DR. ALIREZA HOUSHMANDFAR (Orcid ID : 0000-0003-0592-4926)

DR. GLENN J FITZGERALD (Orcid ID : 0000-0001-6972-4443)

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A reduced tillering trait shows small but important yield gains in dryland wheat production

Alireza Houshmandfar[1,2], Noboru Ota[3], Garry J O'Leary[4,5], Bangyou Zheng[6], Yang Chen[7], Sabine Tausz-Posch[8], Glenn J Fitzgerald[2,4], Richard Richards[9], Greg J Rebetzke[9], Michael Tausz[7]

[1] CSIRO Agriculture and Food, Centre for Environment and Life Sciences, Floreat, WA 6014, Australia

[2] Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, Creswick, VIC 3363 Australia

[3] CSIRO Health and Biosecurity, PO Box 1700, Canberra, ACT 2601, Australia

[4] Agriculture Victoria, 110 Natimuk Road, Horsham, VIC 3401 Australia

[5] School of Agriculture and Food, Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, Parkville, VIC 3010 Australia

[6] CSIRO Agriculture and Food, Queensland Bioscience Precinct, 306 Carmody Road, St. Lucia, Qld 4067, Australia

[7] CSIRO Data61, Goods Shed North, 34 Village St, Docklands, VIC 3008, Australia

[8] Department of Agriculture, Science and the Environment, School of Health, Medical and Applied Science, CQUniversity Australia, Rockhampton, 4700 Qld, Australia

[9] CSIRO Agriculture and Food, PO Box 1700, Canberra, ACT 2601, Australia

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Abstract

Reducing the number of tillers per plant using a tiller inhibition (*tin*) gene has been considered as an important trait for wheat production in dryland environments. We used a spatial analysis approach with a daily time-step coupled radiation and transpiration efficiency model to simulate the impact of the reduced-tillering trait on wheat yield under different climate change scenarios across Australia's arable land. Our results show a small but consistent yield advantage of the reduced-tillering trait in the most water-limited environments both under current and likely future conditions. Our climate scenarios show that whilst elevated [CO_2] (e[CO_2]) alone might limit the area where the reduced-tillering trait is advantageous, the most likely climate scenario of e[CO_2] combined with increased temperature and reduced rainfall consistently increased the area where restricted tillering has an advantage. Whilst long-term average yield advantages were small (ranged from 31 to 51 kg ha^{-1} yr^{-1}), across large dryland areas the value is large (potential cost-benefits ranged from AUD 23 to 60 MIL yr^{-1}). It seems therefore worthwhile to further explore this reduced-tillering trait in relation to a range of different environments and climates, because its benefits are likely to grow in future dry environments where wheat is grown around the world.

Keywords: APSIM next generation, climate change, semi-arid environments, *Triticum aestivum*, water use efficiency

Introduction

Wheat (*Triticum aestivum* L.) containing a reduced-tillering *tin* (tiller inhibition) gene (Atsmon and Jacobs, 1977) has been proposed as an important breeding objective to increase grain yield in dryland environments (Hendriks et al., 2015; Reynolds et al., 2009; Richards, 1988). The advantage of the reduced-tillering trait is in its constraining of excessive tillering and therefore leaf area development and water use during early- to mid-season when temperature and water availability are favourable for tiller initiation (Richards, 1988; Sharma, 1995), shifting soil water availability from pre- to post-anthesis crop growth when drought and temperature stress are frequent (Berry et al., 2003; Richards, 1988; Stephens and Lyons, 1997).

Water availability has long been recognised as a key component and dominant variable affecting crop production in dryland environments, where annual rainfall ranges from about 300 to 600 mm and rainfall variability is substantial (Dawson, 1957). The importance of rainfall varies both temporally and spatially, being a function of rainfall amount and distribution, as well as the ability of respective soils to store water (Stephens and Lyons, 1997). The reduced-tillering trait can be advantageous in some growing environments (i.e. growing seasons and locations) where post-anthesis soil water is critically limiting (Duggan et al., 2005; Moeller and Rebetzke, 2017; Richards, 1988). Whereas in other environments with greater water availability, the free-tillering phenotypes may be superior as tillering provides a greater potential to respond to increasing water availability. The propensity to tiller allows for the development of a greater leaf area and the capacity to capture resources (viz. water, CO_2, solar radiation, and mineral nutrients) needed for increasing biomass and yield (Duggan et al., 2005; Mitchell et al., 2013; Sadras and Rebetzke, 2013). The greater growth and water use, however, in turn may also reduce soil water availability later in the season, worsening terminal drought so that only fewer number of tillers translate into fertile spike. Thus there is uncertainty as to whether the reduced tillering-trait leads to increased or decreased yield when local climate conditions vary. Despite the benefits reported in a number of experimental locations and years (e.g. Mitchell et al. (2012) and Moeller and Rebetzke (2017)), there is a lack of systematic quantification of long-term advantages of the reduced-tillering trait across a range of growing environments, especially taking into account likely future conditions.

Global atmospheric [CO_2] is likely to reach 550 μmol mol^{-1} by 2050 (Solomon et al., 2007), up from just over 400 μmol mol^{-1} at present (2020). Elevated [CO_2] (e[CO_2]) leads to a number of beneficial growth and physiological responses, many of which are interpreted in the context of ameliorating the negative impacts of drought (Leakey et al., 2009; Wullschleger et al., 2002). Elevated [CO_2] decreases stomatal conductance (e.g. Ainsworth and Rogers (2007) and Houshmandfar et al. (2015)), which, in turn, can translate into a proportional reduction in canopy level transpiration (e.g. Houshmandfar et al. (2018) and Leakey et al. (2009)), depending on other determinates of canopy level transpiration, e.g. leaf area index. The suitability of the reduced-tillering trait to a growing environment may be different under e[CO_2], especially if combined with other likely climate change-related events such as reduced rainfall and higher temperatures (Solomon et al., 2007).

Limited information is available about the reduced-tillering trait performance under e[CO_2]. Results from field experiments under ambient [CO_2] (a[CO_2]) have also been highly variable from site to site and from season to season (e.g. Mitchell et al. (2012) and Houshmandfar et al. (2019)). Experimental approaches aimed at interpreting the interaction between genotype and environment are time-consuming, especially where capturing the impact of long-term climate is needed (Asseng and Turner, 2007; He et al., 2017). Crop simulation modelling is another approach allowing long-term assessment under different growing conditions, and especially valuable where it is based on robust data from rigorous field experiments (Christy et al., 2018; Zhao et al., 2019). In this current paper, we used experimental data from two growing seasons at the Australian Grains Free-Air CO_2 Enrichment (AGFACE) facility together with other published data and crop simulation modelling to (i) better understand the interaction between genetic and environmental components of the reduced-tillering trait in wheat and (ii) extrapolate its potential long-term average benefits across Australia's arable land (i.e. land capable of being used to grow crops). The potential yield advantages under the present climate and likely future warmer and drier climate scenarios under e[CO_2] were considered.

Materials and methods

We analysed data from field experiments conducted in the AGFACE facility, and used published data from multiple sites representing the main environment types in Australia's wheatbelt (Mitchell et al., 2012), to validate the Agricultural Production Systems sIMulator (APSIM) (Brown et al., 2014; Holzworth et al., 2018; Holzworth et al., 2014) to reproduce the reduced-tillering trait in wheat under a range of growing environments and under e[CO_2]. The model was then used to extrapolate potential long-term average benefits of the reduced-tillering trait across Australia's arable land. We used APSIM because it has been widely used in wheat in climate change (e.g. Hochman et al. (2017) and Wang et al. (2018)) and crop trait evaluation (e.g. Zhao et al. (2019)) studies, and has recently been successfully tested against other AGFACE data (O'Leary et al., 2015). The model is capturing the CO_2 effects on assimilation rates through modifiers of radiation use efficiency. Transpiration is a function of daily dry matter increase multiplied by transpiration efficiency, which, in turn, depends on vapour pressure deficit and [CO_2] (Holzworth et al., 2014; O'Leary et al., 2015). Actual transpiration and assimilation rates are reduced if available soil water is inadequate to meet the transpiration demand (Holzworth et al., 2014).

Simulations were set up according to the rules established for quantifying grain yield in previously published studies under rainfed conditions, with non-limiting nutrients and well-controlled biotic stresses. Under such conditions, wheat production is determined by the amount and distribution of rainfall, solar radiation, temperature, atmospheric [CO_2], and fixed physical attributes of the soil (Hochman et al., 2017). These settings were unchanged for the duration of the simulations (1962–2018).

The AGFACE experiments

Two field experiments were conducted in 2011 and 2012 growing seasons at the AGFACE site (Fitzgerald et al., 2016) located in Horsham, Victoria (Fig. 1 and Fig. 2). The site has a Mediterranean type climate but with cooler and drier winters (Hutchinson et al., 2005). Long-term average annual rainfall (1962–2018) of the area is 433.1 mm (standard deviation = 117.0 mm). Long-term average maximum and minimum temperatures are 21.5 °C and 8.2 °C (Australian Bureau of Meteorology).

The soil type is a Vertosol clay with non-dispersive and pedal surface (Isbell, 2016), approximately 35% clay at the top increasing to 60% at 1.4 m depth. The experiment had eight plots (16 m in diameter) of which four were ambient CO_2 (approximately 380 µmol mol^{-1}, average daytime [CO_2]) and four elevated CO_2 (centre concentration set at 550 µmol mol^{-1}). Each elevated CO_2 plot was encircled by horizontal CO_2-release-tubes in an octagonal shape which were progressively raised as the crop grew so that the CO_2 was injected about 15 cm above the canopy. A plot centre [CO_2] of 550 µmol mol^{-1} was maintained for the elevated CO_2 treatment from sunrise to sunset starting from germination. Average plot central [CO_2] were recorded every minute with an infrared gas analyser (IRGA, SBA-4, PP Systems, Amesbury, MA, USA) located at the central part of each plot. The spatial variations in the [CO_2] of the site were described by Mollah et al. (2009).

Two wheat (*Triticum aestivum* L.) genotypes contrasting in presence of the *tin* gene, “Silverstar” and “Silverstar + *tin*”, were sown into two randomly allocated subplots (1.5 × 4 m, row spacing = 0.27 m), one each in opposing halves of the ring under either rainfed or supplemental irrigation. Silverstar is an early maturing cultivar initially bred for low rainfall environments but is also suitable for higher yielding environments, as reported by Riffkin et al. (2003). Silverstar + *tin* was a $BC_2F_{6:8}$ breeding line SsrT65, derived by backcrossing a *tin* donor to the spring wheat variety Silverstar (Mitchell et al., 2013). For the supplemental irrigation treatments, a total of 100- and 120-mm irrigation was applied in five splits from 6 September to 18 October in 2011 and in four splits from 11 September to 29 October in 2012, respectively. This resulted in eight sets of environmental growing conditions: 2 years × 2 [CO_2] × 2 watering regimes. Sowing dates were 25 May in 2011 and 30 May in 2012. Annual rainfall was 552.5 mm in 2011 and 301.8 mm in 2012.

Total aboveground biomass was measured at anthesis (DC65, Zadoks et al. (1974), DC: decimal code) and physiological maturity (DC90, harvest). At each sampling date, plants were hand-harvested and counted for number of plants and number of tillers m^{-2} from 0.675 m^2 (5 rows × 0.27 m row spacing × 0.5 m length, including edge rows) of each subplot. ‘Edge rows’ refers to the sub-plots arranged within the closed canopy of the whole ring, so that any growth stimulation due to edge effects between sub-plots would have been very small. Appreciable edge effects would lead to overestimates of growth and yield, which would introduce significant positive deviations from the 1:1 lines in Fig. 3. The DC65 samples were dried for 72 h at 70°C. The DC90 samples were dried for 72 h at 40°C. The DC90 samples were further processed for grain yield. All parameters were expressed on an area basis. Anthesis and physiological maturity dates were recorded for each treatment year. A preliminary analysis of data from these experiments is given in Löw et al. (2015).

The APSIM model parameterisation

APSIM Next Generation Plant Modelling Framework (Holzworth et al., 2018) was tested against the AGFACE field data (Table 1), ensuring observed phenological stages of DC65 and DC90 were matched. Both Silverstar and Silverstar + *tin* were parameterised identically except for one parameter, potential branching rate (i.e. tiller initiation rate). The tiller inhibition gene restricts tiller number to a maximum of 4 tillers per plant (Duggan et al., 2005; Richards, 1988). Potential branching rate was therefore decreased from the APSIM default of 20 tillers plant^{-1} (total tiller population including non-fertile tilers) in the cultivar Silverstar to 4 tillers plant^{-1} in Silverstar + *tin*. The model reproduces the development of wheat leaves and tillers using a cohort approach based on the coordination of leaf and tiller initiation on main stem and tillers (Brown et al., 2014). Leaves and tillers that initiate at the same time belong to the same leaf or tiller cohorts and grow following the same pattern. Tillering (branching) is simulated with leaf number and a potential rate following the pattern of a Fibonacci series between germination and terminal spikelet. The actual branching rate is the potential branching rate reduced by water and nitrogen deficiencies, and further constrained by carbon assimilate supply (Evers et al., 2006). Tillering stops at terminal spikelet and tiller mortality occurs thereafter. Later initiating tillers with slower growth rate and the smallest tillers will die first. At the terminal spikelet, all tillers with less than four leaves stop growing new leaves (see Zhao et al., 2019).

For each season, the model was initialised to match measured sowing soil water content and available mineral nitrogen content through the soil profile (pooled across the experiment). Irrigation was applied by the model on the actual days of application. Due to variable seedling establishment across treatments, number of plants m^{-2} were highly variable for different treatments and sampling dates (Table 1). Therefore, to have a meaningful test of the model, we used the actual (measured) number of plants m^{-2} for each treatment simulation.

TABLE 1 Summary of the observed number of plants, number of tillers, biomass at anthesis (DC65) and physiological maturity (DC90), as well as the harvested grain yield results from the AGFACE experiment. The values are averages from four replicates each (Löw et al., 2015). ± Standard error.

Sowing date	Rain (mm)	Irrigation (mm)	Measurement	Silverstar		Silverstar + *tin*	
				a[CO_2]	e[CO_2]	a[CO_2]	e[CO_2]
25/04/2011	552.5	0.0	Number of plants DC65 (m^{-2})	110.8±6.0	138.0±32.6	169.2±35.8	109.7±18.9
			Number of tillers DC65 (m^{-2})	539.6±49.0	581.0±66.2	237.2±52.8	303.3±85.5
			Biomass DC65 (kg ha^{-1})	7201±689	9648±461	7377±1624	8371±1223
			Number of plants DC90 (m^{-2})	81.0±8.9	84.2±8.4	97.9±20.4	47.9±6.2
			Number of tillers DC90 (m^{-2})	419.3±44.0	520.7±53.0	171.2±56.2	219.5±22.3

			Biomass DC90 (kg ha^{-1})	13252±908	18742±1323	8956±1753	11707±1388
			Grain yield (kg ha^{-1})	5305±635	7352±557	3889±833	4736±663
25/04/2011	552.5	100.0	Number of plants DC65 (m^{-2})	115.0±12.5	153.3±7.3	122.6±22.1	111.3±21.0
			Number of tillers DC65 (m^{-2})	503.8±66.1	670.2±22.2	388.9±110.4	256.2±35.9
			Biomass DC65 (kg ha^{-1})	8593±1046	11172±541	7721±1209	8976±886
			Number of plants DC90 (m^{-2})	120.7±35.2	110.5±13.6	71.7±20.7	89.0±20.0
			Number of tillers DC90 (m^{-2})	533.0±59.0	576.3±76.0	256.3±35.9	257.5±53.1
			Biomass DC90 (kg ha^{-1})	16033±595	20227±1578	9982±1081	13166±1501
			Grain yield (kg ha^{-1})	6503±612	8447±540	4183±461	5860±571
30/04/2012	301.8	0.0	Number of plants DC65 (m^{-2})	121.9±5.1	88.5±11.8	107.0±14.0	100.7±8.8
			Number of tillers DC65 (m^{-2})	506.6±47.1	463.7±58.6	168.7±12.0	235.1±6.9
			Biomass DC65 (kg ha^{-1})	7451±174	7290±700	5328±188	7417±116
			Number of plants DC90 (m^{-2})	89.6±1.9	91.5±8.3	74.8±5.4	87.0±8.4
			Number of tillers DC90 (m^{-2})	485.4±44.0	430.5±33.8	219.4±21.7	256.3±16.4
			Biomass DC90 (kg ha^{-1})	12487±1177	12678±841	9965±680	12365±1163
			Grain yield (kg ha^{-1})	5555±766	5741±225	4689±210	5635±596
30/04/2012	301.8	120.0	Number of plants DC65 (m^{-2})	76.3±13.3	100.4±7.1	80.0±4.4	104.4±6.2
			Number of tillers DC65 (m^{-2})	488.5±59.4	534.2±49.0	173.2±30.7	222.2±17.1
			Biomass DC65 (kg ha^{-1})	7493±732	9259±734	5532±712	7433±934
			Number of plants DC90 (m^{-2})	85.2±9.3	84.4±8.1	87.0±8.4	89.6±12.4
			Number of tillers DC90 (m^{-2})	436.8±23.1	530.2±81.5	198.3±30.3	236.9±3.7
			Biomass DC90 (kg ha^{-1})	13602±450	18557±1713	11312±1009	15321±715
			Grain yield (kg ha^{-1})	6078±253	8763±853	5568±559	7169±720

The model was further validated using published data in Mitchell et al. (2012). The paper reported grain yield in cultivar Silverstar and Silverstar + *tin* ($BC_2F_{6:8}$ breeding lines SsrT02, SsrT14, and SsrT17) at five locations (Fig. 1), representative of the main environment types in Australia's wheatbelt. The locations were Gatton, Kingsthorpe, and Emerald in Queensland, Balaklava in South Australia, and Junee in New South Wales. The soils at Gatton, Kingsthorpe and Emerald were self-mulching, black-cracking clay Vertosols with high water-holding capacity. At Balaklava, the soil was a hard-setting, red-brown duplex soil with a sandy loam texture, and at Junee soil was a free-draining, red gradational loam (Mitchell et al., 2012). Long-term average annual rainfall (1962–2018) was 776.2 mm in Gatton (standard deviation = 207.7 mm), 687.9 mm in Kingsthorpe (standard deviation = 179.3 mm), 607.7 mm Emerald (standard deviation = 205.0 mm), 331.6 mm in Balaklava (standard deviation = 81.3 mm), and 519.4 mm in Junee (standard deviation = 147.9 mm).

The slopes of the relationships between simulated and observed values were compared using 95% confidence intervals calculated from the standard error (Lentner et al., 1982). Statistical analyses were performed and graphs were produced using R software (v 3.0.3) (R Core Team, 2000). Geospatial analyses were performed using ESRI ArcMap 10.6 (ESRI 2018. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). Water Use Efficiency (WUE) was defined as grain yield per unit water supply, calculated by dividing grain yield in kg ha^{-1} by water supply in mm (water supply = seasonal rainfall + initial plant available water content in soil).

The APSIM model long-term analyses at Horsham and other validation sites

The APSIM model was used to investigate the productivity change resulting from the reduced-tillering trait in wheat at the AGFACE (Horsham) and other validation sites (Mitchell et al., 2012), using SILO gridded daily climate data (Jeffrey et al., 2001) from 1962 to 2018. The long-term modelling conducted at ambient and elevated [CO_2] of 380 and 550 µmol mol^{-1}, respectively for the historic 57-year sequence ("historic climate"), plus two additional climate sequences of "historic climate + 2°C warmer", created by increasing the daily average temperature by 2°C across the 57-year period, and "historic climate + 2°C warmer + 20% less rainfall", created by increasing the daily average temperature by 2°C and decreasing daily rainfall by 20% over the 57-year period. These changes were selected to approximate a warmer and drier climate expected by 2050 (Christy et al., 2018). Silverstar and Silverstar + *tin* sown each year on the same day after the autumn-break, defined as at least 10 mm rainfall in a 5-day period between 14 April and 30 June. In total, 684 simulations were conducted for each location (2 genotypes × 2 [CO_2] × 3 climate scenarios × 57 years).

The APSIM model spatial analysis across Australia

The long-term analyses at the validation sites were extended across all privately owned, arable agricultural land in Australia, the spatial region identified in Fig. 1. The spatial area was divided into 0.05° × 0.05° grid cells for modelling. For each grid cell within this region, the APSIM model was run for 2 genotypes × 2 [CO_2] × 3 climate scenarios × 57 years. Upscaling to a total evaluated area of 68,083,675 ha, the APSIM model simulated 15,394,788 site-years of wheat growth (1962–2018). Daily climate data for each grid cell were sourced from the SILO gridded daily climate data available for each 0.05° × 0.05° across Australia (Jeffrey et al., 2001). Soil data for each grid cell were sourced from the Soil and Landscape Grid of Australia (Grundy et al., 2015). The average annual crop yield potential over the 57-year simulation period at each site and sowing time was based on the total yield for each genotype divided by the number of crops sown in 57 years. To have a realistic comparative analysis across the landscape, all forms of post sowing crop failure were included in the calculation of average annual crop yield (Christy et al., 2018).

Results

Model performance against experimental data

Testing of observed (Table 1 and Mitchell et al. 2012) vs. simulated values indicated that the model was able to accurately reproduce the observed phenology (no difference between the two genotypes were observed, data not shown), tillers number (Fig. 3c), biomass (Fig. 3b), and grain yield (Fig. 3a) for Silverstar and Silverstar + *tin* under ambient and elevated [CO_2]. The slopes of the simulated vs. observed responses were near unity with a calculated root mean square error (RMSE) ranging from 34 to 75 tiller m^{-2} for number of tillers at anthesis, from 23 to 53 tiller m^{-2} for number of tillers at maturity, from 412 to 672 kg ha^{-1} for biomass at anthesis, from 827 to 1730 kg ha^{-1} for biomass at maturity, and from 127 to 710 kg ha^{-1} for grain yield for the two genotypes under ambient and elevated [CO_2]. The parameter estimates for the slope of the relationship between observed and simulated values were not significantly different from each other at any of the measurement dates, i.e. the model accuracy in reproducing the two genotypes and CO_2 conditions were statistically similar.

The lack of a significant treatment effect of the + *tin* gene raises questions as to the usefulness of the gene at the Horsham experimental site or the suitability of the site to express any measurable benefit. The latter appears more likely because in the years that the experiments were conducted the annual rainfall + irrigation ranged from about 300 to 650 mm (Table 1), which is not considered very dry. The impact of drier seasons across Australia was therefore explored with simulation modelling.

Long-term responses at Horsham and other validation sites

The trait difference between the two genotypes (Silverstar and Silverstar + *tin*) was simulated over 57 years of present and future climate scenarios at Horsham and other validation sites (Fig. 4 and Fig. 5). Silverstar + *tin* produced a greater grain yield than Silverstar in 38% of the site-years across all sites and climate scenarios (Fig. 5). These yield advantages however did not result in a greater long-term average yield of Silverstar + *tin* over Silverstar at any of the simulated sites and climate scenarios, except for Emerald where the long-term average yields were greater by 19 to 78 kg ha^{-1} yr^{-1}.

Spatial analysis across Australia's arable land

The application of the model across all privately owned arable agricultural land in Australia showed an average yield advantage of 36.1 kg ha^{-1} yr^{-1} in Silverstar + *tin* over Silverstar in 26% of the total evaluated area under the present-day climate (averaged for 57 years, Fig. 7 and Fig. 8, Table 2).

Under e[CO_2] conditions, grain yield of Silverstar + *tin* was greater than that of Silverstar in 18% of the total evaluated area but the average yield advantage was greater (43.4 kg ha^{-1} yr^{-1}) (Fig. 8 and Table 2). The size of the area where Silverstar + *tin* had a greater yield than Silverstar and the size of the effect were least under + 2°C warmer climate but greatest under + 2°C warmer + 20% less rainfall (Fig. 8 and Table 2). These yield advantages were related to water supply, defined as growing season rainfall plus initial plant available water in soil. On average, the benefit seemed to be greater at growing seasons with water supply of < 184-185 mm under the present-day climate (a[CO_2] (a) and e[CO_2] (b), Fig. 6), < 165-167 mm under the + 2°C warmer (a[CO_2] (c) and e[CO_2] (d), Fig. 6), < 153-156 mm under the + 2°C warmer + 20% less rainfall (a[CO_2] (e) and e[CO_2] (f), Fig. 6), and completely disappeared at growing seasons with water supply of greater than ~1000 mm (Fig. 6).

TABLE 2 Grain yield in the areas where long-term average yield of Silverstar *+ tin* is greater than Silverstar (areas coloured in green in Fig. 8). (a) historic climate and a[CO_2] (380 µmol mol^{-1}), (b) historic climate and e[CO_2] (550 µmol mol^{-1}), (c) historic climate + 2°C warmer and a[CO_2], (d) historic climate + 2°C warmer and e[CO_2], (e) historic climate + 2°C warmer + 20% less rainfall and a[CO_2], and (f) historic climate + 2°C warmer + 20% less rainfall and e[CO_2]. Water Use Efficiency (WUE) was defined as grain yield per unit water supply, calculated by dividing grain yield in kg ha^{-1} by plant available soil water (mm) at sowing + growing season rainfall from sowing to physiological maturity. ±: standard deviation. AUD differences are based on the average area sown to wheat in Australia (= 12.97 M ha yr^{-1}) and average price of AUD 260 t^{-1} (2011-2016).

	a	b	c	d	e	f
Area (M ha)	18.14	12.20	15.26	11.49	26.89	23.77
Average water supply (mm)	266±48	253±39	258±57	242±44	218±54	208±43
Average yield in Silverstar + *tin* (kg ha^{-1} yr^{-1})	3530±717	3661±695	4263±782	2860±808	3050±675	3483±888
Average yield advantage of Silverstar + *tin* (kg ha^{-1} yr^{-1})	36.1±26.3	43.4±34.7	31.6±23.1	41.4±30.8	39.9±28.6	51.0±35.2
Average WUE in Silverstar + *tin* (kg ha^{-1} mm^{-1}yr^{-1})	13.39±2.08	17.02±2.72	11.91±1.59	15.26±2.13	13.13±2.36	16.78±2.95
Average WUE advantage of Silverstar + *tin* (kg ha^{-1} mm^{-1} yr^{-1})	0.14±0.12	0.19±0.18	0.13±0.09	0.18±0.15	0.19±0.13	0.26±0.19
AUD differences attributed to + *tin* genetic coefficient ($MIL)	32.5	26.2	23.9	23.6	53.2	60.1

Discussion

We used a spatial modelling approach to compare grain yields of two genotypes with the same genetic background but contrasting in the expression of the reduced-tillering trait under different climate change scenarios across Australia's arable land. Our study region represents an important proportion of global wheat production and is typical of many dryland cropping environments throughout the world (e.g., CIMMYT Mega environment 1, 2, 4 and 8, Braun et al. (1996)) experiencing significant changes in climate (Christy et al., 2018). The seasonal variability in climatic variables (e.g. water availability and temperature) and sowing times in the spatial analysis allowed evaluating the reduced-tillering trait in a range of different water-limited and favourable environments. Our results show that the contribution of the reduced-tillering trait to grain yield is strongly influenced by environment. Due to the complex physiological processes and their interactions during the growing period for yield formation, the reduced-tillering trait may not be beneficial when all growing seasons are considered but becomes important in low-yielding, water-limited seasons (Fig. 6). Accounting for the long-term variability of rainfall, the reduced-tillering trait showed a greater yield in 26% of the total evaluated area of 68.01 M ha, under the present-day climate (Fig. 8 and Table 2). Genetic gain in dry environments is less reliable than in wetter regions or where irrigation is available (Richards et al., 2002), because the variable environmental conditions allow the most favourable environment × genotype interaction only in a fraction of growing season. Data from previous studies suggest an average overall rate increase of 18 kg ha^{-1} yr^{-1} by Australian wheat genotypes from 1958 to 2007 (Sadras and Lawson, 2013). Our data suggests that under the present-day climate the reduced-tillering trait has the potential to improve yield by 36 kg ha^{-1} on 3.4 M ha of the total 12.97 M ha sown to wheat in Australia each year (equals to a potential annual cost-benefit of AUD 32 MIL, see Table 2). The grain yield improvements reported herein and in Sadras and Lawson (2013) are for attainable yields achievable through skilful use of the best available technology (Connor et al., 2011).

Growth under the most likely future conditions (e[CO_2] + 2°C warmer + 20% less rainfall) advantage the reduced-tillering trait compared to the present in a larger area, but temperature increase and e[CO_2] in general mitigates that advantage somewhat (Fig. 8 and Table 2). In our simulations we assumed a uniform temperature increase throughout the growing season. Water-saving effects of e[CO_2] on transpiration efficiency may compensate for the increased evaporative demand caused by this temperature increase, but this compensation seemed insufficient to overcome an additional 20% decrease in rainfall. Our extrapolations confirm the trait value for particularly water-limited conditions, as predicted in previous evaluations of the reduced-tillering trait (e.g. Houshmandfar et al. (2019)). The interactions between e[CO_2] and transpiration efficiency are not straightforward, as potential water saving effects are dependent on timing and extent of drought and rainfall events (Houshmandfar et al., 2016; Tausz-Posch et al., 2019). Our modelled results capture these interactions well where they depend on the relationship between biomass growth, water supply and transpiration efficiency, and are robust in the extrapolation of the relative differences between the cultivars (Zhao et al., 2019).

We used a number of different lines that were all derived by backcrossing a *tin* donor to the spring wheat variety Silverstar (Mitchell et al., 2013), to validate the model employing the exact same setup. Tiller production is dependent on genetics-by-environment-by-management interactions (Innes et al., 1981). The presence of the *tin* gene provides a genetic control on the potential number of tillers produced by a plant, but this varied from line to line depending on unknown modifier genes controlling the level of *tin* expression to affect tiller numbers (Mitchell et al., 2013). Reduced-tillering lines can be therefore classified as restricted or semi-restricted lines (Mitchell et al., 2013), based on the maximum number of tillers produced per plant (Mitchell, 2010). The lines we employed to validate the model (viz. SsrT65, SsrT02, SsrT14 and SsrT17) were all restricted tillering lines, each producing a maximum of 4 tillers plant^{-1} (Mitchell, 2010).

In conclusion, we suggest a small but consistent yield advantage conferred by the reduced-tillering trait in the most water-limited environments both under current and likely future conditions. Our climate scenarios show that whilst increasing [CO_2] alone might limit the area where the reduced-tillering trait is advantageous, the most likely climate scenario with CO_2 combined with increased temperature and reduced rainfall consistently increased the area where restricted tillering has an advantage. Whilst yield advantages are small, it seems worthwhile to further explore this reduced-tillering trait in relation to a range of different environments and climates, because its benefits are likely to grow in future dry environments.

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ORCID

Alireza Houshmandfar https://orcid.org/0000-0003-0592-4926

Data Availability Statement

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

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Figure legends

Figure 1 Long-term average (1962–2018) annual rainfall (mm) within Australia's arable land for the two wheat genotypes and the location of the experimental sites used to validate the APSIM model. Bar graphs show the long-term average monthly rainfall from January to December, respectively.

Figure 2 Daily min (black dashed line) and max (black solid line) temperatures (°C) as well as rainfall (grey solid line) (mm) in 2011 (a) and 2012 (b) at the AGFACE (Horsham).

Figure 3 Simulated vs. observed values of Silverstar (●○●○) and Silverstar + *tin* (■□■□). (a) grain yield data from the AGFACE (Horsham) site at a[CO_2] (□○) and e[CO_2] (■●), and from the other validation sites at a[CO_2] only (□○) (Mitchell et al., 2013). (b) biomass at anthesis (■□●○) and at physiological maturity (■□●○) from the AGFACE site. (c) number of tillers at anthesis (■□●○) and at physiological maturity (■□●○) from the AGFACE site (c). Tables on top of panels show fitting parameter statistics for the linear fits to data subsets as indicated in the row titles to the left, and in the first row of each table. RMSE: root mean squared error. SE: standard error. Dashed line is 1:1 line.

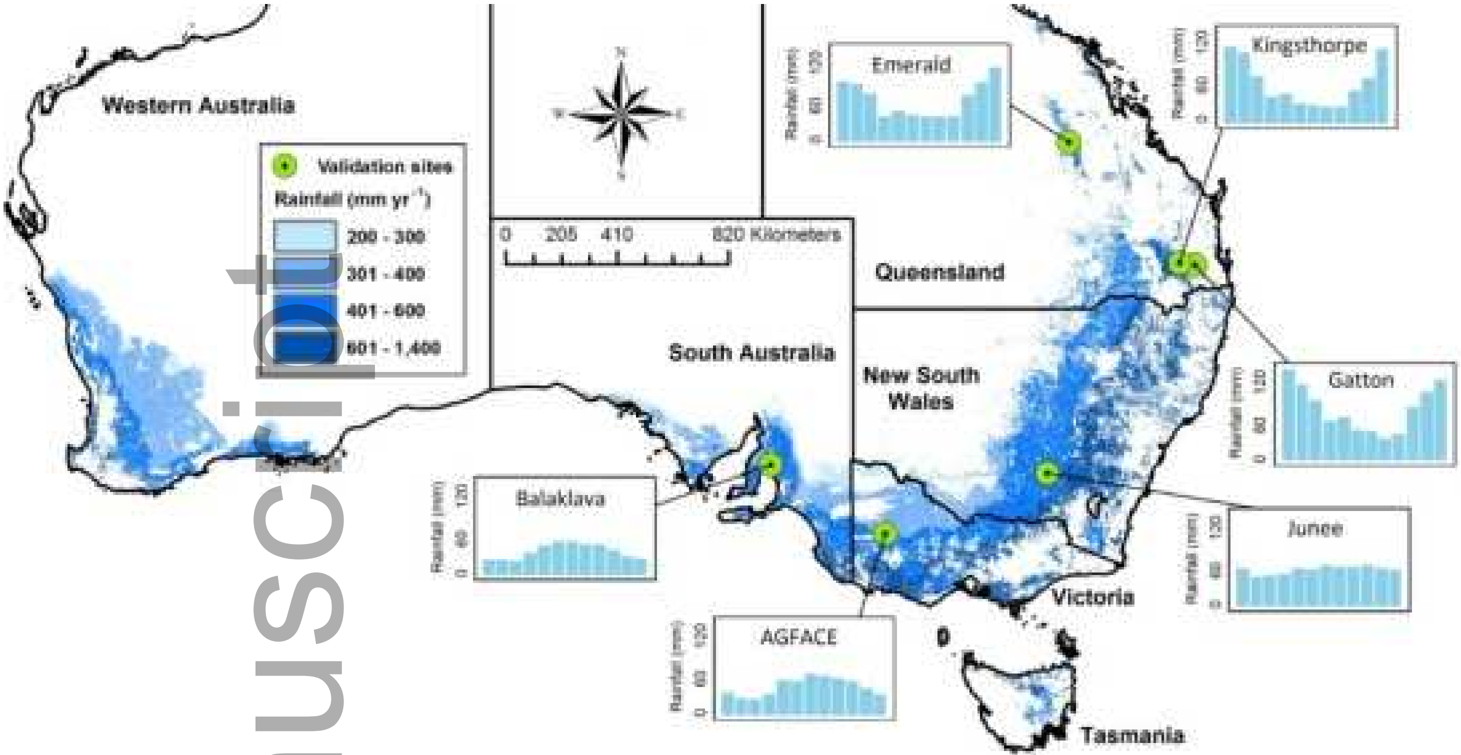
Figure 4 Grain yield (kg ha^{-1}) for (a) Silverstar + *tin* at Horsham, (b) Silverstar + *tin* at Balaklava, (c) Silverstar + *tin* at Emerald, (d) Silverstar at Horsham, (e) Silverstar at Balaklava, (f) Silverstar at Emerald, (g) Silverstar + *tin* at Gatton, (h) Silverstar + *tin* at Junee, (i) Silverstar + *tin* at Kingsthorpe, (j) Silverstar at Gatton, (k) Silverstar at Junee, and (l) Silverstar at Kingsthorpe showing lower (25^{th} percentile – 1.5 × (75^{th} quantile – 25^{th} quantile)) and upper (75^{th} percentile + 1.5 × (75^{th} quantile – 25^{th} quantile)) limits (whiskers), 25^{th}-75^{th} percentile (box) and median (horizontal line) over 57 years (1962-2018) under (H) historic climate, (W) historic climate + 2°C warmer, and (D) historic climate + 2°C warmer + 20% less rainfall at a[CO_2] (380 µmol mol^{-1}) and e[CO_2] (550 µmol mol^{-1}). Asterisks are points that fall outside the limits of the whiskers.

Figure 5 Grain yield advantage (kg ha^{-1}) of Silverstar + *tin* over Silverstar showing lower (25^{th} percentile – 1.5 × (75^{th} quantile – 25^{th} quantile)) and upper (75^{th} percentile + 1.5 × (75^{th} quantile – 25^{th} quantile)) limits (whiskers), 25^{th}-75^{th} percentile (box), median (horizontal line) and mean (dot) over 57 years (1962-2018) at (a) Horsham (AGFACE), (b) Balaklava, (c) Emerald, (d) Gatton, (e) Junee, and (f) Kingsthorpe) under (H) historic climate, (W) historic climate + 2°C warmer, and (D) historic climate + 2°C warmer + 20% less rainfall at a[CO_2] (380 µmol mol^{-1}) and e[CO_2] (550 µmol mol^{-1}). Asterisks are points that fall outside the limits of the whiskers.

Figure 6 Grain yield advantage (kg ha^{-1}) of Silverstar + *tin* over Silverstar in relation to water supply (< 3000 mm). Each point is coloured according to the percentage of results from simulations across Australia's arable land (1962-2018) under (a) historic climate and a[CO_2] (380 µmol mol^{-1}), (b) historic climate and e[CO_2] (550 µmol mol^{-1}), (c) historic climate + 2°C warmer and a[CO_2], (d) historic climate + 2°C warmer and e[CO_2], (e) historic climate + 2°C warmer + 20% less rainfall and a[CO_2], and (f) historic climate + 2°C warmer + 20% less rainfall and e[CO_2]. White points indicate that there were no simulation results. Water supply is seasonal rainfall plus initial plant available water content in soil.

Figure 7 Long-term average (1962-2018) grain yield (kg ha^{-1} yr^{-1}) for (a) Silverstar + *tin* under historic climate and a[CO_2] (380 µmol mol^{-1}), (b) Silverstar + *tin* under historic climate and e[CO_2] (550 µmol mol^{-1}), (c) Silverstar under historic climate and a[CO_2], (d) Silverstar under historic climate and e[CO_2], (e) Silverstar + *tin* under historic climate + 2°C warmer and a[CO_2], (f) Silverstar + *tin* under historic climate + 2°C warmer and e[CO_2], (g) Silverstar under historic climate + 2°C warmer and a[CO_2], (h) Silverstar under historic climate + 2°C warmer and e[CO_2], (i) Silverstar + *tin* under historic climate + 2°C warmer + 20% less rainfall and a[CO_2], (j) Silverstar + *tin* under historic climate + 2°C warmer + 20% less rainfall and e[CO_2], (k) Silverstar under historic climate + 2°C warmer + 20% less rainfall and a[CO_2], and (l) Silverstar under historic climate + 2°C warmer + 20% less rainfall and e[CO_2]. Max and min are 0.01 and 0.99 percentiles of all long-term yields, respectively. Boxplots represent frequently.

Figure 8 Long-term average (1962-2018) yield advantage (kg ha^{-1} yr^{-1}) of Silverstar + *tin* over Silverstar under (a) historic climate and a[CO_2] (380 µmol mol^{-1}), (b) historic climate and e[CO_2] (550 µmol mol^{-1}), (c) historic climate + 2°C warmer and a[CO_2], (d) historic climate + 2°C warmer and e[CO_2], (e) historic climate + 2°C warmer + 20% less rainfall and a[CO_2], and (f) historic climate + 2°C warmer + 20% less rainfall and e[CO_2]. Boxplots represent frequently.



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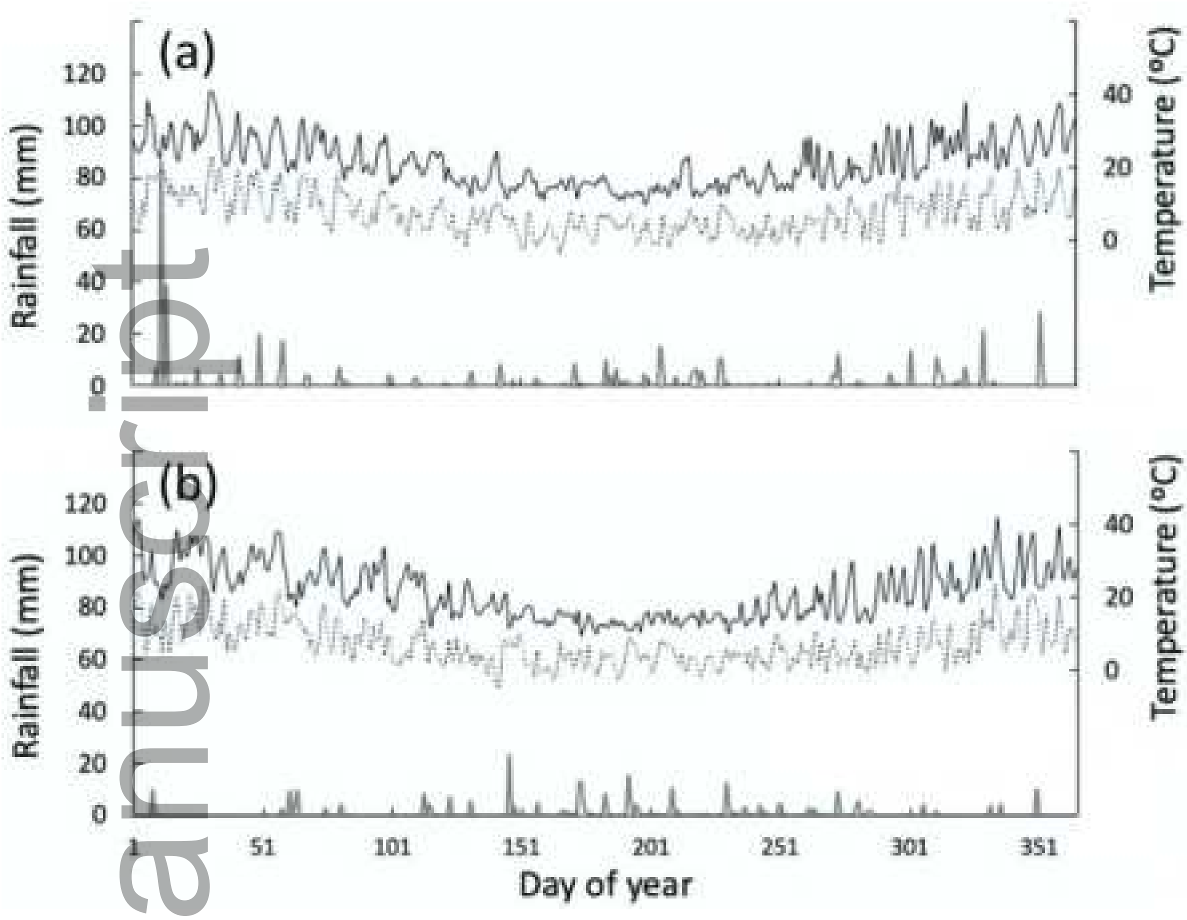

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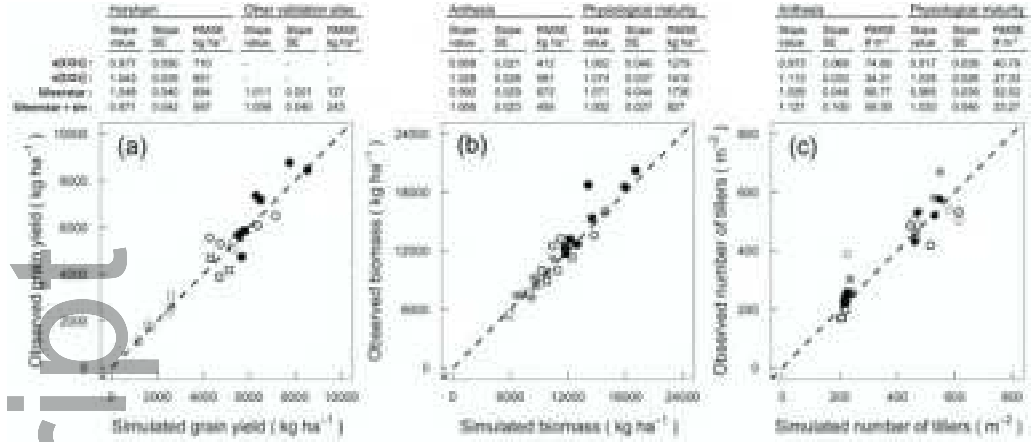

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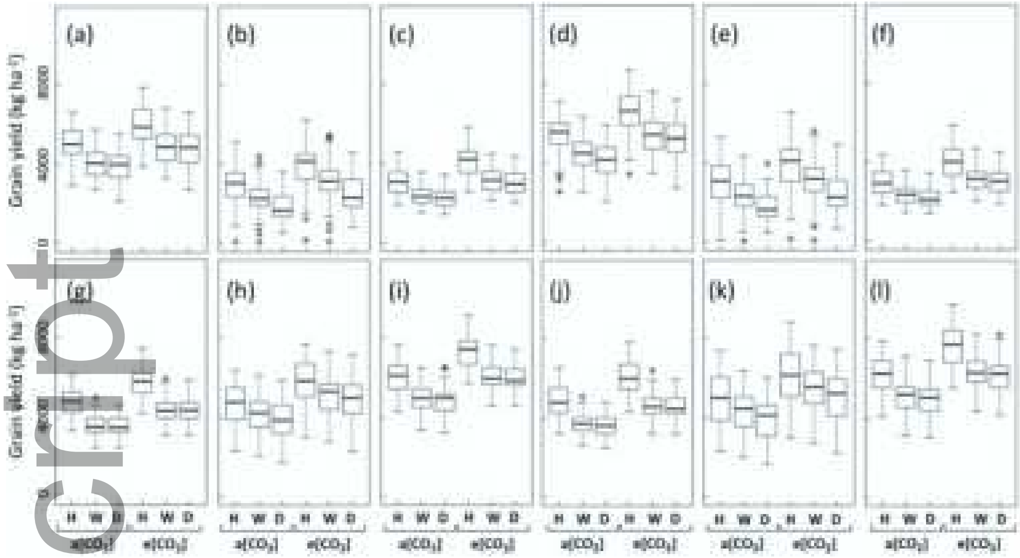

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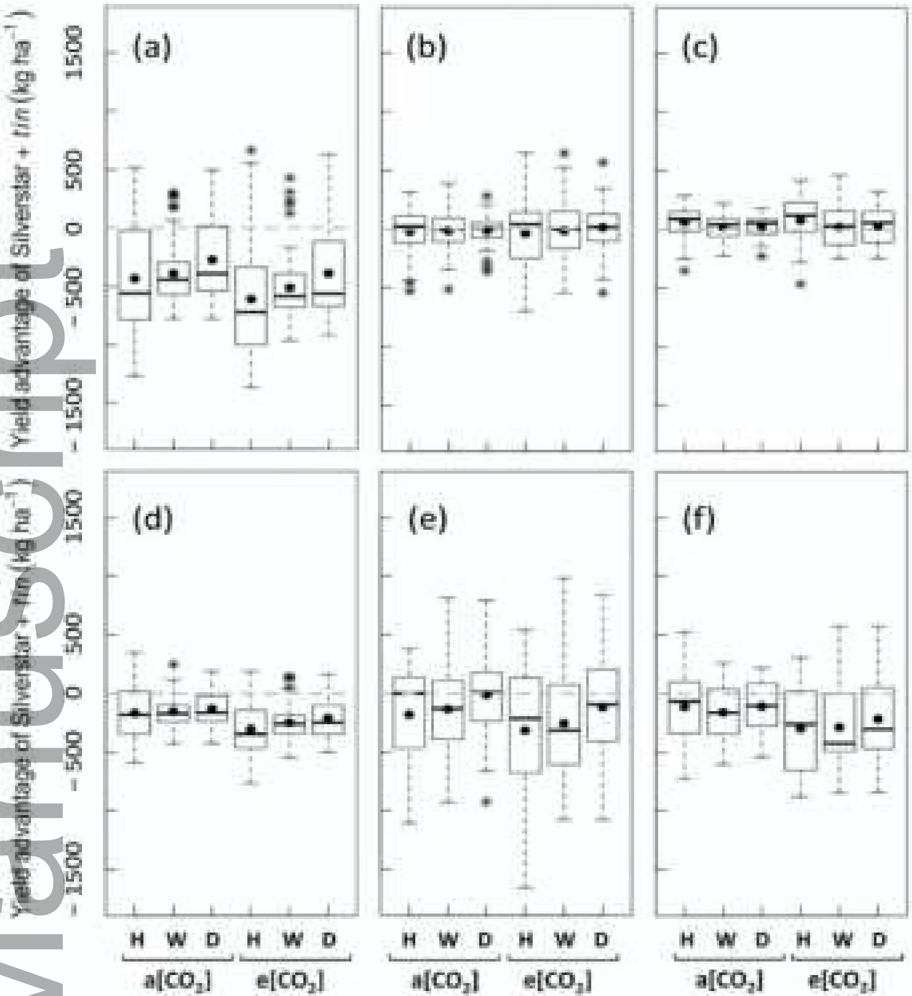

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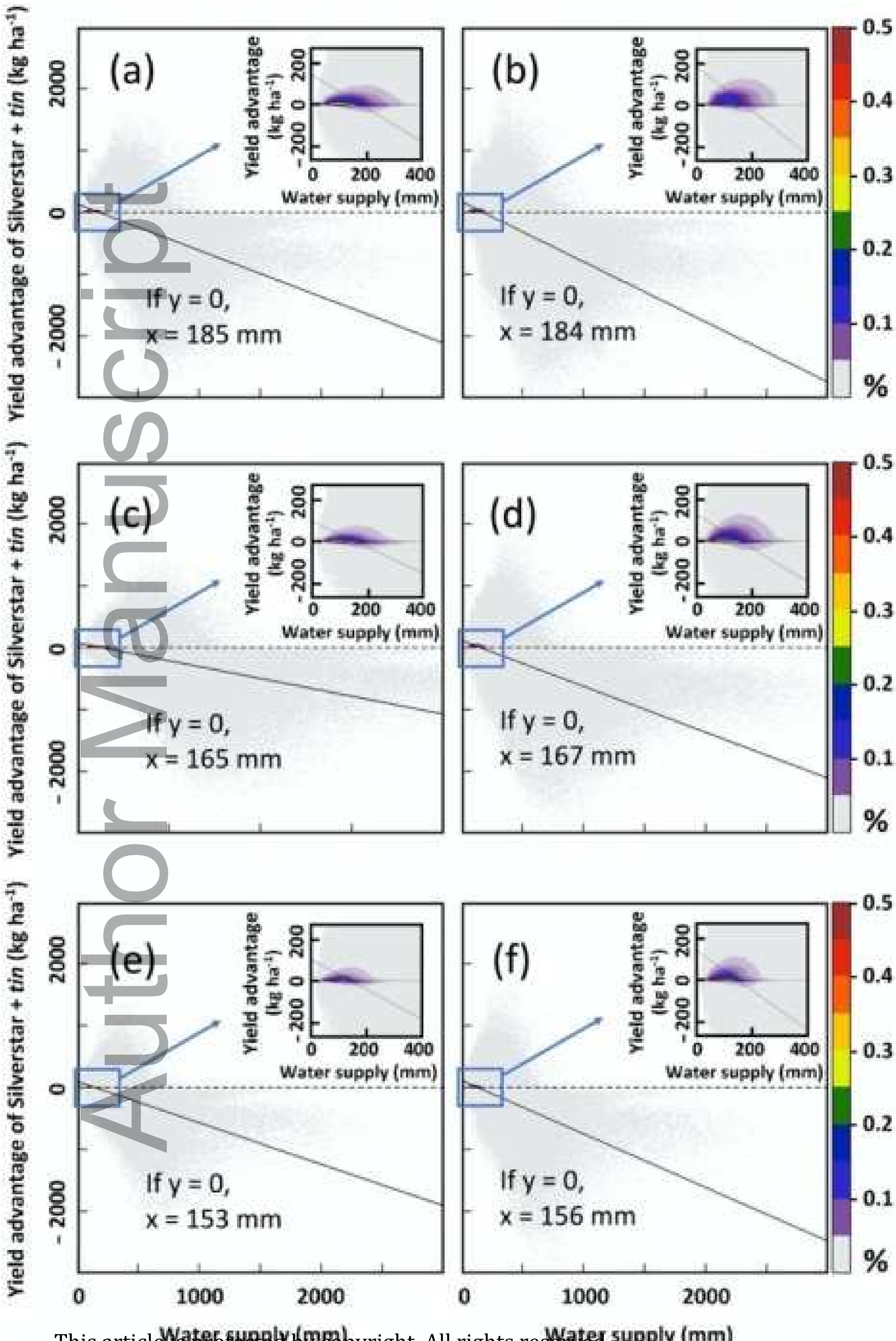

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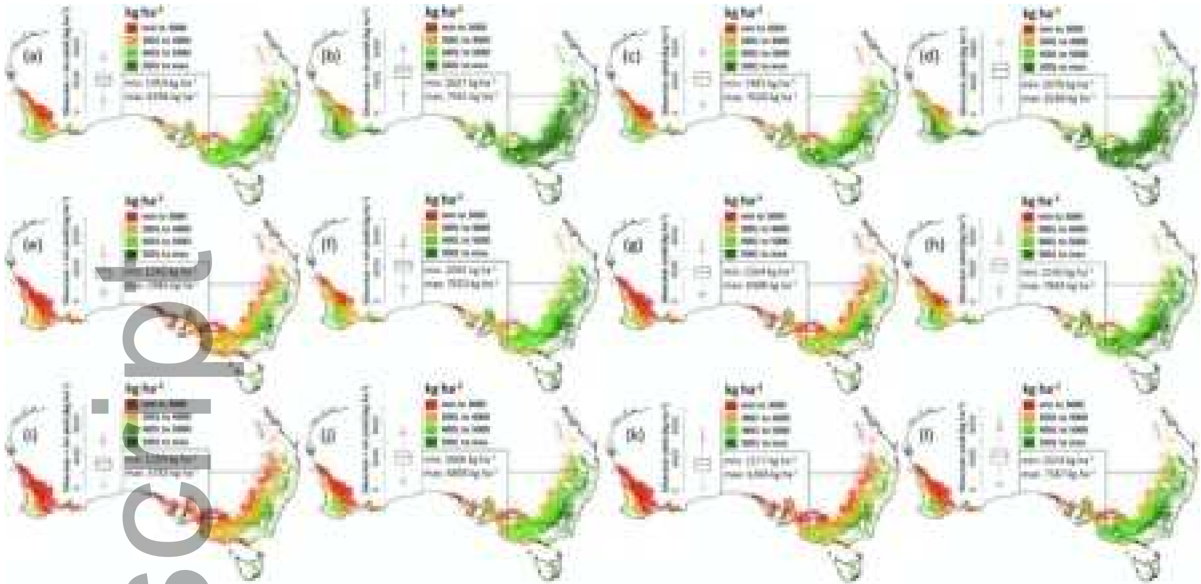

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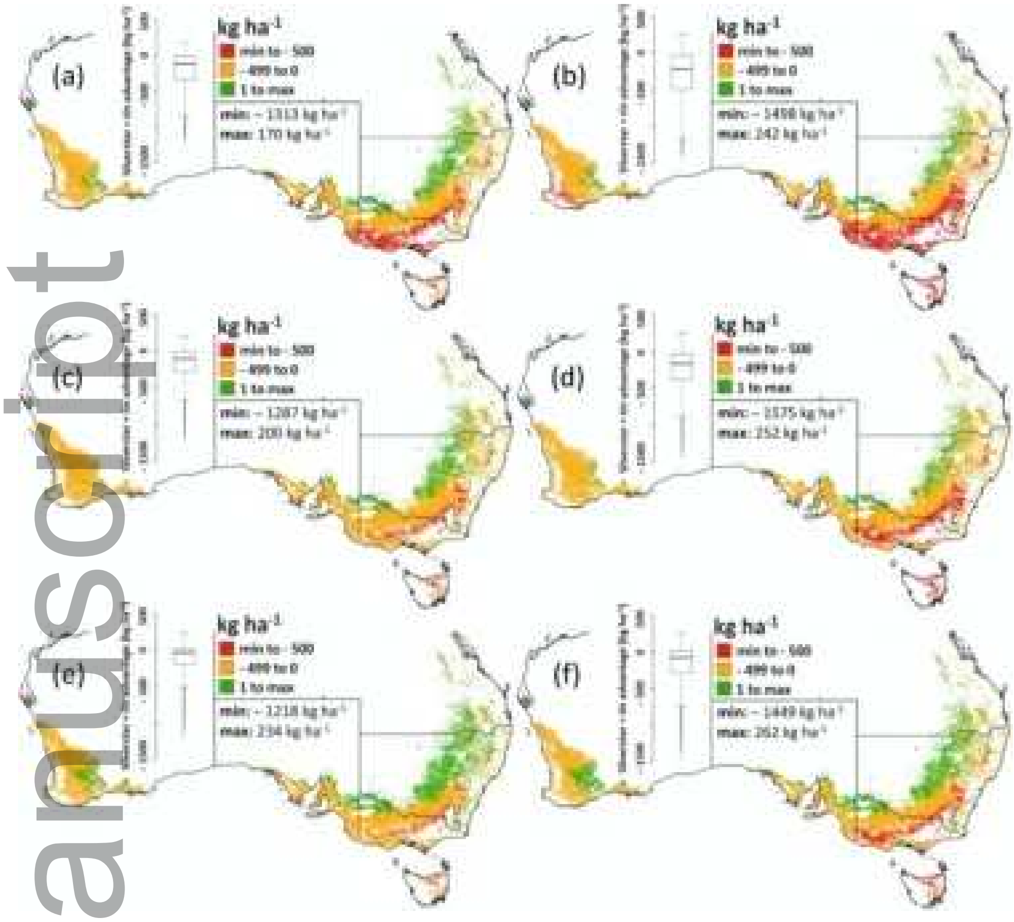

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