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Benefits of increasing transpiration efficiency in wheat under elevated CO_2 for rainfed regions

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Abstract

Higher transpiration efficiency (TE) has been proposed as a mechanism to increase crop yields in dry environments where water availability usually limits yield. The application of a coupled radiation and TE simulation model shows wheat yield advantage of a high-TE cultivar (cv. Drysdale) over its almost identical low-TE parent line (Hartog), from about −7 to 558 kg/ha (mean 187 kg/ha) over the rainfed cropping region in Australia (221–1,351 mm annual rainfall), under the present-day climate. The smallest absolute yield response occurred in the more extreme drier and wetter areas of the wheat belt. However, under elevated CO_2 conditions, the response of Drysdale was much greater overall, ranging from 51 to 886 kg/ha (mean 284 kg/ha) with the greatest response in the higher rainfall areas. Changes in simulated TE under elevated CO_2 conditions are seen across Australia with notable increased areas of higher TE under a drier climate in Western Australia, Queensland and parts of New South Wales and Victoria. This improved efficiency is subtly deceptive, with highest yields not necessarily directly correlated with highest TE. Nevertheless, the advantage of Drysdale over Hartog is clear with the benefit of the trait advantage attributed to TE ranging from 102% to 118% (mean 109%). The potential annual cost-benefits of this increased genetic TE trait across the wheat growing areas of Australia (5 year average of area planted to wheat) totaled AUD 631 MIL (5-year average wheat price of AUD/260 t) with an average of 187 kg/ha under the present climate. The benefit to an individual farmer will depend on location but elevated CO_2 raises this nation-wide benefit to AUD 796 MIL in a 2°C warmer climate, slightly lower (AUD 715 MIL) if rainfall is also reduced by 20%.

KEYWORDS
climate change, vapor pressure deficit, water use efficiency

1 | INTRODUCTION

Higher transpiration efficiency (TE) has been proposed as a mechanism to increase crop yields in dry environments where reduced water supply limits biomass and yield (Craufurd, Austin, Acevedo, & Hall, 1991; Ehdaie, Hall, Farquhar, Nguyen, & Waines, 1991; Martin & Thorstenson, 1988; Passioura, 1977). Crop level TE can be defined as the ratio of biomass gain over transpiration, and is related to leaf-level TE and approximations of TE that include soil evaporation (e.g., evapotranspiration or total water use, also termed water use

efficiency). The nature of TE, comprising components of biomass and transpiration, contributes to it being a complex trait from a breeding point of view (Richards & Condon, 1993). This complexity is increased because of TE's dependence on environmental factors like vapor pressure deficit (VPD) of the atmosphere, whereby TE is reduced as VPD increases (Tanner & Sinclair, 1983). As such, it is difficult to separate the genetic components of TE from the environmental components, but as Sinclair (2012) showed, it is possible to do this by defining TE as an inverse function of VPD (TE = k_d/VPD). The resulting crop-dependent transpiration coefficient (k_d) offers a way to normalize TE against changing VPD. Under typical dryland field conditions, TE for wheat varies from around 3 to 9 g of biomass growth per kg water transpired with k_d typically ranging from 4 to 6 Pa (Kemanian, Stöckle, & Huggins, 2005). Older cultivars appear to have a lower potential ("unstressed") TE (i.e., when measured under ample water supply and low VPD) than more recently released cultivars, and that has been attributed to rising atmospheric CO_2 concentrations over recent years (Fletcher & Chenu, 2015). Crop TE itself can vary more than the assumed constant k_d, particularly when water stressed under high VPD or under increasing atmospheric CO_2. However, varied assumptions of total biomass accumulation (i.e., shoot + root or shoot only) and consistent VPD algorithms for the sampling period contribute to the observed variance for which more complex models of TE apply (Kemanian et al., 2005).

The stable isotope (δ^{13}C) signature in biomass has been used as a surrogate for leaf-level TE, to produce high-TE wheat cultivars (Condon, Richards, Rebetzke, & Farquhar, 2004; Rebetzke, Condon, Richards, & Farquhar, 2002). This was based on the original work relating carbon isotope discrimination (CID) to TE in wheat (Farquhar & Richards, 1984). This original work also delineated the important distinction between carbon isotope composition, δ^{13}C, and the biologically meaningful process of CID. Field evaluation of the high-TE cultivar (Quarrion) showed significant gains in TE (11%–21%) over a season measured against a low-TE cultivar (cv. Matong) but realizing final yield was more complex than just biomass gain (Condon & Richards, 1993). The complexity comes from disproportionate changes in transpiration and biomass, with changes in assimilate partitioning considered independent of those factors that primarily control TE (e.g., VPD). This partitioning is particularly important when considering grain yield, because grain growth occurs later in the season when crops are typically water-limited and experiencing terminal drought and crops have the capacity to shift varying amounts of C assimilated earlier in the season into the grain. This early work showed significant advantage of related high-TE lines over low-TE lines in drier locations (e.g., Rebetzke et al., 2002) but the benefits over a wider range of environmental conditions remain largely unknown. An independent assessment of the value of TE was undertaken separately by Australian Grains Technology® breeding company. They grew a high-TE cultivar, Drysdale, side-by-side with its closely related low-TE parent Hartog across 60 site-year combinations throughout the Australian wheat belt (Rebetzke et al., 2009). Their studies confirmed the significant yield benefit of greater TE across a broader range of environments ranging in yield from 0.3 to

6 t/ha, and a particular benefit of high TE at yields of 4 t/ha and below.

Among changing environmental factors, increasing atmospheric CO_2 will increase leaf-level TE for virtually all plants because elevated CO_2 promotes C assimilation and at the same time decreases stomatal conductance and therefore transpiration. Recent work from the Australian Grains Free-Air Carbon Dioxide Enrichment (AGFACE) facility provided some evidence that a high-TE trait might still be an advantage under higher atmospheric CO_2 concentrations (Tausz-Posch, Norton, Seneweera, Fitzgerald, & Tausz, 2013; Tausz-Posch, Seneweera, Norton, Fitzgerald, & Tausz, 2012). High-TE cultivar Drysdale was grown side-by-side with low-TE parent Hartog and while both cultivars in this analysis had improved TE under elevated CO_2, differences between the two cultivars indicated greater TE for Drysdale with growth under elevated CO_2 potentially increasing the response of this trait. The exact mechanisms for this increasing advantage were not entirely clear (Tausz-Posch et al., 2012). Additionally, the AGFACE experiment does not fully represent a future climate even at its present location in Horsham, Australia. We therefore used crop simulation modeling to (1) better understand the genetic and environmental components of TE in these experiments, and (2) extrapolate experimental observations to other environments beyond this site. Specifically, we explored potential benefits of increased TE in wheat across the wheat growing areas of Australia employing a validated model considered sufficiently mechanistic to model water-limited wheat crop growth and yield. We consider these effects under the present climate and likely future warmer and drier climate scenarios under elevated atmospheric CO_2 concentrations. This study region represents a large proportion of global wheat production areas and is typical of many rainfed cropping environments throughout the world experiencing significant changes in climate (e.g., CIMMYT Mega environment 1, 2, 4, and 8; CIMMYT 2014).

2 | MATERIALS AND METHODS

We reanalyzed the published data from Tausz-Posch et al. (2012) using the CAT-wheat model (O'Leary et al., 2015). The model (CAT-Wheat) is a landscape-scale model that has recently been successfully tested against other AGFACE data (O'Leary et al., 2015). The advantage of the CAT model is its unique feature of analyzing crop performance across diverse landscapes (Christy et al., 2013).

2.1 | Experimental site and growing conditions

A detailed description of the site set-up is given in Mollah, Norton, and Huzzey(2009). Briefly, the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility is located at Horsham, Victoria, Australia (36°45′07″S, 142°06′52″E, 127 m above mean sea level). The site is a clay vertosol (Isbell, 1996), which has ~35% clay at the soil

surface increasing to 60% at 1.4 m depth. Four ambient CO_2 (a [CO_2], 375 mol/mol) and four elevated CO_2 (e[CO_2], 550 mol/mol) plots (each 12–16 m in diameter) were used. Plots are randomly allocated within each ring.

In 2009, one experimental series was sown within the time frame of standard local practice (23 June 2009; Table 1) and a second experimental series was sown later (19 August 2009; Table 1) in order to create a set of drier and hotter growing conditions. In 2010, a third experimental series was run, sown within the time frame of standard local practice (sowing date 27 May 2010; Table 1). In addition, each of the three experimental series was run under rainfed conditions and supplemental irrigation. This resulted in three additional sets of environmental growing conditions (Table 1). Closely related cultivars "Drysdale" and "Hartog" were sown into flat beds at 0.27 m row spacing on the plots. The high-TE Drysdale was selected from a backcross-2 population (Hartog × 3/Quarrion) using Hartog as the low-TE recurrent parent. Summarizing, a total of six different environments were tested under both ambient CO_2 (375 mol/mol) and elevated CO_2 (550 mol/mol) concentrations, using differing combinations of water supply, seasonal, and sowing date variations (Table 1).

2.2 | Biomass, grain yield, and morphological measurements

For each experimental series, total above-ground biomass (leaves, stems, spikes) was measured at flowering (growth stage DC65; Zadoks, Chang, & Konzak, 1974) and at physiological maturity (DC90). As phenological development was similar for both cultivars and in both CO_2 treatments, both cultivars grown under ambient and elevated CO_2 were sampled on the same dates. At each sampling

date, plants from 0.5 m^2 of each subplot ("whole sample") were hand-harvested and then dried for 72 hr at 70°C (DC65) or 40°C for 72 hr (DC90). The DC65 samples were weighed while DC90 samples processed for grain yield, above-ground biomass and 1,000 kernel weight. All parameters were expressed on an area basis (m^2).

2.3 | The CAT-Wheat model

The CAT-Wheat model originally calculated crop growth by a radiation use efficiency (RUE) approach whereby reduced water supply, nutrient stress or photoperiod factors reduced RUE by relative differences (O'Leary et al., 2015). The minimum value of these factors (i.e., the most limiting) was used to reduce RUE. While that version of the model performed satisfactorily in testing the response to elevated CO_2, it did not simulate transpiration reduction directly as a consequence of high CO_2. The model was modified here to increase its utility in simulating water dynamics similar to other contemporary models. Initial parameter adjustments were made using the OLEARY-CONNOR model (O'Leary & Connor, 1996) utilizing parameters driven by TE for determining growth, and software coding modifications to establish realistic amendments that were subsequently transferred to the landscape CAT-Wheat model. These two models are not identical and differ in assimilate partitioning and water and nitrogen simulation calculations.

Transpiration reduction and efficiency changes due to elevated CO_2 were added to CAT based on a formulation adapted from Stöckle, Williams, Rosenberg, and Jones (1992) as incorporated into the CROPSYST (Stöckle, Donatelli, & Nelson, 2003) and STICS (Brisson et al., 2003) models. A correction to RUE is applied and the associated correction to TE, without double accounting, was made after O'Leary

TABLE 1 Summary of data underlying the results reported in Tausz-Posch et al. (2012). Three times of sowing, growing season rainfall, and irrigation applied. Observed above-ground biomass (at DC65 and DC90) and grain yield for both Hartog and Drysdale at ambient and elevated CO_2 concentrations (averages from four replicates each)

Time of sowing	Rain (mm)	Irrigation (mm)	Measurement	Hartog		Drysdale	
				a[CO_2]	e[CO_2]	a[CO_2]	e[CO_2]
23/06/09	223	0	Biomass DC65 (g/m^2)	821.7	1,104.9	764.4	952.6
			Biomass DC90 (g/m^2)	843.6	876.8	870.9	1,109.6
			Grain yield (g/m^2)	221.3	200.2	252.2	277.8
23/06/09	223	70	Biomass DC65 (g/m^2)	817.2	836.4	889.8	998.0
			Biomass DC90 (g/m^2)	923.0	984.2	1,046.2	1,035.2
			Grain yield (g/m^2)	246.2	219.6	287.6	270.2
19/08/09	187	0	Biomass DC65 (g/m^2)	453.1	507.7	358.0	496.7
			Biomass DC90 (g/m^2)	505.8	535.7	444.4	686.2
			Grain yield (g/m^2)	136.1	136.7	122	163.0
19/08/09	187	60	Biomass DC65 (g/m^2)	473.4	585.4	422.4	621
			Biomass DC90 (g/m^2)	497.9	686.6	485.2	757.3
			Grain yield (g/m^2)	125.1	172.6	122.9	228.2
27/05/10	296	0	Biomass DC65 (g/m^2)	937	1,114.1	1,000.1	1,224.2
			Biomass DC90 (g/m^2)	1,546.1	1,712.8	1,429.4	1,714.4
			Grain yield (g/m^2)	467.7	576.6	500.5	598.8
27/05/10	296	80	Biomass DC65 (g/m^2)	939.3	1,114.2	943.6	1,209.4
			Biomass DC90 (g/m^2)	1,666.1	1,939.9	1,624.4	2,067.3
			Grain yield (g/m^2)	591.9	631.5	537.6	776.0

et al. (2015). The fertilization effect of elevated CO_2 is achieved by multiplication of TE by a factor (TECC) that is derived from a RUE factor (RUECC) from Stöckle et al. (1992) with simplifying assumptions of aerodynamic resistance of crop canopy 300 s/m and canopy resistance of 36 s/m at 350 µmol/mol CO_2 (O'Leary et al., 2015);

$$RUECC = \max\left[1, \frac{1.7 \times CO_2 \times \left(\frac{-1.7}{350(1-1.7)}\right)}{1.7 + CO_2 \times \left(\frac{-1.7}{350(1-1.7)}\right)}\right], \quad (1)$$

$$TECC = \frac{\frac{RUECC}{\delta + \left(\frac{\gamma(r_s + 300)}{300}\right)}}{\delta + \frac{\gamma\left(\left(\frac{r_s \times CO_2}{350 \times RUECC}\right) + 300\right)}{300}}, \quad (2)$$

where, CO_2 is the atmospheric CO_2 concentration (µmol/mol) and γ (kPa/°C) and δ (kPa/°C) are the psychometric constant and slope of saturated vapor pressure–temperature curve, respectively such that RUECC = 1, 1.18 and 1.23 at 350, 550, and 650 µmol/mol, respectively. We calculated γ and δ as follows:

$$\gamma = \frac{0.1651 \times \left(\frac{293 - 0.0065 \times El}{293}\right)^{5.26}}{2.501 - T \times 0.002361}, \quad (3)$$

$$\delta = \frac{4,098\left(0.6108 \times EXP\left(\frac{17.27 \times T}{(T + 237.3)}\right)\right)}{(T + 237.3)^2}, \quad (4)$$

where, T is the daily mean air temperature (°C) and El is the height above sea level (m) (Allen, Pereira, Raes, & Smith, 1998). Potential crop transpiration is reduced by elevated CO_2 in proportion to the ratio of RUECC/TECC that provides a TECC of 1.27 at 650 µmol/mol CO_2. At very high levels of CO_2, RUECC asymptotically approaches 1.7.

2.4 | The CAT-Wheat model–Crop parameterization

This modified CAT-Wheat model was parameterized against the field data of cultivars Drysdale (high TE) and Hartog (low TE, near isogenic to Drysdale), ensuring observed phenological stages of DC65 and DC90 were matched. To reflect the similar genetic background, both Hartog and Drysdale were parameterized identically with the exception of two parameters, viz; crop transpiration coefficient and crop canopy resistance (Table 2). For each time of sowing, the model was initialized to match measured sowing soil water content and available mineral N content through the soil profile (pooled across the experiment). Irrigation and fertilizer were applied by the model on the actual days of application.

Previous studies have demonstrated a yield advantage between 2% and 15% for low-CID lines (Drysdale) (Rebetzke et al., 2002, 2009) when compared with high discrimination lines (Hartog). The

yield advantage of low-CID selected lines was associated with increases in aerial biomass and greater partitioning of dry matter to grain. Therefore, to simulate these increases, the crop transpiration coefficient (k_c) of Drysdale was increased from the CAT-Wheat default of 5.8–6 Pa while that of Hartog was decreased to 5.2 Pa. These changes reflected the biomass growth response of the experimental observed ambient CO_2 data. An increase in TE is typically simulated with an approximately equal weighting to growth increase and transpiration decrease. We further increased the weighing on transpiration decrease for Drysdale by increasing the canopy resistance (r_s) from 36 (for Hartog) to 44 s/m (for Drysdale), thereby further altering the calculation of potential evapotranspiration by CAT and the TECC response in Equation (6) but reducing RUECC to maintain the desired genetic transpiration coefficient of 6 Pa for Drysdale. Based on the differences in observed elevated CO_2 response of Drysdale and Hartog, the RUECC term calculated with the fertilization effect of elevated CO_2 (Equation 1) was altered by the proportion of the crop transpiration coefficient divided by 5.8 Pa, replacing Equation (1) with Equation (5).

$$RUECC = \max\left[1, \frac{1.7 \times \left(\frac{k_c}{5.8}\right) \times CO_2 \times \left(\frac{-1.7}{350(1-1.7)}\right)}{1.7 + CO_2 \times \left(\frac{-1.7}{350(1-1.7)}\right)}\right], \quad (5)$$

$$TECC = \frac{\frac{RUECC}{\delta + \left(\frac{\gamma(r_s + 300)}{300}\right)}}{\delta + \frac{\gamma\left(\left(\frac{r_s \times CO_2}{350 \times RUECC}\right) + 300\right)}{300}}, \quad (6)$$

where, r_s is the crop canopy resistance (s/m).

2.5 | The CAT-Wheat model– Long-term analysis at Horsham

The CAT-Wheat model was applied to consider the productivity change resulting from increasing TE in wheat at the FACE experimental site using daily climate data from 1962 to 2015 resulting in 54 crop years of modeled data. Daily climate data for the Horsham (Horsham Polkemmet Rd, Station number 79023 (36°39′41″S, 142°04′07″E)) climate station (located 10 km from the site) were sourced from the Australian Bureau of Meteorology (www.longpaddock.qld.gov.au/silo, accessed 25 January 2018). The long-term modeling conducted considered both Hartog and Drysdale at ambient (375 µmol/mol) and elevated (550 µmol/mol) CO_2 concentrations for the whole historic 54 year sequence (Historic climate), plus two additional climate sequences: the first additional sequence was created by increasing the daily average temperature by 2°C over the 54-year period (Historic climate 2°C warmer), while the second sequence increased the daily average temperature by 2°C and decreased daily rainfall by 20% (Historic climate 2°C warmer and 20% less rainfall). These changes were selected to approximate a warmer and drier climate expected by 2050 in this region to indicate

TABLE 2 Key parameters used to define wheat growth in CAT-Wheat for cultivar Hartog and Drysdale

Parameter definition	Value		Units
	Hartog	Drysdale	
Base photoperiod	0	0	hr
Optimal photoperiod	24	24	hr
Base temperature for vernalization	2	2	°C
Max temperature for vernalization	9	9	°C
Vernalization days required	24	24	day
Threshold temperature for thermal requirement: sowing to emergence	4	4	°C
Threshold temperature for thermal requirement: sowing to stem elongation	4	4	°C
Threshold temperature for thermal requirement: sowing to anthesis	4	4	°C
Threshold temperature for thermal requirement: anthesis to maturity	8	8	°C
Thermal time between sowing and crop emergence	78	78	°C day
Thermal time between sowing and stem elongation	430	430	°C day
Photothermal time between sowing and anthesis	340	340	hr °C day
Thermal time between anthesis and maturity	550	550	°C day
Maximum photosynthetic (leaf + stem) area index	5	5	m^2/m^2
Proportion of Max PAI (1st point)	0.05	0.05	0 to 1 scalar
Proportion of growing season (1st point)	0.20	0.20	0 to 1 scalar
Proportion of Max PAI (2nd point)	0.95	0.95	0 to 1 scalar
Proportion of growing season (2nd point)	0.50	0.50	0 to 1 scalar
Crop transpiration coefficient	**5.2**	**6.0**	**Pa**
Crop canopy resistance	**36**	**44**	**s/m**
Maximum grain growth rate	2	2	mg/day
Maximum grain size	50	50	mg
Grain number coefficient (intercept)	2,000	2,000	grains/m^2
Grain number coefficient (slope)	10.51	10.51	grains/g
Maximum proportion of biomass at anthesis that can be translocated to grain	20	20	%

Highlighted in bold are the two parameters distinguishing these cultivars (Crop transpiration and Canopy crop resistance). Photothermal time is calculated by multiplying the thermal time by the relative photoperiod (actual/optimum photoperiod). The vernalization requirement is also added by multiplying the thermal time by the relative vernalization attained (actual/required vernalization days).

expected sensitivity of the crop traits. The CAT-Wheat model was applied for the two wheat cultivars sown each year after the "autumn-break" (defined as at least 20 mm rainfall in a 5-day period between 14 April and 30 June). In summary, 12 separate 54 year simulations were conducted that comprised two cultivars by three climates by two CO_2 concentrations totaling 648 years of simulations.

To reduce the confounding effect of "carry-over" stored soil water from the previous year's crop, the stored soil water status was reset 75 days before sowing to 10% plant available water for each soil depth increment to a total depth of 1 m, and a full plant available water profile below that depth.

2.6 | The CAT-Wheat model– Spatial analysis across Australia

The long-term analysis at Horsham was extended across Australia over a 54-year period using historic climate and the two additional climate sequences using the same method applied for the long-term analysis at Horsham. Model simulation was conducted on all privately owned, arable agricultural land (defined as slopes <5%) within the spatial region identified in Figure 1. The spatial area was divided into 1-km^2 grid cells for modeling. For each grid cell within this region, the CAT-Wheat model was applied for the two wheat cultivars sown each year after the "autumn-break," with crop yield response demonstrating intraseasonal variability associated with climate patterns and soil water availability.

For the long-term, single site at Horsham, 648 annual simulations were conducted to represent all scenarios. Upscaling to a total area evaluated of 71.3×10^6 ha (Figure 1), the CAT-Wheat model simulated 462,085,560 years of wheat growth, by being applied to each 1 km × 1 km grid cell on a daily basis using the 54 years of historic climate data (1962–2015), scaled to each grid pixel from the meteorological climate station of nearest proximity. The point location of each climate recording station is used to create a Voronoi diagram that identifies the nearest climate station for each point in a catchment. Daily climate data for each climate station are sourced from the Bureau of Meteorology (www.bom.gov.au/silo, accessed 5th June 2016). The daily data are "patched point data" and contain rainfall, minimum and maximum temperatures and solar radiation. The data combine original Bureau of Meteorology measurements for a given climate station with a process for infilling any gaps in the record using interpolation methods discussed in Jeffrey, Carter, Moodie, and Beswick (2001). As climate stations are located sparsely, daily rainfall and temperature data are scaled according to interpolated mean annual spatial layers. Interpolated surfaces were created using the ANUClim software (Hutchinson, 2001) that combines a digital elevation model and temporal climatic data to generate a smoothed climate surface.

The dominant soil type for each grid cell (sourced on June 2013 from http://www.asris.csiro.au/themes/Atlas.html) was described and mapped under a Northcote (1979) classification and attributed using the 50 percentile predictions of soil properties described in McKenzie, Jacquier, Ashton, and Cresswell (2000). For each year of
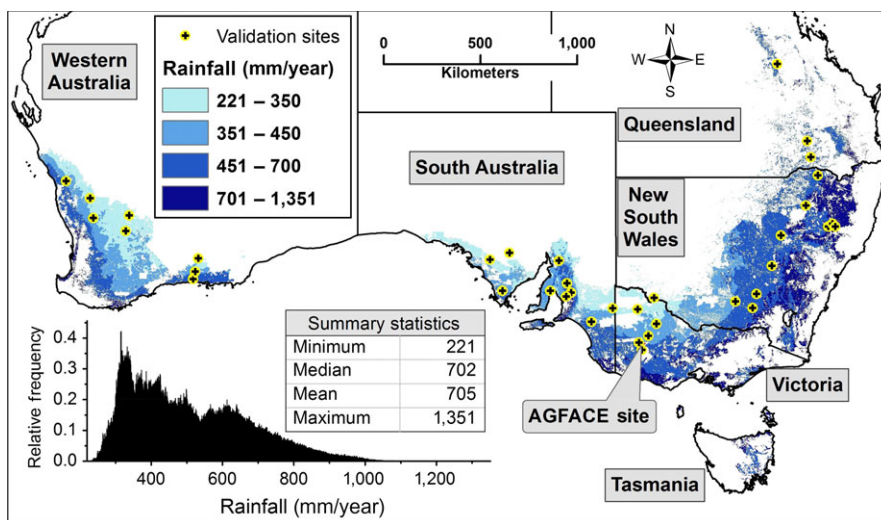
FIGURE 1 The area evaluated above 220 mm/year rainfall within wheat belt for the two wheat cultivars and the location of the Australian Grains Free-Air Carbon Dioxide Enrichment experimental site used for CAT-Wheat parameterization. Graph shows frequency distribution of mean annual rainfall (mm/year, 1975–2005) across study region. Validation site symbols indicate the 60 locations of the validation data for Hartog and Drysdale shown in Figure 2d

simulation at each grid cell, simulations were conducted with unlimited nitrogen to avoid confounding sequencing factors that can be managed by farmers. To reduce the confounding effect of "carry-over" stored soil water from the previous year's crop, the stored soil water status was reset 75 days before sowing to 10% plant available water for each soil depth increment to a total depth of 1 m, and a full plant available water profile below that depth.

For the two wheat cultivars tested (always sown at a site on the same day of the autumn-break), average annual crop yield over the 54-year simulation period, at each site and sowing time, was based on the total yield for each cultivar divided by the number of crops sown within that 54-year period. All forms of crop failure postsowing were included in the calculation of average annual crop yield. This provided a realistic comparative analysis across the landscape, irrespective of whether crop failure was due to a false break in the sowing window or subsequent stress.

An additional validation dataset was sourced from two sources and was used to evaluate spatial model response for multiple locations across Australia. First, crop yield data were obtained 60 locations which evaluated both Drysdale and Hartog in the years 2004 and 2005 from Australian Grains Technologies (S. Jefferies, CEO AGT, 2006, personal communication). Second, 5 years (2011–2015) of crop data, with and without irrigation were source from a multi-environment experiment conducted at Narrabri and Yanco (NSW) and Merredin (WA) (Rebetzke et al., 2013). We did not amend any calibrated parameters in this validation.

3 | RESULTS

3.1 | Model performance against experimental data at the AGFACE site

We were able to reproduce an accurate simulation against the observed biomass at anthesis and maturity and grain yield for both Drysdale and Hartog across the various irrigation and CO_2 treatments (Figure 2). The slope of the simulated vs. observed response was near unity (range of 0.93–1.03) with a calculated root mean square error

(RMSE) of 94, 91, and 74 (g/m^2) for biomass at anthesis and maturity, and grain yield, respectively. Similarly, across our larger dataset the model is seen to be unbiased (slope of 0.998 and 0.982) with similar accuracy with a RMSE 71 g/m^2 (Figure 2d). The cumulative simulated transpiration by Drysdale to anthesis for the 12 crops was 17 mm (1.4%) lower than Hartog, resulting in an additional 60 mm (5.1%) plant available water being available for Drysdale for grain filling. The slope values in Figure 3 are a representation of the growth response (observed and modeled) of a number of variables to elevated CO_2 as by default, this slope value reports the response to elevated CO_2 by dividing the elevated measurement (e.g., grain yield) by the ambient measurement. Based on these slope values, the model simulated (within 3%) the large differential yield response between Drysdale and Hartog to elevated CO_2 which is consistent with the empirical data reported by Tausz-Posch et al. (2012; Figure 3) by using two cultivar-parameters (Table 2), the TE coefficient and crop canopy resistance. The exception was the grain yield CO_2 response for Drysdale (Figure 6f) with its observed slope of grain response to elevated CO_2 being 27.5% above unity compared to the modeled 18.3%.

3.2 | Long-term responses at Horsham

We applied the simulated trait differences between Drysdale and Hartog over 54 years of present and future climate scenarios at Horsham (Figure 4). As sowing data were based on an amount of rainfall falling at an "autumn-break," there was no impact on the average sowing date by raising temperature by 2°C. However, the third climate sequence of reduced rainfall delayed the average sowing date by 16 days (Table 3). The increase in temperature did decrease the length of growing season which resulted in reduced growing season rainfall for the two climate sequences which were elevated by 2°C (Table 3).

Irrespective of the negative and positive effects of temperature and rainfall, the increased TE trait appears of consistent benefit at Horsham. The yield advantage ranged from around 127 to 152 kg/ha under present-day CO_2 concentration and a likely future 550 ppm scenario, respectively (Figure 4a,b).

	Slope value	Slope S.Error	RMSE g/m²
Drysdale	0.969	0.029	91.2
Hartog	1.011	0.035	95.9

	Slope value	Slope S.Error	RMSE g/m²
Drysdale	0.987	0.022	90.4
Hartog	1.028	0.023	91.6

	Slope value	Slope S.Error	RMSE g/m²
Drysdale	0.958	0.058	79.7
Hartog	0.933	0.049	67.3

	Slope value	Slope S.Error	RMSE g/m²
Drysdale	0.998	0.023	71.9
Hartog	0.982	0.024	70.2
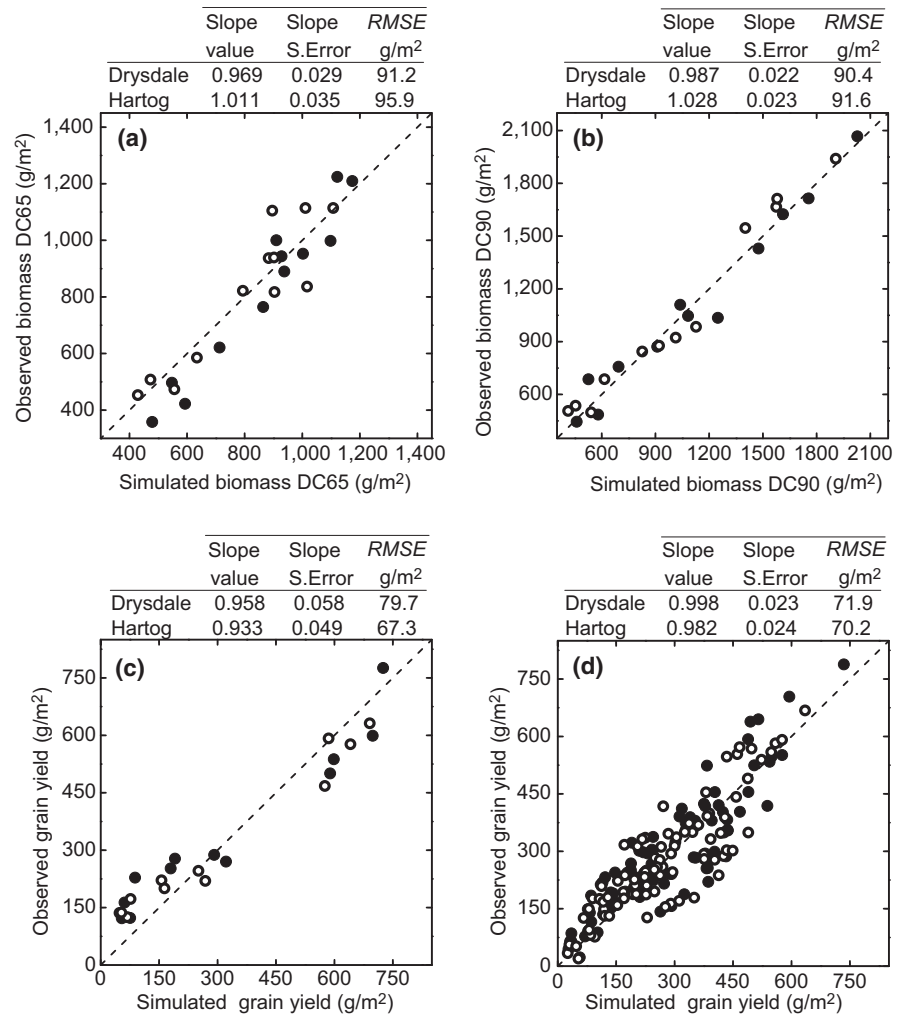
FIGURE 2 Simulated vs. observed values of both Hartog (open circles) and Drysdale (closed circles). Data from Australian Grains Free-Air Carbon Dioxide Enrichment, Horsham with and without supplementary irrigation, at ambient and elevated CO_2 (a) Total biomass at anthesis (DC65) (b) Total biomass at physiological maturity (DC90) and (c) Grain yield. Additional model validation data (60 Australia-wide locations (2004–2005) sourced from Australian Grain Technologies and three sites over 5 years (2011–2015) with and without supplementary irrigation (d) Grain yield

The variation in yield advantage of Drysdale under the likely future 550 ppm scenario had a wider distribution of response compared to current climate, with a greatly enhanced (>10%) yield in 22% of the years tested. However, in poorer seasons this yield advantage tended toward a yield loss (5% of years), reflecting a possible resource limitation during grain filling of Drysdale resulting from early enhanced vegetative growth during these seasons. For example, with the historic climate, 375 ppm scenario, our modeling predicted that Drysdale's yield was lower than Hartog's in the 1984 and 2014 seasons at Horsham. In both these years, the model predicted low plant available water at anthesis and the total rainfall between anthesis and harvest was only 20 mm. At anthesis, in these years, Drysdale's biomass was 5% higher which resulted in greater predicted water stress over the grain fill period. Overall, the range of yield advantage between the 25 and 75 percentiles was wider for the current climate compared to the future 550 ppm scenarios.

3.3 | Responses across Australian arable land

The application of the model across all arable land between 221 and 1,351 mm annual rainfall under the present-day climate showed a mean yield advantage of Drysdale over Hartog from about −7 to 558 kg/ha (mean 187 kg/ha) (Figure 5a). However, there was large spatial variance, with the smallest response in the drier areas of Western Australia, South Australia New South Wales and Queensland, along with the higher rainfall regions of Western Australia, South Australia and Victoria. Under elevated CO_2 conditions, the response of Drysdale was much greater overall, ranging from 51 to 866 kg/ha (mean 284 kg/ha), with the greatest response tending toward the wetter areas (Figures 1 and 5b). Under warmer, drier climates (Figure 5e,f) yield advantage of Drysdale declined more in the higher rainfall regions of the study area.

In these simulations, part of these differences was attributed to changes in TE with a median 8% greater TE of Drysdale over Hartog under the present climate (Figure 6a). This difference in TE increased marginally to 9% under elevated CO_2 (Figure 6b).

Spatial differences in simulated TE were seen across Australia with notably increased areas of higher TE under a drier climate in Queensland, Western Australia and parts of New South Wales and Victoria (Figure 6e,f). Improved efficiency is subtly deceptive because highest yields are not necessarily directly correlated with highest TE. Nevertheless, the portion of the yield advantage of Drysdale over Hartog attributed to TE under current climate conditions ranged from 187 (ambient CO_2) to 284 kg/ha under an elevated
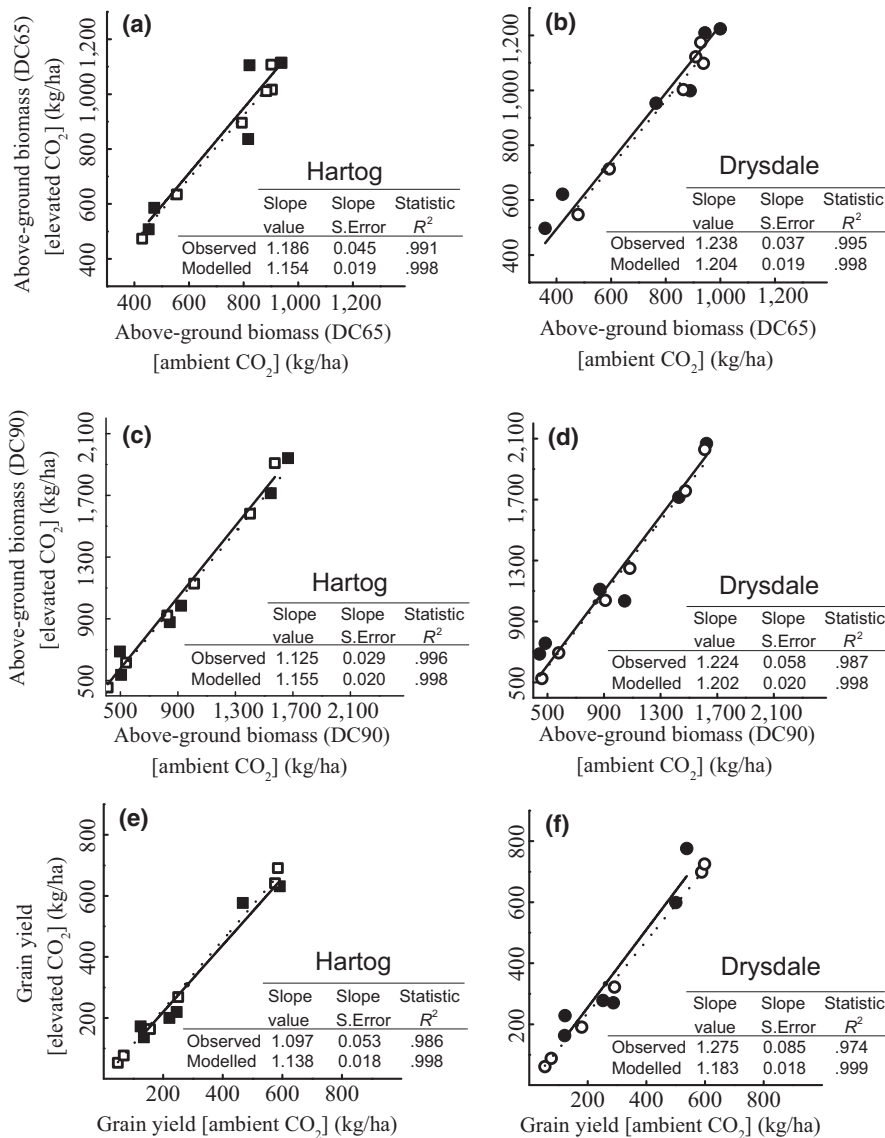
FIGURE 3 Observed and simulated growth response of biomass at anthesis (DC65) (a and b), biomass at physiological maturity (DC90) (c and d) and grain yield (e and f) for Hartog (■ and solid fitted lines) and Drysdale (● and solid fitted lines) and simulated growth response of Hartog (□ and dotted fitted lines) and Drysdale (○ and dotted fitted lines) to elevated CO_2 compared to daytime ambient conditions (375 μmol/mol)

CO_2 environment, while in a drier warmer climate the range was from 143 (ambient CO_2) to 212 (elevated CO_2) kg/ha (Table 4). The potential benefits of this increased genetic TE trait across the average area sown to wheat of Australia from 2011 to 2016 (12.97 Mha), totaled AUD 631 MIL with an average of 187 kg/ha (5 year average wheat price of AUD/260 t) under the present climate. The benefit to individual farmers will depend on location but elevated CO_2 raises this nation-wide benefit to an annual AUD 796 MIL in a 2°C warmer climate, and to a lesser, but still very significant extent, with 20% less rainfall (AUD 715 MIL/year).

4 | DISCUSSION

Using a simulation model validated against data contrasting the high-TE Drysdale and its near-isogenic low-TE parent Hartog, we have demonstrated under present climate an important yield advantage from the high-TE genetic trait in rainfed wheat crops over much of

Australia. This yield advantage was smallest in the extremely dry regions of Western Australia, South Australia, New South Wales and Queensland, along with the higher rainfall regions of Western Australia, South Australia and Victoria (Figure 5). However, under elevated CO_2 conditions, the yield response of Drysdale was much greater overall. It ranged from 51 to 866 kg/ha (mean 284 kg/ha), with the greatest response in the higher rainfall areas and despite the highest TE occurring in the dry to intermediate areas of the Australian cropping region (Figure 6). While the large land area used in our study magnifies the value of the TE trait (Table 4), if applied over the whole of the existing grain producing area the yield advantage of Drysdale varied widely, from −7 to 866 kg/ha under the present climate (Figure 5a,b) and from −18 to 659 kg/ha under elevated CO_2, increased warming and reduced rainfall (Figure 5e,f), depending on location. The seasonal variance in climate (rainfall, temperature, and vapor pressure), sowing times and variability in soil properties in the spatial modeling analysis permitted testing of the TE trait under both water-limited and favorable conditions.
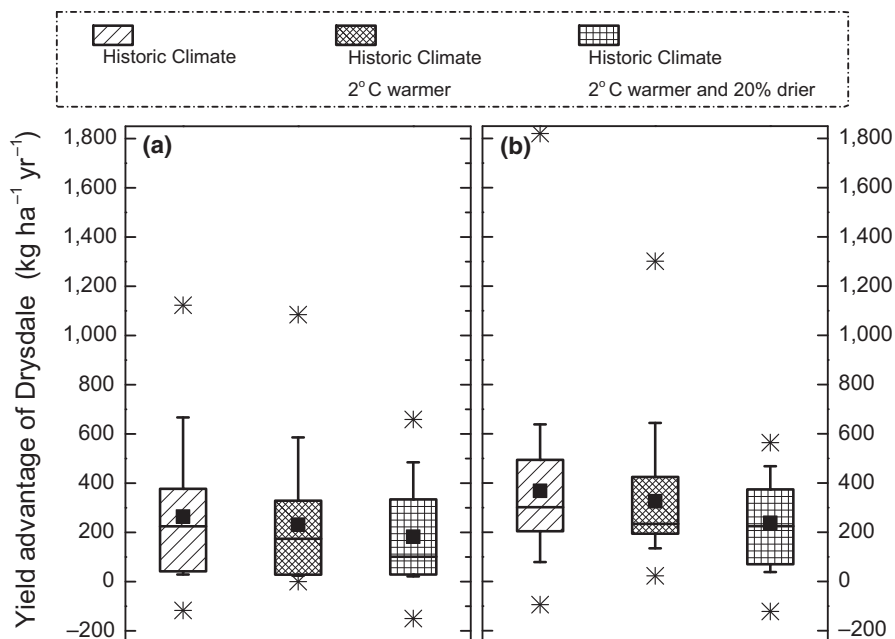
FIGURE 4 Grain yield advantage of Drysdale over Hartog showing 10 percentile, 25 percentile, median (line), average (■), 75 percentile, 90 percentile over 54 years at Horsham under Historic climate (▨), Historic climate 2°C warmer (▦), Historic climate 2°C warmer and 20% less rainfall (▦) at (a) ambient CO_2 (375 mol/mol) (b) elevated CO_2 (550 mol/mol). The absolute minimum and maximum yield advantage achieved is shown as an asterisk on graph

TABLE 3 Average sowing and physiological maturity date, growing season rainfall (mm) and temperature (°C) for wheat cultivars sown on the "autumn-break" (defined as at least 20 mm rainfall in a 5-day period between 14 April and 30 June) resulting from the "historic climate sequence" and the two synthetic sequences of "2°C warmer" and "2°C warmer and 20% less rainfall"

	Average sowing date	Average physiological maturity date	Average growing season rainfall	Average growing season temperature
Historic climate	17-May	9-Dec	320	12.2
Historic climate 2°C warmer	17-May	26-Nov	300	13.6
Historic climate 2°C warmer and 20% less rainfall	2-Jun	30-Nov	226	13.8

Therefore, the result of this modeling reflects TE dependence on environmental factors like vapor pressure deficit (VPD) of the atmosphere whereby TE is reduced as VPD increases (Vadez, Kholova, Medina, Kakkera, & Anderberg, 2014). It provides results at an industry-relevant scale needed to assess the value of the TE trait and its value proposition in commercial breeding (Fischer, 2011; Rebetzke et al., 2013). This confirms the robust nature of the enhanced-TE trait for future climatic conditions and reflects the advantage of low-CID lines in buffering against intermittent water stress that may occur during the growing season (Rebetzke et al., 2002).

The cultivar Drysdale used here as a high-TE example was bred by selecting for low-CID in leaf tissue accumulated immediately prior to stem elongation when soil moisture conditions are favorable. A major advantage of selecting using CID is that TE is integrated over the lifetime that the plant material is sampled (Condon et al., 2004; Farquhar & Richards, 1984). Genetic variation in CID can arise from variation in

both photosynthetic capacity and stomatal conductance and it is likely that the high-TE Drysdale has both a higher photosynthetic capacity at the leaf level and a reduced stomatal conductance (Condon et al., 2004). Both of these are likely to be advantageous at the crop level when there is insufficient soil water as there generally is in most of the Australian cropping regions. The additional assimilation should benefit biomass production whereas the reduced stomatal conductance may conserve soil water prior to anthesis, so that it can be used during the critical grain filling period where crop water use efficiency for grain production is high (Kirkegaard, Lilley, Howe, & Graham, 2007). The small increases in assimilation together with small reductions in stomatal conductance were confirmed in AGFACE field measurements of leaf physiology (Tausz-Posch et al., 2013). However, these physiology measurements also showed that the leaf-level TE advantages of Drysdale only manifest under certain conditions, and can be transient throughout the season. Nonetheless, CID measurements that "store" an assimilation-weighted, longer term signal of TE differences confirm that Drysdale has, on average, higher TE than Hartog.

The difference between Drysdale and Hartog in TE and canopy conductance shows the importance of saving some soil water early for later use during grain formation. By anthesis, our modeling showed that Drysdale had transpired 17 mm less water and conserved 60 mm more soil water than Hartog. This is in agreement with previous experimental evaluation of near-isogenic Hartog wheat lines varying in CID where it was determined that the yield advantage was achieved by a mixture of increased areal biomass growth together with greater partitioning of biomass to grain attributed to greater postanthesis water use (Rebetzke et al., 2002). In our model, increased biomass resulting from increased TE (increased crop transpiration coefficient and increased canopy resistance, Table 2) matched the experimental results in biomass (at both anthesis and maturity), and was sufficient to explain the grain yield advantage observed in the experiment.
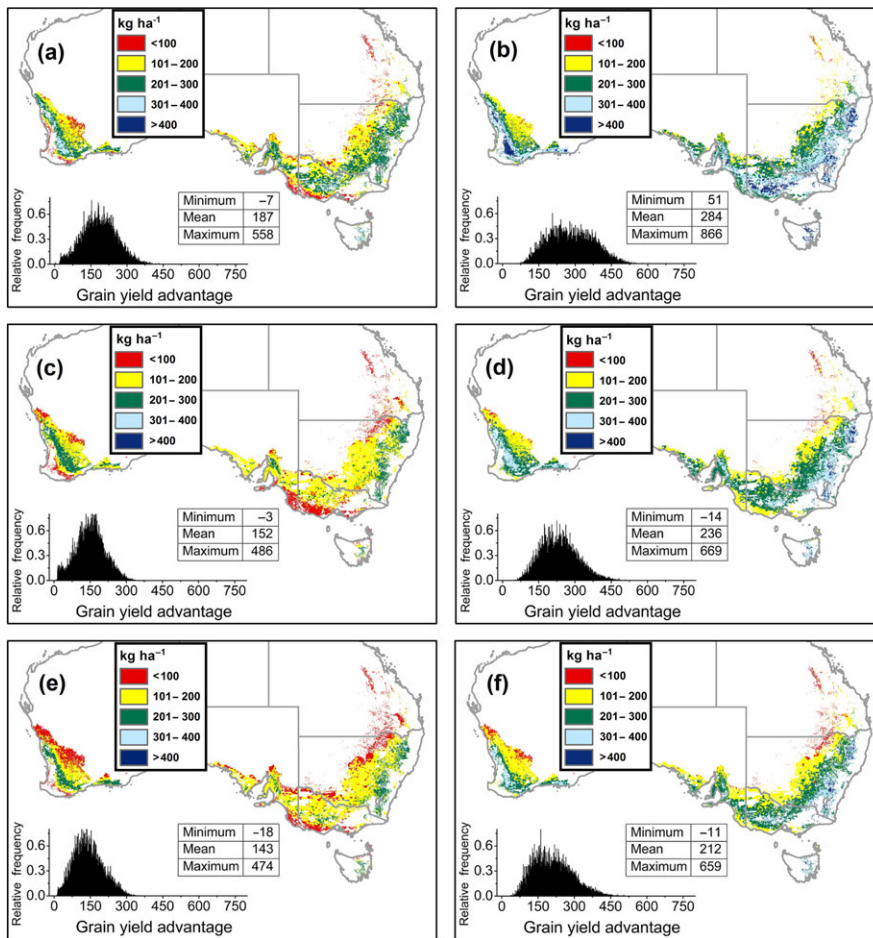
FIGURE 5 Grain yield advantage of Drysdale over Hartog (over 54 years 1962–2015) at (a) Historic climate and ambient CO_2 (375 mol/mol) (b) Historic climate and elevated CO_2 (550 mol/mol) (c) Historic climate, 2°C warmer and ambient CO_2 (375 mol/mol) (d) Historic climate, 2°C warmer and elevated CO_2 (550 mol/mol) (e) Historic climate, 2°C warmer, 20% less rainfall and ambient CO_2 (375 mol/mol) (f) Historic climate, 2°C warmer, 20% less rainfall and elevated CO_2 (550 mol/mol)

Elevated CO_2 is known to increase assimilation and decrease stomatal conductance and therefore increase leaf-level TE of all crops (Leakey et al., 2009). It is commonly assumed that the benefit from elevated CO_2 in growth and yield is greater under drier conditions. Yet despite the greater TE in the drier areas (Figure 6), the highest yield comes predominately from the wetter areas, where both high TE and high transpiration can occur (Figure 5). Correspondingly, a modeling study on earlier AGFACE results did not confirm this general trend toward greater CO_2-benefit under drier conditions (O'Leary et al., 2015), and neither did a recent meta-analysis that summarized only experiments where two different water treatments were compared side-by-side (van der Kooi, Reich, Löw, De Kok, & Tausz, 2016). This may be because higher TE promotes faster leaf area growth and thus greater total transpiration, despite lower conductance. A consequence may be faster depletion of soil water in low rainfall environments where transpired water is not replaced by rainfall to carry the crop through flowering and grain filling. Previous AGFACE studies (Tausz-Posch et al., 2012, 2013) also did not support the assumption that with elevated CO_2, where all crops become more transpiration-efficient, a high-TE trait may become obsolete. In contrast, and as underlined by our model extrapolations in this study, benefits from the high-TE trait may become even greater, at least in rainfed environments experiencing high climate variability. This presumably reflects the more complex crop level responses over a whole season that cannot be directly inferred from infrequent measurements at the leaf level. More detailed modeling is needed to capture improvements of known effects of subdaily changes in transpiration, partitioning and harmonizing energy balance approaches (e.g., Webber et al., 2017) that can be extrapolated over large areas for future work. Our work has shown what is possible with a sufficiently suitable daily time-step model.

It has been demonstrated in this study that selection for CID to improve TE can have a profound yield advantage across most of Australia. Clearly, there is scope to raise wheat grain yields in Australia by increasing biomass TE coefficient despite increased risks of water stress later in the season. Under dryland field conditions, TE for wheat can vary from 3 to 9 g of biomass growth per kg water transpired (Kemanian et al., 2005). This variance raises an obvious question: what is the upper threshold that TE can be increased to for beneficial increases in growth and particularly yield? Crop TE can be increased through both crop management and breeding. Sowing earlier so that there is more crop growth when VPD is low is one easy way of achieving increased TE and this has been shown to be a valuable practice (Gomez-MacPherson & Richards, 1995; Kirkegaard & Hunt, 2010). However in Australia, earlier sowing, as a management tool, has to be matched with an appropriate flowering time (through cultivar choice) to avoid the yield losses associate with frost around flowering and drought and high temperatures post flowering.

FIGURE 6 Transpiration efficiency advantage of Drysdale over Hartog (over 54 years 1962–2015) at (a) Historic climate and ambient CO_2 (375 mol/mol) (b) Historic climate and elevated CO_2 (550 mol/mol) (c) Historic climate, 2°C warmer and ambient CO_2 (375 mol/mol) (d) Historic climate, 2°C warmer and elevated CO_2 (550 mol/mol) (e) Historic climate, 2°C warmer, 20% less rainfall and ambient CO_2 (375 mol/mol) (f) Historic climate, 2°C warmer, 20% less rainfall and elevated CO_2 (550 mol/mol)
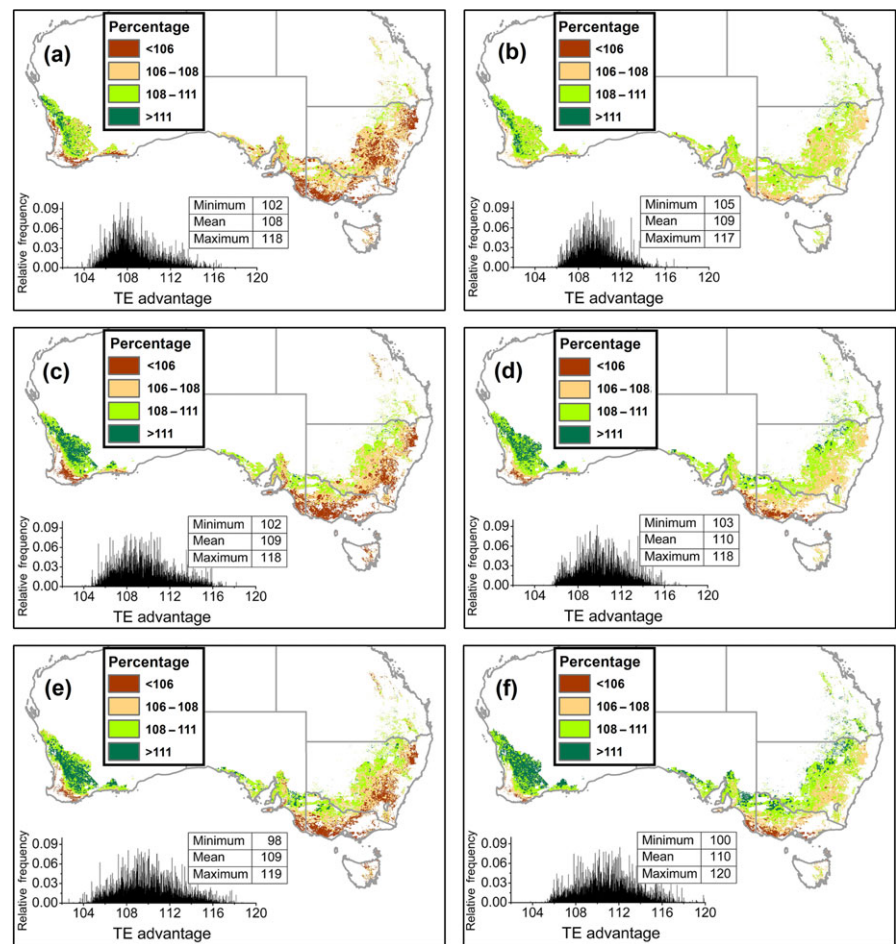
TABLE 4 Grain yield advantage of Drysdale over Hartog under ambient CO_2 (375 mol/mol) and current climate, and elevated CO_2 (550 mol/mol)

Climate	CO_2 (mol/mol)	Mean yield difference (kg/ha)	AUD ($MIL) difference attributed to transpiration efficiency genetic coefficient
Current	375	187	631
Current	550	284	958
Current + 2°C	375	152	513
Current + 2°C	550	236	796
Current + 2°C −20% rainfall	375	143	482
Current + 2°C −20% rainfall	550	212	715

Breeding can also be important for TE in other ways, as is evident from the comparison here between the near-isogenic wheat cultivars Drysdale and Hartog characterized by differences in CID. A range of opportunities for breeding are outlined in Richards et al. (2010), however increasing TE, through lowering CID has been shown to disproportionally lower crop transpiration compared to increased biomass growth. Therefore, further exploration of TE is warranted to further help mitigate against the impacts of future climate change.

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