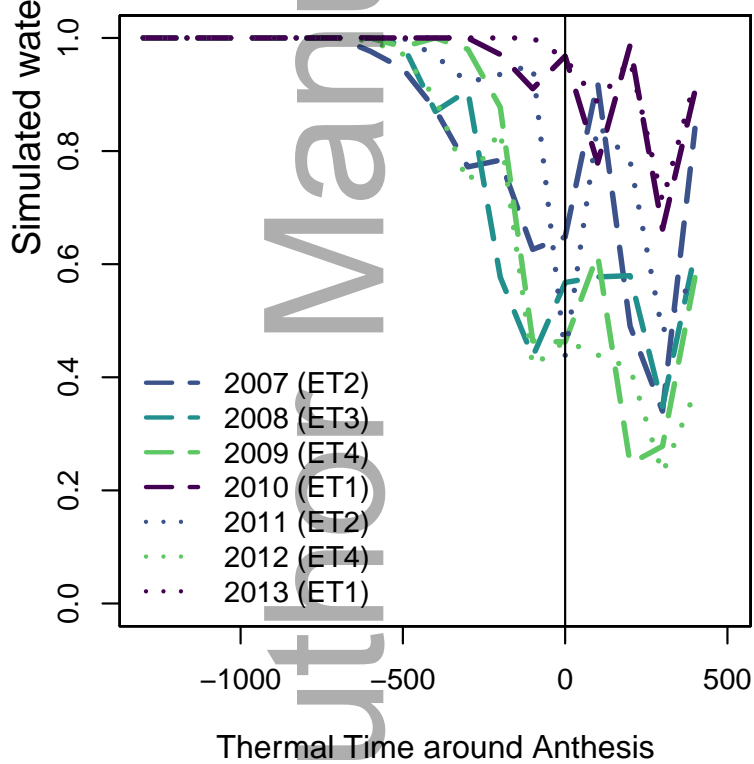
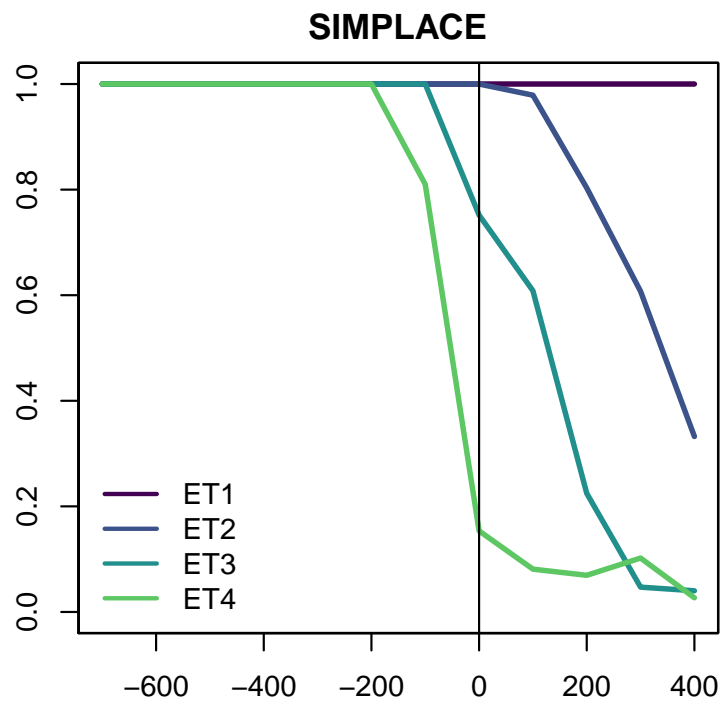
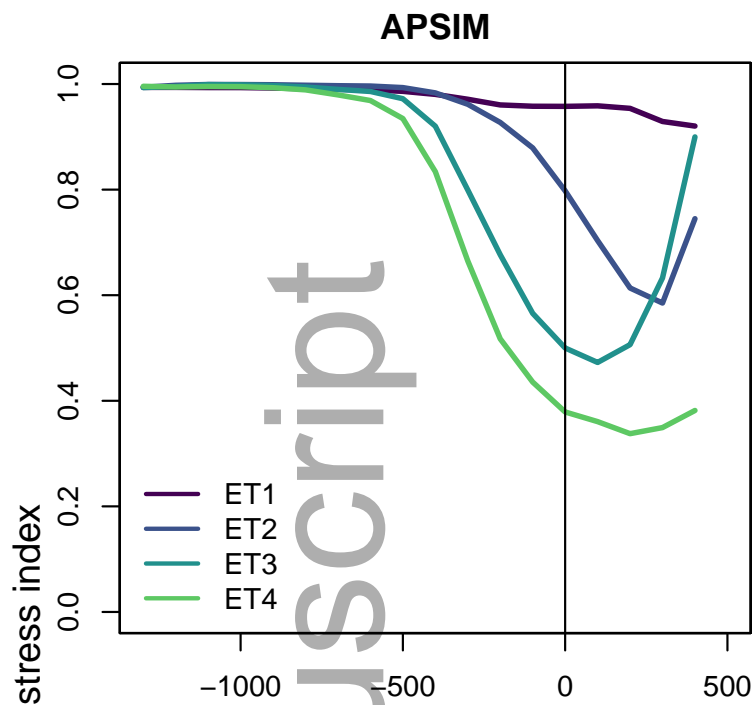
Table 4: Environmental characterisation of AGFACE experimental data with APSIM and SIMPLACE simulations outputs, according to methodology by Chenu *et al.* (2013). The four environment types describe four different drought patterns: no stress or negligible stress (ET1), moderate water stress post-anthesis (ET2), moderate to severe water stress beginning before anthesis but relieved during grain filling (ET3), or that continued through to maturity as a severe terminal drought (ET4).

Year	Cultivar	APSIM Outputs				SIMPLACE Outputs			
		Rainfed		Supplemental		Rainfed		Supplemental	
		a[CO ₂]	e [CO ₂]	a[CO ₂]	e [CO ₂]	a[CO ₂]	e [CO ₂]	a[CO ₂]	e [CO ₂]
2007	Janz	ET2	ET2	ET2	ET2	ET2	ET2	ET2	ET2
	Yitpi	ET2	ET3	ET2	ET2	ET3	ET3	ET2	ET2
2008	Janz	ET2	ET2	ET2	ET2	ET4	ET4	ET3	ET3
	Yitpi	ET3	ET3	ET3	ET3	ET4	ET4	ET4	ET4
2009	Hartog	ET4	ET4	ET2	ET3	ET3	ET3	ET2	ET2
	Janz	ET2	ET2	ET2	ET2	ET3	ET3	ET2	ET2
	Yitpi	ET4	ET4	ET2	ET2	ET3	ET3	ET2	ET2
2010	Hartog	ET2	ET2	ET1	ET1	ET2	ET2	ET1	ET1
	Janz	ET1	ET1	ET1	ET1	ET2	ET2	ET1	ET1
	Yitpi	ET1	ET1	ET1	ET1	ET2	ET2	ET1	ET1
2011	Janz	ET2	ET2	ET1	ET1	ET2	ET2	ET1	ET1

	SB062	ET2	ET2	ET2	ET1	ET2	ET2	ET1	ET1
	SsrT65	ET1	ET1	ET1	ET1	ET1	ET1	ET1	ET1
	Yitpi	ET2	ET2	ET1	ET1	ET2	ET2	ET1	ET1
2012	Janz	ET2	ET2	ET1	ET2	ET4	ET3	ET2	ET2
	SB062	ET4	ET4	ET2	ET2	ET4	ET4	ET2	ET2
	SsrT65	ET1	ET1	ET1	ET1	ET3	ET3	ET1	ET1
	Yitpi	ET4	ET4	ET2	ET2	ET4	ET4	ET2	ET2
2013	Bolac	ET1	ET1	ET1	ET1	ET2	ET2	ET2	ET2
	Spitfire	ET1	ET1	ET1	ET1	ET1	ET1	ET1	ET1

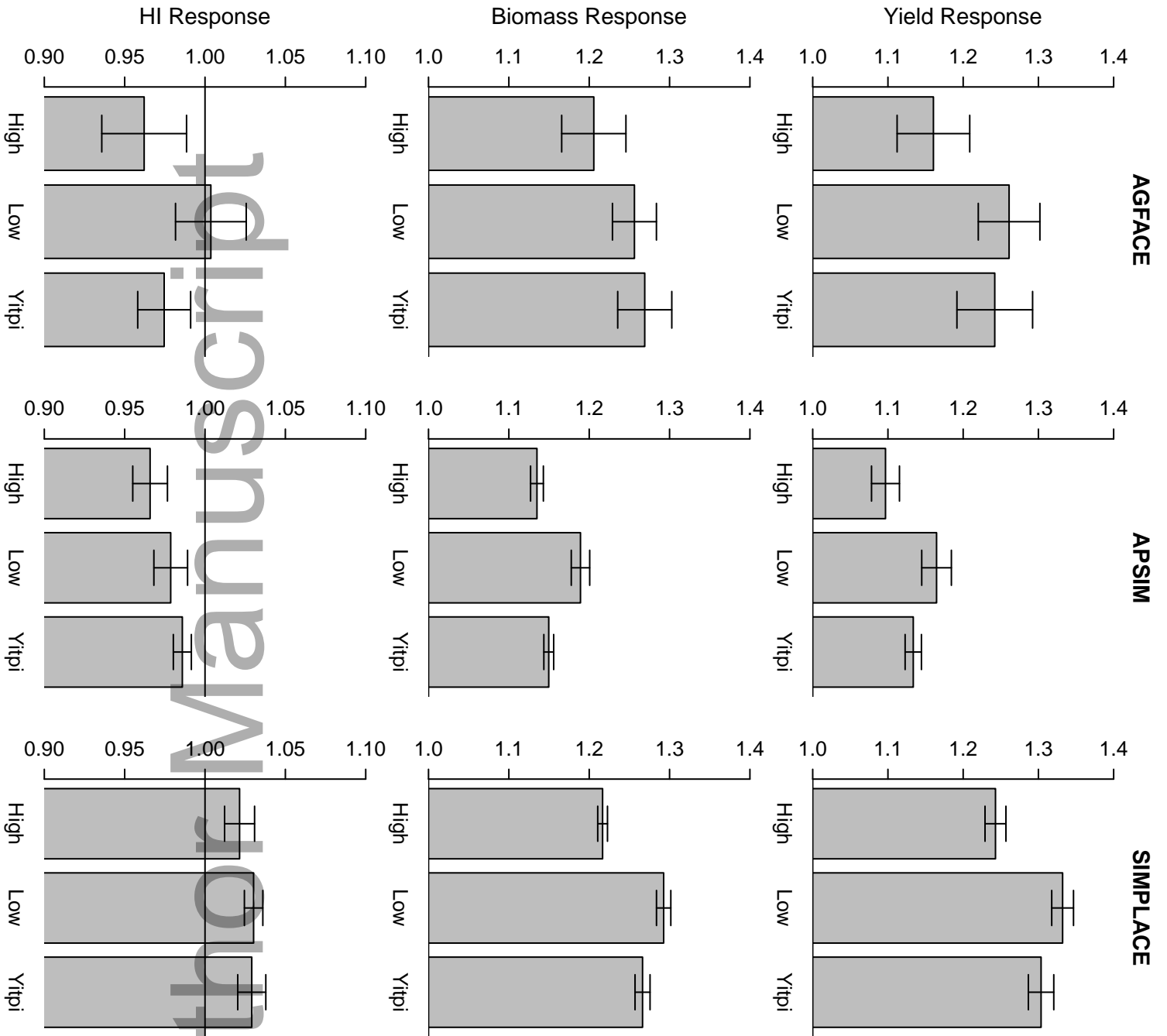


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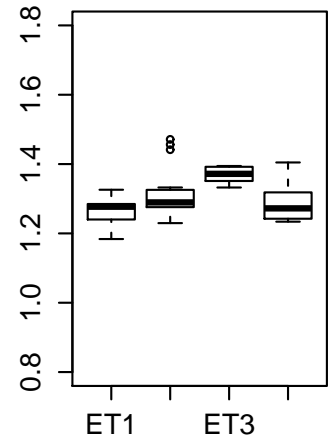
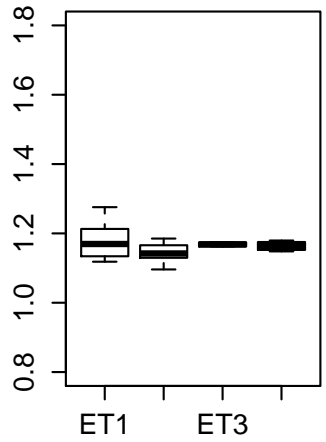
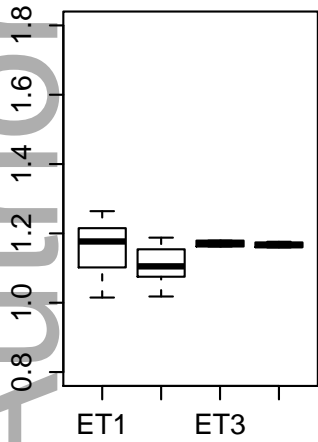
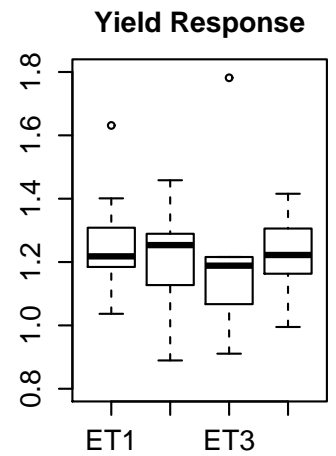
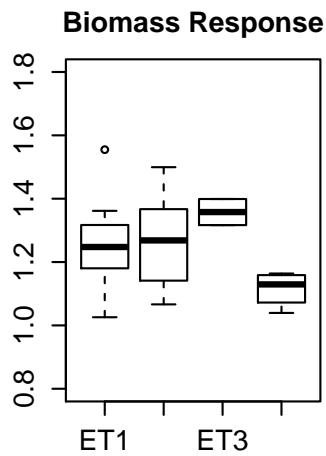
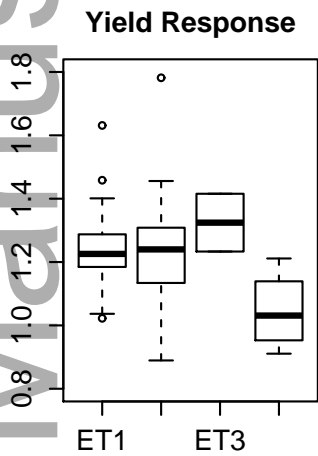
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Relative Response to Elevated [CO₂]



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Simulated Response to e[CO₂] Experimental Response to e[CO₂]

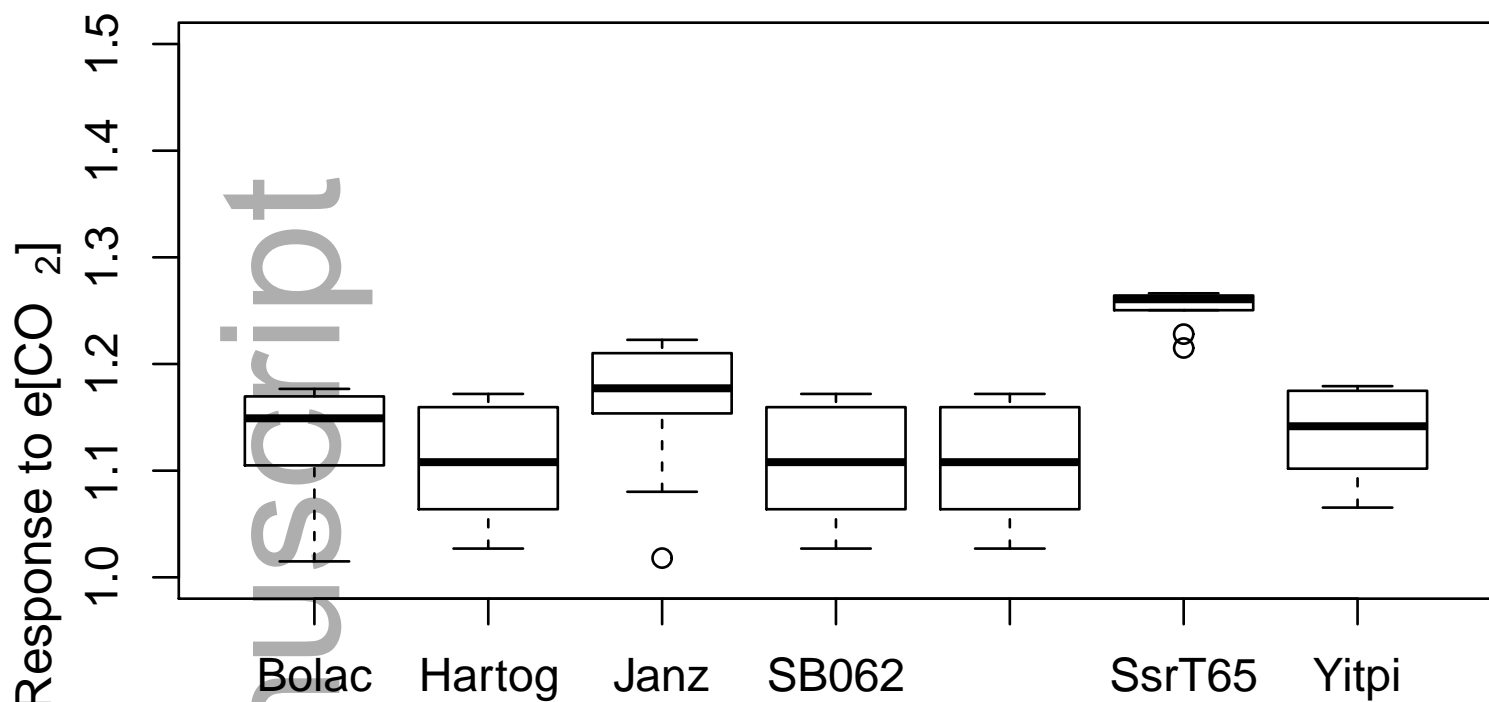


APSIM ET Characterization

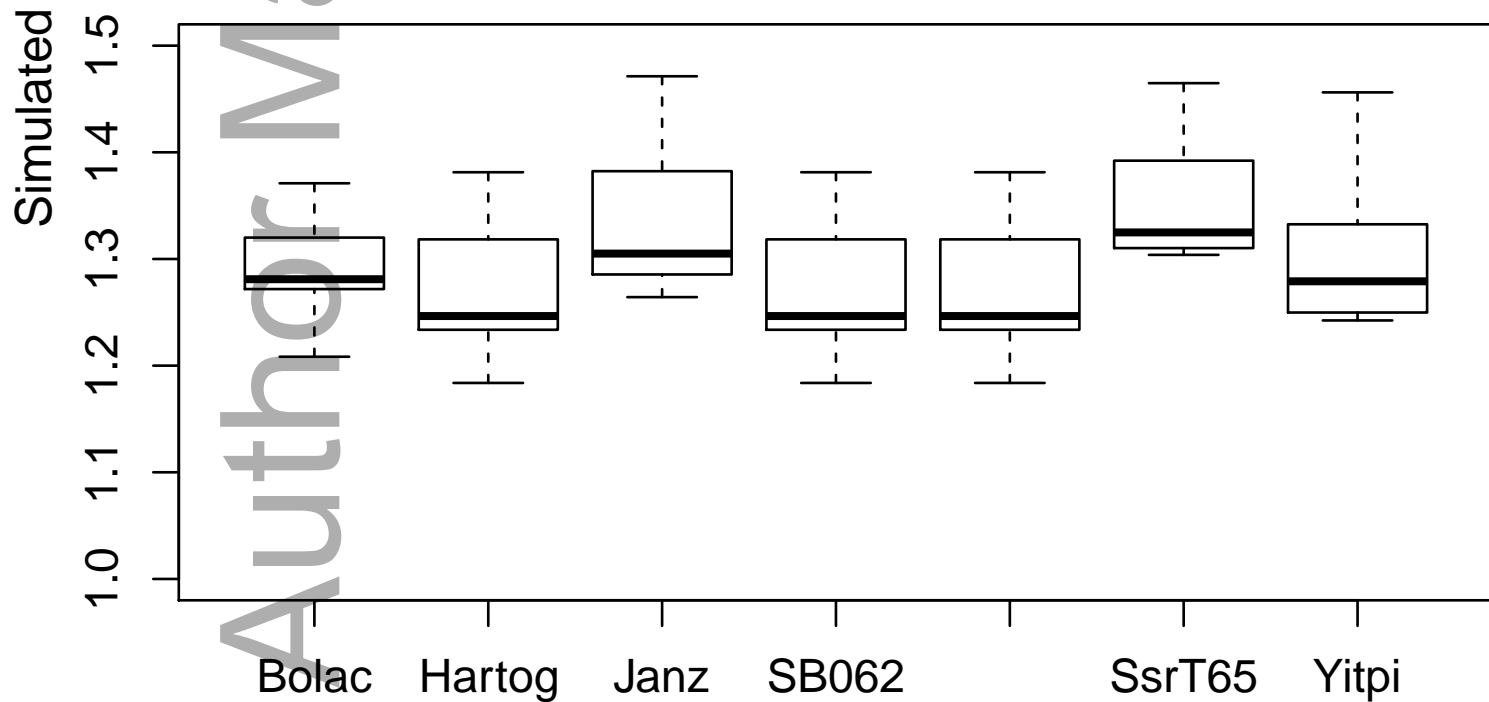
SIMPLACE ET C

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APSIM



SIMPLACE



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