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Limiting transpiration rate in high evaporative demand conditions to improve Australian wheat productivity

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ABSTRACT

Limited-transpiration rate at high evaporative demand ('LTR' trait) has potential to improve drought adaptation, crop water productivity and food security. The quantification of the implications of LTR for water consumption, biomass accumulation and yield formation requires the use of dynamic crop modelling to simulate physiological and environmental processes and interactions in target environments. Here, a new transpiration module was developed for the Agricultural Production Systems sIMulator (APSIM NextGen) and used to simulate atmospheric and edaphic water stress on wheat crops. This module was parameterized with (i) data from a lysimeter experiment assessing genotypic variability in the LTR trait for four genotypes contrasting in transpiration efficiency, and with (ii) a more pronounced response to high evaporative demand. The potential of the LTR trait for improving crop productivity was investigated across the Australian wheatbelt over 1989–2018. The LTR trait was simulated to allow an increase in national yield by up to 2.6 %, mostly due to shift in water use pattern, alleviation of water deficit during grain filling period and a higher harvest index. Greatest productivity gains were found in the north-east (4.9 %, on average) where heavy soils allow the conserved water with the LTR trait to be available later at more critical stages. The effect of the LTR trait on yield was enhanced under the future climate scenario, particularly in the north-east. Limiting transpiration at high evaporative demands appears to be a promising trait for selection by breeders, especially in drought-prone environments where crops heavily rely on stored soil moisture.

KEYWORDS: APSIM NextGen; breeding; climate change; crop adaptation; drought resilience; water conservation.

1. INTRODUCTION

Nearly 40 % of the world's food supply is provided by wheat crops (FAO 2013). To satisfy the projected demand for food, wheat yields need to increase at much higher rates than the current annual increase (Ray *et al.* 2013; Keating *et al.* 2014). A common challenge faced by wheat growers and breeders is the lack of soil moisture available for the plant, which often limits crop production (Araus *et al.* 2002). In Australian rain-fed production regions, drought is a major factor limiting wheat production (e.g. Murphy and Timbal 2008; Chenu *et al.* 2011, 2013; Rebetzke *et al.* 2013). In addition, high temperature is increasingly impacting wheat productivity due to suboptimal temperature (Zheng *et al.* 2016; Hunt *et al.* 2018; Ababaei and Chenu 2020) and its impact on evaporative demand (Lobell *et al.* 2013). In the future, drought and heat-shocks are expected to remain major issues if no adaptation is considered (Lobell *et al.* 2015; Watson *et al.* 2017; Webber *et al.* 2018, 2020; Ababaei and Najeeb 2020).

Identification of key target traits for selection of drought and heat adaptation strategies requires an understanding of the implications for grain yield from realistic manipulations of the phenotypic expression of those traits in target production environments. Crop models that have the biological functionality required to capture context-dependencies are valuable tools to quantify the value of candidate traits in a diverse range of environments (e.g. Hammer *et al.* 1997, 2019; Chenu *et al.* 2017, 2018; Webber *et al.* 2018; Ababaei and Chenu 2019; Ramezani Etedali *et al.* 2019; Rincent *et al.* 2019; Nazari *et al.* 2020) and can thus assist breeding progress (e.g. Cooper *et al.* 2014).

Great attention has been given to limiting transpiration at elevated vapour pressure deficit (VPD), also referred to as the 'limited transpiration rate' trait (LTR; Sinclair *et al.* 2005), which is involved in both heat and drought tolerance (Lobell *et al.* 2013). This trait results from hydraulic restrictions within the plant (Sinclair *et al.* 2017), which slow down the water transfer to the leaves. While this makes leaves vulnerable to dehydration under high VPD, partial stomatal closure is required to match transpiration rate (TR) with water flux to the leaves and avoid leaf desiccation and senescence (Bunce 2006). Reducing transpiration at high VPD allows crops to save soil water (e.g. Kholová *et al.* 2010; Vadez *et al.* 2013; Messina *et al.* 2015) and leads to improved daily transpiration efficiency (TE; Sinclair *et al.* 1984), i.e. more biomass produced per unit of water transpired. Genotypic variation in limiting transpiration at high VPD has been observed in many species (Sinclair *et al.* 2017), including wheat (Schoppach and Sadok 2012; Schoppach *et al.* 2014, 2017; Tamang *et al.* 2019). In many cereals, genotypes with restricted TR per unit of green leaf area tend to have higher plant-level TE (wheat, Li *et al.* 2017; sorghum, Mortlock and Hammer 1999; pearl millet, Kholová *et al.* 2010; rice, Impa *et al.* 2005; and maize, Ryan *et al.* 2016), though some studies reported weaker correlations between plant-level TE and TR per unit of green leaf area (e.g. Hammer *et al.* 1997; Geetika *et al.* 2019). By definition, higher TE leads to 'more crop per drop' and more biomass can led potentially higher yield (Passioura 1977; Marris 2008).

Importantly, reducing transpiration at high VPD can allow crops to conserve water in soil profile and change the dynamics of water availability and use. Saving water early in a growing season can be valuable to support crop physiological activities at more sensitive growth stages later in the season (e.g. Passioura 1977; Sinclair *et al.* 2005; Schoppach and Sadok 2012; Lobell *et al.* 2013; Devi *et al.* 2014; Vadez *et al.* 2014; Messina *et al.* 2015) when water deficit in rainfed production systems is particularly common, as is the case in Australia (Chenu *et al.* 2013). However, limiting transpiration can also have a cost, as any reduction in stomatal conductance also influences CO_2 fluxes from/into leaves and may result in lower photosynthesis rates with potential reductions in biomass accumulation. Therefore, the productivity value of limiting transpiration at high VPD depends on the environment in which the crop is cultivated, and in particular, the frequency of high VPD (e.g. winter vs. summer crops) and the ability of the soil to retain the conserved water for later demand.

Analyses of Australian wheat cultivars released over the last decades highlighted an increasing trend in yield (Sadras *et al.* 2012) together with a decreasing trend in TR per unit of leaf area at high VPD (Schoppach *et al.* 2017), an increasing trend in TE (Fletcher and Chenu 2015), but no evident increasing trend in light-saturated photosynthetic rate (Sadras *et al.* 2012). The LTR trait has also been incorporated to commercial maize hybrids (AQUAmax®) destined to drought-prone regions (Gaffney *et al.* 2015), as well as some soybean cultivars (Sinclair *et al.* 2017).

The aim of this study was (i) to assess the potential impact on yield of the LTR trait in wheat (i.e. a winter crop) across the Australian wheatbelt based on existing genotypic variations, and (ii) to evaluate the potential trade-offs in productivity that reduced stomatal conductance can induce via limitation in photosynthetic activity and biomass production. In other words, would a limited transpiration at high VPD result in a higher grain yield, where and how often? To answer these questions, a new transpiration module was developed for Agricultural Production Systems sIMulator (APSIM NextGen) (Holzworth *et al.* 2014, 2018) improved for canopy development (Zheng *et al.* 2019). A lysimeter experiment was conducted to assess genotypic variability in the LTR trait for genotypes contrasting in TE. The yield impact of such observed genotypic variability as well as some increased variability in the LTR trait was simulated at 60 locations across the Australian wheatbelt for 1989–2018 and an average future climate scenario for 2050. The future scenario corresponded to a 10 % reduction in precipitation as well as 1.6 and 2 °C increase in daily minimum and maximum temperatures, i.e. average changes from 33 global climate models (Lobell *et al.* 2015), over the wheat growing season (April–November; B. Collins and K. Chenu, unpubl. data), which were applied on the base weather data (1976–2005).

2. MATERIALS AND METHODS

2.1 A new transpiration module for APSIM NextGen

A new transpiration module was implemented in APSIM NextGen (Holzworth *et al.* 2018) that was improved with a canopy module recently developed by Zheng *et al.* (2019). The module developed in current study simulates photosynthesis using the Soil–Plant–Atmosphere System Simulation (SPASS) model developed by Wang (1997), with a few modifications including (i) a downscaling to hourly time step with the temperature diurnal pattern estimated using the approach proposed by Parton and Logan (1981) and (ii) a more accurate estimation of radiation around sunrise and sunset. The hourly potential accumulation of dry matter ($\Delta DM_{pot,t}$, i.e. amount of CO_2 fixed by photosynthesis; g m^{-2}) is then used to calculate hourly potential transpiration ($TR_{pot,t}$, mm) depending on hourly VPD (VPD_t; Equation (2)) and the TE coefficient (TE_c, Fig. 1A):

$$TR_{pot,t} = \frac{\Delta DM_{pot,t} \times VPD_t}{TE_c \times F_r \times F_{CO_2}} \quad \text{sunrise} \leq t \leq \text{sunset} \qquad (1)$$

where the TE coefficient (TE_c) is set at 0.006 (g m^{-2} mm^{-1} kPa) from crop emergence to maturity, as in APSIM v7.9 (Keating *et al.* 2003; Holzworth *et al.* 2014; Zheng *et al.* 2015). As this TE_c does not consider photorespiration (Respiration), a conversion coefficient ($F_r \geq 1$) is calculated at the beginning of each day as the ratio of $\Delta DM_{pot,d-1}$ and $\Delta DM_{pot,d-1}$ – Respiration_{d-1}, where d denotes the day. The F_{CO_2} factor was used to account for the increasing effect of atmospheric [CO_2] on TE_c, which increases from 1 to 1.37 when

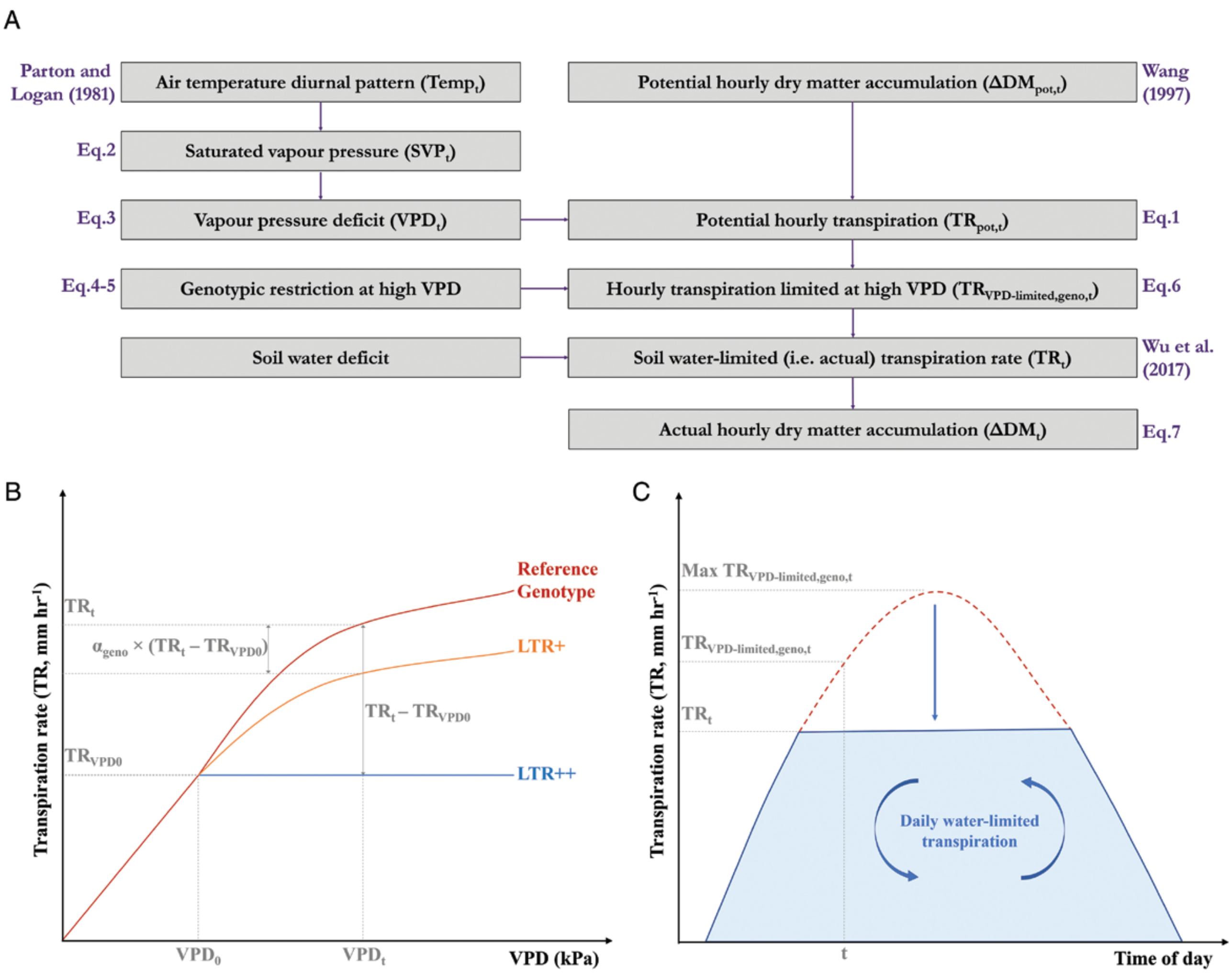

Figure 1. Schematics of the new crop transpiration module: (A) different steps of the module implemented into APSIM NextGen, (B) genotypic variations in limited transpiration at high evaporative demand (LTR) and (C) effect of the edaphic water stress on TR (following Wu *et al.* 2017). For the two virtual genotypes tested in this study, α_{geno} was set to 0.3 (LTR+) and 1.0 (LTR++) and a VPD threshold (VPD_0) to 1.3 kPa, based on observations.

[CO_2] rises from 350 to 700 ppm, as in APSIM v7.9 (Reyenga *et al.* 1999).

VPD_t (kPa) at time *t* is calculated as the difference between hourly saturated vapour pressure (SVP_t; kPa) and SVP at minimum temperature (kPa; Messina *et al.* 2015) as follows:

$$SVP_t = 0.61078 \times \exp(17.269 \times Temp_t/(237.3 + Temp_t)) \quad (2)$$

$$VPD_t = SVP_t - SVP_{T_{min}} \quad (3)$$

where $Temp_t$ is air temperature at time *t*. The potential transpiration is then adjusted based on (i) the sensitivity of the genotype to high evaporative demand and (ii) edaphic water stress, when applicable. So, first, genetic limitation on hourly transpiration at a high VPD ($TR_{VPD\text{-limited},geno,t}$) is calculated as follows:

$$TR_{VPD_0} = \frac{\Delta DM_{pot,VPD_0} \times VPD_0}{TE_c \times F_r \times F_{CO_2}} \quad (4)$$

$$Reduction_{geno,t} = \max(0,\ TR_{pot,t} - TR_{VPD_0}) \times \alpha_{geno}\ for\ VPD_t > VPD_0 \quad (5)$$

$$TR_{VPD\text{-limited},geno,t} = TR_{pot,t} - Reduction_{geno,t} \quad (6)$$

where VPD_0 is the threshold VPD above which TR may be genetically limited, TR_{VPD_0} is the TR at VPD_0 (mm h^{-1}), $\Delta DM_{pot,VPD_0}$ is the interpolated hourly growth at VPD_0 (g m^{-2}), α_{geno} is the fractional reduction due to genotypic characteristic at a high VPD when hourly TR exceeds TR_{VPD_0} and $Reduction_{geno,t}$ is the reduction in hourly TR (mm h^{-1}).

Then actual hourly transpiration (TR_t) is calculated by accounting for any soil water limitation ($TR_{water\text{-limited}}$). Hourly transpiration is capped starting from the maximum $TR_{VPD\text{-}limited,geno}$ at midday until the total available soil water to the plant can meet the crop daily water demand (Fig. 1C; Wu *et al.* 2017). Finally, actual hourly increase in dry matter (ΔDM_t) is calculated based on actual TR (TR_t), as follows:

$$\Delta DM_t = \frac{TR_t \times TE_c \times F_r \times F_{CO_2}}{VPD_t} \quad (7)$$

2.2 Lysimeter experiment

An experiment was conducted in a high-throughput automated lysimeter platform (Fig. 2). The system, as described by Chenu *et al.* (2018), combines the concept of a constant water table (developed by Hunter *et al.* 2012) with automatic monitoring and irrigation management. The platform, located in a solar weave enclosure consists of 560 lysimeters (4-L black ANOVApot®, top diameter: 137 mm, bottom diameter: 116 mm, height: 140 mm; Anova Solutions). Watering and weighing are performed fully automatically at 10-min intervals.

Four genotypes with contrasting TE (Drysdale, Janz, Scout and Suntop) were sown with six replicates on 24 April 2018. Four plants per pot were grown in a potting medium mixed with 2.8 g L^{-1} of Osmocote Exact 3-4 month fertilizer (NPK of 21.2:1.9:5.7), under well-watered conditions and variable VPD. Plastic sleeves were used to cover the soil to minimize soil evaporation. Additional pots without plants were used to measure any remaining soil evaporation. A weather station located in the centre of the facility was used to monitor environmental conditions at 10-min intervals. From sowing to harvest, the average air temperature was 15.9 °C, the average radiation was 8.63 MJ m^2 day^{-1} and the average diurnal VPD was 0.83 kPa.

Plants were harvested on 30 July, i.e. 1500 °Cd after planting when plants were on average at anthesis, i.e. Z65 growth stage (Zadoks *et al.* 1974). Plants were cut at the soil level and above-ground fresh biomass was oven-dried at 70 °C for 72 h and then weighed to record dry biomass. Green leaf area was measured with a LI-3100C leaf area meter (LI-COR, Inc., Lincoln, NE, USA).

2.3 Normalized TR

To avoid difficulties related to measurements or estimations of the green leaf area throughout the season, a new approach was taken to indirectly account for variations in canopy size by daily normalization of TR. For each pot and each day, TR values under high-radiation conditions (>0.84 MJ m^{-2} h^{-1} or 486 μmol m^{-2} s^{-1} of photosynthetically active radiation, i.e. typically between 0900 and 1500 h on a sunny day) were normalized (TR_{norm}) with the TR of the same pot at a reference VPD of 1.2 kPa, under which no significant genotypic differences in TR_{norm} were observed (unpublished data). A linear interpolation was applied to estimate TR at reference VPD on each day using all the 10-min TR values of the same pot between 08:00 and 11:00 am. Due to the low sensitivity of the lysimeter platform to very small changes in pot weights when plant leaf area is small in earlier growth stages, the analysis was performed on data from 750 °Cd after sowing onwards. Note that average TR_{norm} for VPD ≥ 1.3 kPa was significantly correlated ($P < 0.05$) with the cumulated transpiration over the last 7 days of the season normalized by green leaf area ($TR7_{norm}$ in g mm^{-2}; data not shown). Therefore, TR_{norm} can be used as a surrogate for TR normalized with green leaf area (i.e. the trait commonly used in similar studies), which is hard to calculate due to difficulty of precisely estimating green leaf area non-destructively in species like wheat.

2.4 Simulation setup

Daily weather data for 1989–2018 were obtained from the SILO point climate dataset (Jeffrey *et al.* 2001) for 60 selected sites in four major wheat-producing regions across the Australian wheatbelt (Fig. 3A). Five sowing dates, five initial soil moisture levels at sowing and local

A

B

Figure 2. High-throughput lysimeter platform at The University of Queensland in Gatton, Australia: (A) water container positioned on a load cell, and (B) pots with wheat plants.

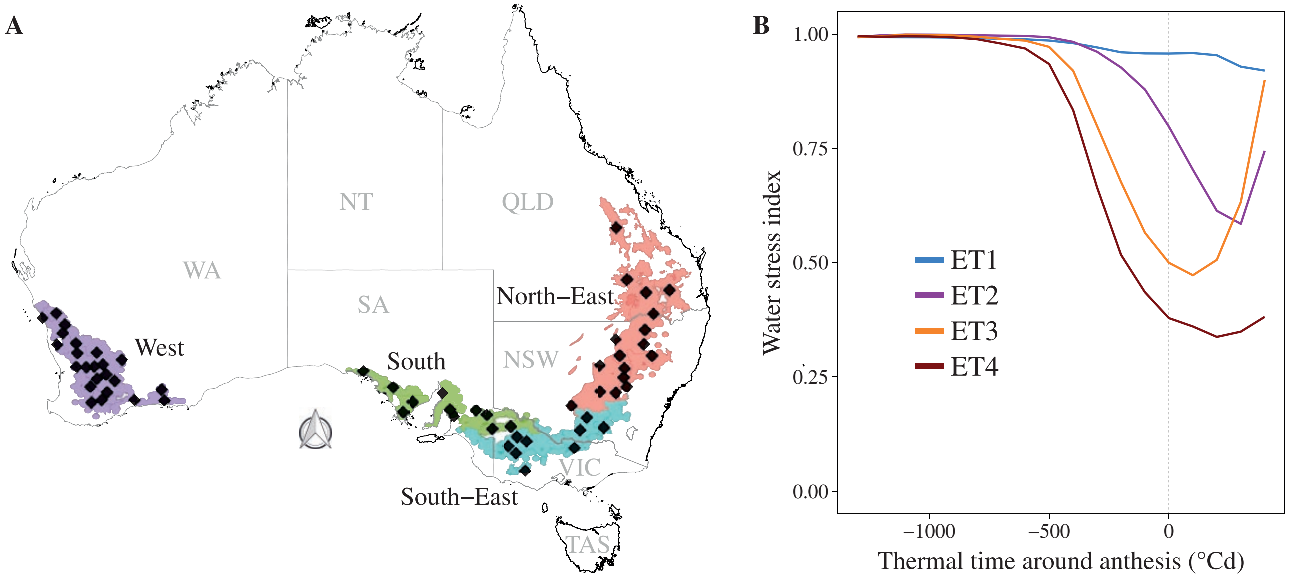

Figure 3. The Australian wheatbelt and the 60 studied sites in the North-East (red), South-East (blue), South (green) and West (purple) (A), along with simulated water stress index for four drought ETs identified across the Australian wheatbelt (B; adapted from Chenu *et al.* 2013). The water stress index is represented as a function of cumulative thermal time relative to anthesis, from crop emergence to 450 °Cd after anthesis, after which senescence greatly reduces plant transpiration. See Supporting Information—Fig. S1 for the frequency of ETs in each region and across the Australian wheatbelt. The abbreviations of state names are presented in grey.

N application rates were adopted at each site to represent local wheat cropping systems (see Table 1 in Chenu *et al.* 2013). Atmospheric CO_2 concentration was updated daily according to observations at Cape Grim (Ziehn *et al.* 2016).

A climate scenario representing the period of 2036–65 (2050s) was also used to explore the potential value of the LTR trait in the future. Atmospheric [CO_2] was set at 541 ppm, as projected by the RCP8.5 scenario (IPCC 2014), which assumes 'business as usual' CO_2 emissions. A 10 % reduction in precipitation as well as 1.6 and 2 °C increase in daily minimum and maximum temperatures were applied on the base weather data (1976–2005). These changes were based on the average of the monthly outputs of 33 global climate models (e.g. Lobell *et al.* 2015) over the wheat growing-season (April–November; B. Collins and K. Chenu, unpubl. data).

Simulations were run for cv. Hartog (of which transpiration was considered as the reference, i.e. not restricted by VPD), and a genotype with TR above TR_{VPD_0} (i.e. above TR at VPD = 1.3 kPa) reduced by 30 % at high VPD (LTR+) as observed experimentally, and a virtual genotype with a TR reduced by 100 % at high VPD (LTR++). Genotypic differences were simulated for VPD greater than 1.3 kPa (i.e. VPD_0 in Equations (4) and (5)), which corresponds to the VPD threshold above which significant genotypic variations in normalized TR were observed (Fig. 4; B. Collins and K. Chenu, unpubl. data).

2.5 Environment characterization

In the simulations, water stress was quantified using the daily water supply-demand ratio (SDR) as a stress index. Crop water demand is the daily amount of water the crop would transpire in the absence of soil water limitation, and water supply is the soil water extractable by the roots. Lower values of SDR correspond to more severe stress. Daily SDR values were averaged over 100 °Cd periods cantered around anthesis day, from crop emergence to 450 °Cd after anthesis after which senescence greatly reduces plant transpiration. The daily patterns of SDR from all simulations of the reference cv. Hartog were compared to the four drought patterns representative of the Australian wheatbelt (drought 'environment types' (ETs); Fig. 3B; Chenu *et al.* 2013) and classified across ETs based on Euclidean distances. Average pre-anthesis SDR (SDR_{Pre}) was calculated from 550 °Cd before anthesis (i.e. about when SDR starts to decrease for ET4 in Fig. 3B) up to anthesis, and average post-anthesis SDR (SDR_{Post}) was calculated between anthesis and 450 °Cd after anthesis.

3. RESULTS

3.1 Model performance

The modified APSIM NextGen model was evaluated for wheat in five experiments in Gatton, Australia in which cv. Hartog was cultivated under a wide range of management practices, with different irrigation levels, N application rates, stubble managements, row spacings and planting dates. The model captured biomass and grain yield variations slightly better than the original APSIM NextGen [**see Supporting Information—Fig. S2**], with a R^2 of 0.86 and 0.71 for the two traits, respectively, and mean absolute error of 126.7 and 78 g m^{-2} [**see Supporting Information—Fig. S2C**] as compared with 135.3 and 88 g m^{-2} for the unchanged version of the model [**see Supporting Information—Fig. S2A**], and 154.6 and 86.4 g m^{-2} for

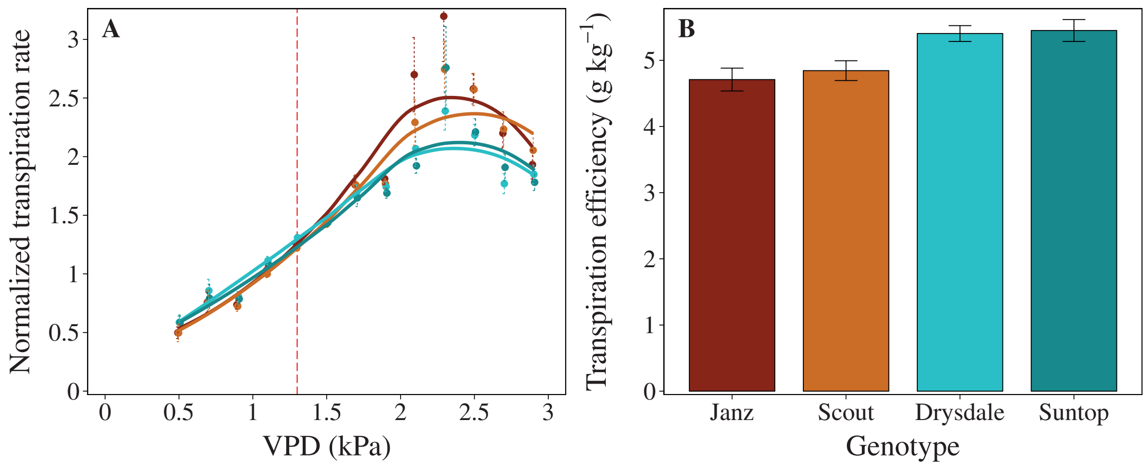

Figure 4. Genotypic differences in (A) the response of normalized transpiration rate (TR_{norm}) to air VPD, and (B) TE of four commercial Australian cultivars grown in a high-throughput automated lysimeter platform (Fig. 2). In (A), the vertical red dashed line corresponds to the VPD threshold of 1.3 kPa above which genotypic differences in TR_{norm} were significant. In (B), TE was calculated with above-ground biomass and cumulated transpiration between sowing and anthesis of an average plant; error bars correspond to standard errors.

the version modified by Zheng *et al.* (2019) without the new module [**see Supporting Information—Fig. S2B**].

3.2 Genotypic variation in TR at high VPD

Environmental effects on TR were analysed in detail by using sub-hourly VPD and TR data. Significant variability was found in TR_{norm} for VPD ≥ 1.3 kPa (Fig. 4A) with an average TR_{norm} for VPD ≥ 1.3 kPa of 2.0 for the low-TE cv. Janz and 1.75 for the high-TE cv. Suntop in these experimental conditions (Fig. 4). In contrast, averages TR_{norm} for VPD < 1.3 kPa were not significantly different between the two genotypes. There was a 28 % variation in the response of TR_{norm} for VPD ≥ 1.3 kPa (i.e. $TR_{norm} - TR_{norm,VPD_0}$) between cultivars with the lowest (Janz) and highest (Suntop/Drysdale) maximum TR_{norm} (a_{geno} = 0.28 in Equation (5)).

3.3 Limiting TR at high VPD led to substantial reduction in post-anthesis water stress and higher yield across the Australian wheatbelt

The impacts of the LTR trait on wheat crops were simulated by comparing the well-parameterized cv. Hartog as a reference, and two virtual genotypes that differed for TR when VPD ≥ 1.3 kPa. For the first virtual genotype (LTR+), the reduction in TR above 1.3 kPa ($TR - TR_{VPD_0}$) was 30 % compared to the reference genotype (a_{geno} = 0.3 in Equation (5); Fig. 1B), i.e. similar to observed variation between high-TE Suntop and low-TE Janz (a_{geno} = 0.28; Fig. 4A), which has a TE comparable to Hartog (Fletcher and Chenu 2015). For the second virtual genotype (LTR++), a 100 % reduction was applied for any TR above 1.3 kPa, i.e. TR was equal to TR at 1.3 kPa (TR_{VPD_0}) for VPD above 1.3 kPa (a_{geno} = 1; Fig. 1B). The impact of the LTR trait was evaluated on a selected set of crop traits: cumulative transpiration (TR_{Mat}), biomass at maturity (DM_{Mat}), transpiration efficiency (TE_{Mat}), average water supply-demand ratio (SDR) for pre- (SDR_{Pre}) and post-anthesis (SDR_{Post}), harvest index (HI) and grain yield (Yield).

With the LTR++ genotype, average reduction in TR_{Mat} was estimated to be 8.9 % across the Australian wheatbelt while LTR+ had a 1.8 % reduction as compared with the reference genotype (Fig. 5). Despite the reduction in TR_{Mat}, national average DM_{Mat} was almost sustained, resulting in an increased average TE_{Mat} by 1.6 and 7.4 % for LTR+ and LTR++, respectively. Harvest index improved by an average 0.8 and 4.1 % with LTR+ and LTR++, respectively. These changes were driven by lower water stress (higher SDR values), especially post-anthesis (SDR_{Post}), which often translated into a better grain-filling and higher individual grain weight. Across the Australian wheatbelt, these impacts resulted in an average yield gain of 1.0 and 2.6 % for LTR+ and LTR++, respectively.

Largest yield gains associated with the LTR trait were simulated in Queensland (especially in the northernmost sites) and central New South Wales (Fig. 5A) where crops often heavily rely on stored soil moisture, as well as in the western central at sites heavily prone to drought and with relatively heavy soils for the region. Regionally, average yield increased by 2.0, 0.4, 0.5 and 0.7 % with LTR+ and 4.9, 0.9, 1.8 and 1.8 % with LTR++, in the North-East, South-East, South and West, respectively (Fig. 5B). Larger positive impact of the LTR trait on grain yield in the North-East was associated with a significant reduction in TR_{Mat} (2.2 and 12 % with LTR+ and LTR++) which allowed water saving from early stages that could be used later in the crop cycle, as indicated by considerable decrease in post-flowering water stress (increases in SDR_{Post} by 5.0 and 22 %), increase in HI (1.2 and 5.8 %) and increase in TE_{Mat} (2.7 and 12.3 %; Fig. 5B).

3.4 Drought-prone environments benefit more from the LTR trait

Under drought conditions, the LTR trait led to a relatively similar improvement in DM_{Mat} regardless of the timing and intensity of the water stress (e.g. national average of 2.0 to 2.5 % in ET2–4 for LTR+; Fig. 6). Changes in the pattern of water use were found in all drought ETs with reduced water stress before flowering (i.e.

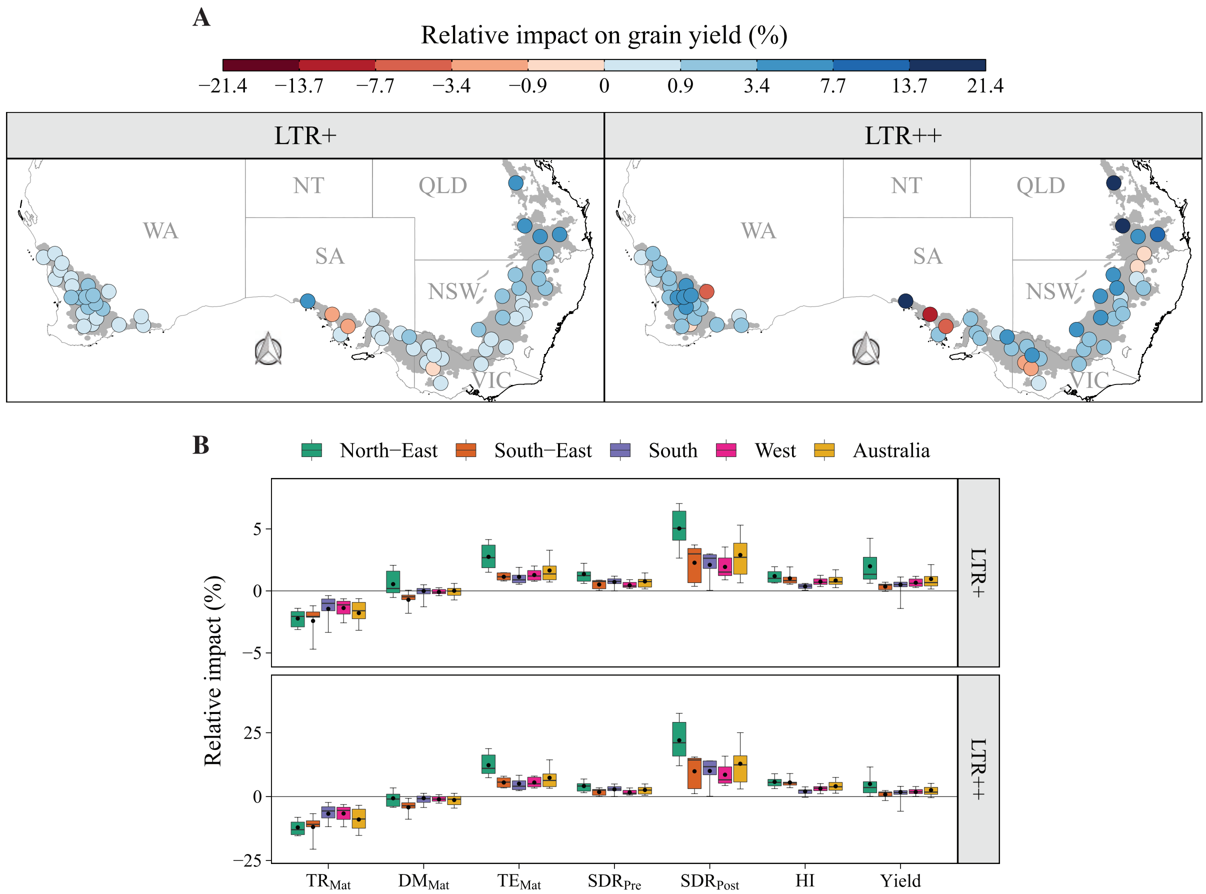

Figure 5. Long-term average relative impact of the limited transpiration (LTR) trait at (A) the 60 studied locations across the Australian wheatbelt as well as (B) regionally and nationally, under the current climate (1989–2018) for two virtual genotypes with TR reduced by 30 % (LTR+) or 100 % (LTR++) for TRs above the TR corresponding to VPD = 1.3 kPa (Fig. 1B). Selected traits are cumulative transpiration (TR_{Mat}), biomass at maturity (DM_{Mat}), transpiration efficiency (TE_{Mat}), water supply-demand ratio for pre- (SDR_{Pre}) and post-anthesis (SDR_{Post}), HI and grain yield (Yield). For the boxplots in (B), the middle line of the box represents the median; the upper and lower edges represent the 75th and 25th percentiles and the whiskers show the 10th and 90th percentiles; black points correspond to the averages across locations. Note: panels in (B) have different scales.

higher SDR_{Pre}) in ET2–4, and a major decrease in water stress post flowering (i.e. higher SDR_{Post}). The reduction in pre-flowering stress was most strongly associated with yield in environments classified as ET3 ($R = 0.31$ and R = NS for LTR+ and LTR++, respectively; **see Supporting Information—Fig. S5**) and ET4 ($R = 0.46$ and $R = 0.40$) in which early water stress typically affects wheat crops (Fig. 3B). The decrease in post-flowering stress was most evident in ET2 (6.6 and 34 % for LTR+ and LTR++, respectively) and ET4 (6.3 and 40 %) and strongly correlated to yield ($R = 0.49$ and $R = 0.50$ for LTR+ and LTR++ in ET2; $R = 0.19$ and $R = 0.10$ in ET3) compared to ET3 (3.8 and 23 %; $R = 0.14$ and R = NS for LTR+ and LTR++, respectively). This could be because in ET2, there was typically no pre-flowering water stress (Fig. 3B) and all the water saved by the LTR trait during this period was available (in environments where pedo-climatic conditions allowed it) to reduce the stress later in the cycle.

In ET4 environments, the post-flowering stress is typically very severe and each millimetre of extra water during this period may have a greater impact than under less severe post-flowering stress from ET3 environments. As a consequence, the largest yield gain due to the introduction of the LTR trait was simulated in ET4 (national increase by 2.5 and 13.2 % for LTR+ and LTR++, respectively) followed by ET2 (2.0 and 6.6 %) and ET3 (1.5 and 5.2 %). In all ETs with substantial drought (ET2–4), yield was strongly and positively correlated to DM_{Mat}, TE_{Mat} and HI ($R > 0.40$ except for LTR++ in ET3; **see Supporting Information—Fig. S5**). Overall, yield gains were simulated in 87|82|97 % of the seasons classified as ET2|ET3|ET4 with the LTR+ genotype and 82|77|98 % with LTR++. A national increase in yield of 1 % or more occurred in 60|50|71 % of the simulated seasons for LTR+ and 74|68|96 % for LTR++.

By contrast, when no or only light water stress occurred (ET1), the impact of LTR on DM_{Mat} and yield was negative or only slightly

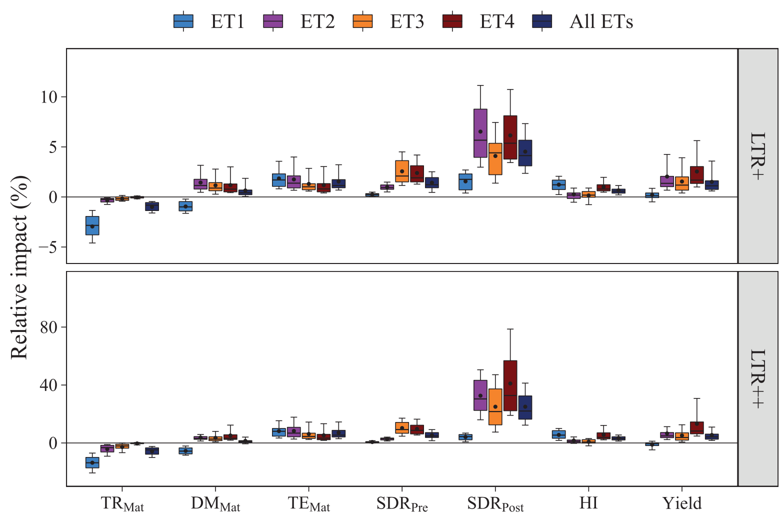

Figure 6. Average relative impact of the limited transpiration (LTR) trait on selected traits and variables across drought ETs for two virtual genotypes with TR reduced by 30 % (LTR+) or 100 % (LTR++) for TRs above the TR corresponding to VPD = 1.3 kPa (Fig. 1B). Simulations for 1989–2018. Selected traits and variables are cumulative transpiration from emergence to maturity (TR_{Mat}), biomass at maturity (DM_{Mat}), transpiration efficiency (TE_{Mat}) defined as the ratio between DM_{Mat}/TR_{Mat}, average water supply-demand ratio for the pre- (SDR_{Pre}) and post-anthesis (SDR_{Post}) periods, HI and grain yield (Yield). Environment types were characterized for the reference cv. Hartog. For the boxplots, the middle line of the box represents the median; the upper and lower edges represent the 75th and 25th percentiles and the whiskers show the 10th and 90th percentiles; black points correspond to the averages across locations. Note: panels have different scales.

positive due to significantly greater reduction in TR_{Mat} and in overall photosynthesis levels compared to drought environments. In such conditions, water saving had negligible or relatively small impact on water stress (i.e. almost no change in SDR_{Pre} and a slight increase in SDR_{Post}) as soil water limitations were only light or inexistent. Across environments, variations in LTR+ yield were strongly and positively correlated with changes in TR_{Mat}, DM_{Mat} and HI (R = 0.61, 0.59, 0.86, respectively) while for LTR++ the correlation was strong only with HI [**see Supporting Information—Fig. S5**]. National yield in ET1 was increased by 0.2 % with LTR+ and decreased by 1.1 % with LTR++, with 62 and 70 % of the seasons experiencing a national yield loss for LTR+ and LTR++, respectively. A yield loss of 1 and 5 % was simulated in 13 and 6 % of the seasons, respectively, for LTR+, and 25 and 15 % of the seasons for LTR++.

3.5 Higher yield gains on soils with high water holding capacity

Soils were ranked based on their plant available water capacity (PAWC) across all the 60 sites and classified in four quartiles (Q1: 34–79 mm, Q2: 82–112 mm, Q3: 119–153 mm, Q4: 159–272 mm). Soil with high water holding capacity are more common in the North-East (65 and 29 % of PAWC-Q3 and PAWC-Q4, respectively) followed by the South-East (44 and 33 %) while none of these soils exist in the South and West [**see Supporting Information—Fig. S3**].

Greatest impacts of the LTR trait on yield, TR_{Mat}, DM_{Mat}, HI and TE_{Mat} were simulated in sites with high water-holding soils (PAWC Q3–Q4). Mostly located in Queensland and northern New South Wales, these sites receive summer rainfall and experience higher average temperatures as compared with sites located in the South, South-East and South-West (Ababaei and Chenu 2020). As a consequence, crops in these regions are typically subject to greater evaporative demand. They also strongly depend on stored water in the soil, which increases potential benefits from the LTR trait. Yield gain associated with the LTR trait during severe drought (ET4) in sites with PAWC-Q4 soil was estimated to be 4 and 22 % with LTR+ and LTR++, respectively, while across all sites, yield gains in ET4 were only was 1 and 8 % for LTR+ and LTR++, respectively.

3.6 Climate change is expected to enhance the impact of the LTR trait on grain yield in the North-East

The effect of the LTR trait on yield was enhanced under the average future climate scenario (Fig. 7). The spatial pattern of yield gain/loss was projected to be similar to that of the current climate (Fig. 5) with, for instance, the largest yield gains due to the LTR trait in the North-East and central West. Greatest yield gains were projected for the North-East (3.0 and 12.1 %), followed by the West (0.9 and 3.0 %), South (0.7 and 2.8 %) and South-East (0.4 and 1.6 %) for LTR+ and LTR++, respectively. Overall, the LTR trait was projected to benefit the national yield by 1.4 and 5.3 % on average, for LTR+ and LTR++, respectively, under the 2050 climate scenario (Fig. 7B).

Nationally, the positive impact of the LTR trait on TE_{Mat} was not significantly improved under the average future climate scenario compared with the improvement simulated under current climate (0.1 and 0.4 % improvement for LTR+ and LTR++, respectively; Figs 5B and 7B). Change in climate with reduced rainfall and increased

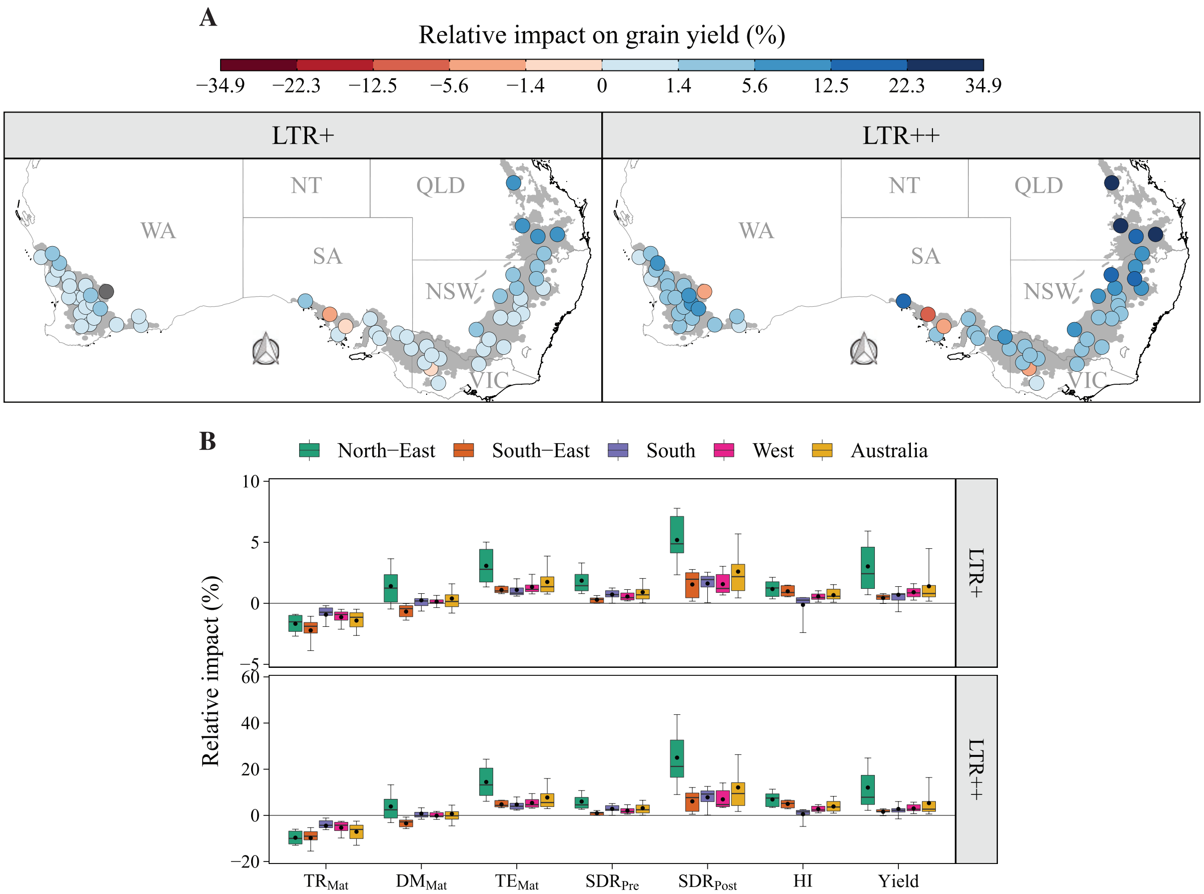

Figure 7. Projected average relative impact of the limited transpiration (LTR) trait at (A) the 60 studied locations across the Australian wheatbelt and (B) averaged across regions, under the future climate (2050s) for two virtual genotypes for two virtual genotypes with TR reduced by 30 % (LTR+) or 100 % (LTR++) for TRs above the TR corresponding to VPD = 1.3 kPa (Fig. 1B). Selected traits are cumulative transpiration (TR_{Mat}), biomass at maturity (DM_{Mat}), transpiration efficiency (TE_{Mat}), water supply-demand ratio for pre- (SDR_{Pre}) and post-anthesis (SDR_{Post}), HI and grain yield (Yield). Environment types were characterized for the reference cv. Hartog. For the boxplots in (B), the middle line of the box represents the median; the upper and lower edges represent the 75th and 25th percentiles and the whiskers show the 10th and 90th percentiles; black points correspond to the averages of the 60 locations. Note: panels in (B) have different scales.

temperature, VPD and atmospheric [CO_2], resulted in slight changes in the impact of the LTR trait on TR_{Mat} (increased by 0.4 and 1.9 % for LTR+ and LTR++, respectively), DM_{Mat} (increased by 0.4 and 2 %), HI (reduced by 0.2 % for both LTR+ and LTR++) and yield (increased by 0.4 and 2.8 %). At the regional level, largest increase in yield due to the LTR trait as compared to the current climate occurred in the North-East, with a high impact for LTR++ (7.1 %) but a much smaller impact for LTR+ (1.0 %).

3.7 The LTR trait translates to more benefits than losses in Australian production environments

Across the wheatbelt, respectively 61 and 55 % of the simulated LTR+ and LTR++ crops benefited from the LTR trait under the current climate scenario (Fig. 8). National yield gains|losses greater than 1 % were achieved in 34|13 % of the simulated seasons for LTR+, and 46|25 % for LTR++. For impacts larger than 5 %, these numbers reduced to 6|6 % for LTR+, and 26|15 % for LTR++. The North-East (71 and 60 % with LTR+ and LTR++, respectively) and South-East (41 and 37 %) regions had the largest and smallest proportion of simulated seasons experiencing positive impact of the LTR trait on grain yield.

Yield gains >1 % were simulated for 40 % or more of the seasons in almost 50 % of sites with both LTR+ and LTR++ under current climate (Fig. 8A). The greatest occurrence of yield gains >1 % was found in Queensland, northern New South Wales and the central West. Growing LTR++ instead of LTR+ would lead to a higher number of seasons experiencing considerable yield gain, but at the cost of the risk of having slightly more seasons with yield loss in the North-East (Fig. 8B).

For the studied future climate scenario, the average probability of yield gains >1 % across the 60 sites was 37 and 55 % with LTR+ and

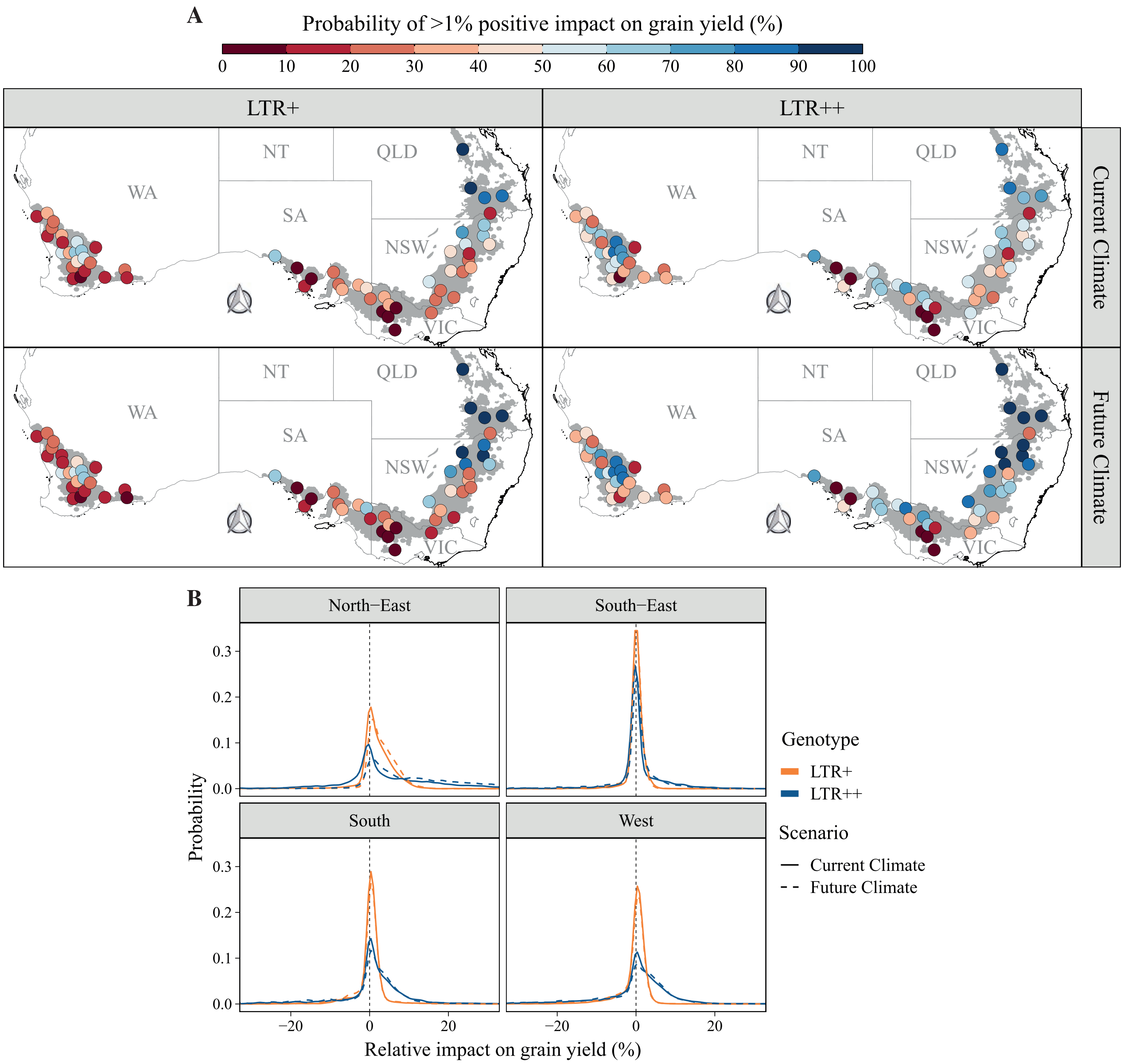

Figure 8. Risk associated to the limited transpiration (LTR) trait in the current (1989–2018) and future (2050) climates: (A) Probability of positive impact (>1 %) of the LTR trait on grain yield across the Australian wheatbelt and (B) the probability densities of relative impacts of the LTR trait across regions for two virtual genotypes with TR reduced by 30 % (LTR+) or 100 % (LTR++) for TRs above the TR corresponding to VPD = 1.3 kPa (Fig. 1B). See Supporting Information—Fig. S6 for empirical cumulative distribution functions of yield impact across regions. See Supporting Information—Fig. S7 for probability of positive impact on grain yield >0 % and >5 %.

LTR++, respectively, up from 34 and 46 % under the current climate (Fig. 8A). For the future climate, yield losses >1 % were only simulated in 13 and 25 % of the simulated cropping seasons with LTR+ and LTR++. Spatial pattern of the probability of positive impacts were similar to that of the current climate. The greatest and smallest average proportions of simulated seasons with >1 % positive impact on yield were simulated in the North-East (54 and 53 % for LTR+ and LTR++, respectively) and in the South-East (17 and 25 %), respectively. Under the future climate, TE_{Mat} was improved by at least 1 in 60 % (vs. 59 % under current climate) and 93 % (vs. 93 %) of the simulated seasons for LTR+ and LTR++.

4. DISCUSSION

4.1 The potential of the LTR trait to increase wheat productivity in Australia

Genotypic variation in the LTR trait has been observed in wheat (Fig. 4; Schoppach and Sadok 2012; Schoppach *et al.* 2017; Medina *et al.* 2019) as well as many other crops, including sorghum (Gholipoor *et al.* 2010; Shekoofa *et al.* 2014; Chenu *et al.* 2018), soybean (Fletcher *et al.* 2007; Sadok and Sinclair 2009), maize (Yang *et al.* 2012) and peanut (Devi *et al.* 2010). Differences in LTR are typically reported as a segmented response of TR per unit of leaf area to VPD. In wheat, genotypic variations were identified in the 'first' slope (for VPD lower than the VPD breakpoint), the VPD breakpoint and the 'second' slope (for higher VPD) (e.g. Schoppach and Sadok 2012). By contrast, no significant differences in normalized TR for VPDs lower than the breakpoint were found among genotypes in the experiments carried in our lysimeter platform under fluctuating VPD (Fig. 4; B. Collins and K. Chenu, unpubl. data). This may be due to the fact that the VPD breakpoint identified when using weeks of data recorded at 10-min intervals was typically significantly lower (1.3 kPa) than in experiments carried out with far fewer measurements done (i) over short periods at controlled VPD levels or (ii) over 2 days at 1-h interval in fluctuating VPD (breakpoint varying from 2.4 to 3.9 kPa in Schoppach and Sadok 2012; from 1.86 to 2.35 in Schoppach *et al.* 2017). However, Medina *et al.* (2019) found in durum wheat a low and unique VPD breakpoint (~1.1 kPa) across genotypes with segmented TR–VPD responses, which is close to the breakpoint at 1.3 kPa found in current study, in an experiment with relatively low number of measurements performed at different levels of controlled VPD. In other cereals, the VPD breakpoint has also been shown to depend on temperature (Sermons *et al.* 2012; Yang *et al.* 2012; Sunita *et al.* 2014).

In any case, the potential value of the limited-transpiration at high VPD (LTR) highly depends on the VPD threshold as well as the frequency of occurrence of high VPD in the target environments. The greater the VPD breakpoint, the lower the LTR impact is expected to be, at least when there is no genetic variability below this VPD breakpoint (e.g. Fig. 4B). In our glasshouse experiment in Gatton (subtropical climate), 65 % of the data analysed (high radiation and from 750 °Cd after sowing up to flowering) had a VPD above 1.3 kPa, against only 22 % had a VPD of 2 kPa. Across the 60 sites selected for simulations, 57, 46 and 19 % of days in an average season experienced a maximum diurnal VPD exceeding 1.1, 1.3 and 2.0 kPa, respectively, under the current climate, with largest proportion of such days occurring in the North-East (74, 63 and 28 %, respectively; **see Supporting Information—Fig. S8**). Climate warming is expected to raise the proportion of high-VPD days to 63, 50 and 20 % for the three thresholds, averaged across 30 years and 60 sites.

As found in other crops and regions around the world (Sinclair *et al.* 2005, 2010; Messina *et al.* 2015; Sinclair 2018), the LTR trait appears to be a trait with substantial potential to improve grain yield. For the Australian wheatbelt, a national long-term yield gain of 1.0 % was simulated (Fig. 5) when only accounting for observed variation in LTR across four tested genotypes (Fig. 4; LTR+). The national yield gain increased to 2.6 % with an increased level of genotypic variability (Figs 1B and 5). Almost similar levels of genotypic variation were observed when phenotyping a diverse panel of genotypes in another experiment in the lysimeter platform under fluctuating VPD (B. Collins and K. Chenu, unpubl. data).

The risk of yield loss was relatively low (e.g. 39 and 37 % for LTR+ under the current and future climate scenarios, respectively) compared to yield gain (61 and 67 %) across the wheatbelt (Fig. 8B), with a high probability of yield gain simulated for a large portion of the Australian wheatbelt (Fig. 8). In wet seasons in which no yield gain was achieved, only small yield losses were simulated for genotypes with the LTR trait. For instance, national yield losses of >5 % were only simulated in 6 % of the seasons under current climate for LTR+. These findings concurs with results for other crops and regions, where considerable yield benefits were identified in dry seasons and only small yield penalties in wet seasons (in maize, Messina *et al.* 2015; in soybean, Sinclair *et al.* 2010).

The greatest benefits of the LTR trait were simulated in the North-East, with a long-term yield gain of 2.0 % for LTR+ and 4.9 % for LTR++ (Fig. 5B). Average yield gains of up to 20 % were simulated in northern Queensland (Fig. 5A). In the North-East, yield gain above 1 % occurred 54 % of the seasons against only 8 % of the seasons been simulated to loss more than 1 % yield, for LTR+.

While historically, a decreasing trend has been observed in TR per unit of green leaf area at high VPD in Australian cultivars released over the last decades (Schoppach *et al.* 2014) together with an increasing trend in TE (Fletcher and Chenu 2015), some modern genotypes commonly grown in the North-East, such as Suntop, appear to have the LTR trait and a high TE (Fig. 4). Recently, increased genetic variability has been found for the LTR trait in a diversity panel (B. Collins and K. Chenu, unpubl. data). Hence, the findings for the current study indicate that genetic material carrying the LTR trait has potential to improve wheat germplasm for yield beyond the current levels observed in Australian breeding programs, especially for north-east Australia.

4.2 LTR, a valuable water-saving trait under drought conditions and where crops rely on stored soil moisture

While the LTR trait typically led to significant reductions in the cumulative amount of water transpired (e.g. TR_{Mat}), its impacts on other traits, including yield, were context dependant (Figs 5 and 6). In drought environments, the LTR trait resulted in reduced water stress both pre-flowering and post-flowering. This is due to the fact that limiting water loss during the time of the day when VPD is the highest increases daily TE but also translates into saving water with potential benefits for later stages. Higher availability of water enhances the possibility of sustained crop physiological activity (e.g. staygreen; Borrell *et al.* 2014) and reduced impact of water deficit (e.g. cooler canopies). By shifting the dynamic in water use, the LTR trait can thus result in higher TE, HI and yield (Sinclair 2018), as simulated across Australia (Fig. 5). For instance, in northern Australia, each extra millimetre of water extracted during grain filling was estimated to generate an additional 55 kg ha^{-1} of wheat yield (Manschadi *et al.* 2006).

The conserved water in soil profile early in a growing season due to the LTR trait was most valuable in soils capable of retaining large amount of water (i.e. high PAWC; **see Supporting Information—Figs S3 and S4**). In Australia, such soils are more common in the North-East and South-East. In addition, in the northern half of the North-East, crops heavily rely on stored soil moisture as rainfall predominantly occurs in the summer, i.e. before the wheat season. The benefits of the LTR in those sites were probably also enhanced by the fact that they experience higher average temperatures (Ababaei and Chenu 2020) and likely higher VPDs compared with other regions.

In environments where crops were not or only slightly affected by water stress (ET1), the reduction in stomatal conductance and transpiration due to the LTR trait typically led to reduced photosynthesis and biomass accumulation. In such environments, biomass at maturity (DM_{Mat}) was reduced by 0.9 % in LTR+ and 5.5 % in LTR++ on average nationally (Fig. 6). However, the average impact of the LTR trait on TE_{Mat} was positive in all environments, whether or not they were affected by drought. The LTR trait still had a small positive impact in lightly stressed environments, as it allowed the alleviation of such water deficits, in particular during the grain filling period (higher SDR). Overall, yield in these environments was either negative or only slightly positive.

Overall, limiting stomatal conductance at high evaporative demand appeared to be a promising trait for selection by breeders, especially in drought-prone environments where crops often rely on stored soil moisture. By contrast, the LTR trait may not be desirable in cropping system with no water limitation (Gholipoor *et al.* 2012; Franks and Farquhar 1999) as it has been linked with detrimental impacts on crop productivity. Further work could be done to account for variations in leaf temperature associated with the LTR trait, which can result in complex interaction with the environments. Reduced stomatal conductance from the LTR trait can cause the leaf temperature to rise due to reduction in energy dissipation (Fletcher *et al.* 2007), and thus led to increased risks of heat stress and tissue damage. This effect occurred to some degree in the lysimeter experiment that was used to parameterize the model and was thus already partly accounted for. On the other hand, the LTR trait also allows alleviation of water stress, especially post-flowering, i.e. when heat events are most frequent (Ababaei and Chenu 2020). Hence, the LTR trait can also lead to reduced canopy temperature when crops have access to more water to cool down.

4.3 The benefits of the LTR trait are expected to increase in part of the wheatbelt in the future

Change in climate, with an increase to 541 ppm of atmospheric [CO_2], a 1.6 °C increase in daily minimum temperature, a 2 °C increase in daily maximum temperature and a 10 % reduction in rainfall over April–November enhanced yield benefits due to the LTR trait mainly in the North-East (Fig. 7). This was accompanied with a slight reduction in the risk of crop failure (Fig. 8). As under the current climate, the impact of the LTR trait on yield was the greatest for the drought environments, and more specifically when severe drought occurred (ET4), especially in the North-East. Christy *et al.* (2018) simulated that elevated atmospheric [CO_2] raised the benefit of increasing wheat TE in a 2 °C warmer climate, with slightly lower effect if rainfall was also reduced by 20 %, though they did not directly link the increased benefit with the LTR trait *per se*. Such benefits from a CO_2 enrichment are associated with increases in photosynthetic activity and TE (Fitzgerald *et al.* 2016; Wang *et al.* 2017; Christy *et al.* 2018). In addition, higher VPDs are also expected to play a role to enhance the water-saving effect of the LTR trait. Elevated atmospheric [CO_2] and traits such as the LTR trait have a positive effect on yield and could compensate, at least partly, the adverse effect of other components of climate change in C3 crops (Fig. 7; Lobell *et al.* 2013; Watson *et al.* 2017; Christy *et al.* 2018; Webber *et al.* 2018).

5. CONCLUSION

Genotypic differences in TE are an emergent consequence of different physiological mechanisms. One approach to select genotypes for enhanced TE is to identify genotypes with reduced stomatal conductance under high VPD (i.e. the LTR trait). In some cropping environments, the LTR trait allows water saving and modifies the dynamics of water use and availability, which can benefit wheat productivity. Significant genotypic variations in TE were found among the four studied Australian commercial cultivars that were associated with different levels of expression of the LTR trait.

The impact of the observed variation across the studied genotypes (~30 % variation) in the LTR trait was simulated with a new module integrated to APSIM NextGen. Under the current climate, this observed variation led to an average 1.0 % increase in wheat grain yield across the Australian wheatbelt, with a 2.0 % increase in the North-East, where crops heavily rely on stored soil moisture. Reductions in post-anthesis water stress and increases in HI across regions confirmed the role of this trait in water conservation. The potential value of the LTR trait was also assessed for an increased level of genetic variability (i.e. the capping of TR when VPD exceeds a threshold of 1.3 kPa). This change led to yield gains of 4.9 % on average in the North-East.

For a dryer and warmer climate scenario representing an average Australian climate by 2050, the LTR trait had an enhanced impact on TE in the North-East (14.5 % for LTR++) and on grain yield across the wheatbelt with a national yield gain of 5.3 % (LTR++). Greatest impacts were projected in the North-East, with a 3 % yield increase for LTR+ and a 12.1 % for LTR++. Hence, limiting TR at high VPD appears to be a promising trait for selection in north-eastern growing region of Australia in the current climate, and in other regions too in a warmer and dryer climate.

SUPPORTING INFORMATION

The following additional information is available in the online version of this article—

Figure S1. Frequency of four environment types (ETs; Chenu *et al.* 2013) across the Australian wheatbelt and regions for two virtual genotypes with different levels of the limited transpiration (LTR) expression: LTR+ with transpiration rate (TR) above TR at vapour pressure deficit (VPD) = 1.3 kPa reduced by 30 % (LTR+) or 100 % (LTR++).

Figure S2. Evaluation of Agricultural Production Systems sIMulator (APSIM NextGen) for dry biomass at harvest (first row) and grain yield (second row) for the released version of the model (Holzworth *et al.* 2018; A), a modified version with a canopy module recently developed by Zheng *et al.* (2019) without (B) and with (C) the addition of the new transpiration module. The models were evaluated for wheat in five experiments at Gatton, Australia in which cv. Hartog was cultivated under a wide range of management practices, with different irrigation levels, N application rates, stubble management, row spacings and planting dates. Experiments included: (i) APS2: sowing on 30th of May and 30th of July in 1991; (ii) APS14: four N application rates (0, 40, 80, 200 kg ha^{-1}) and three pre-sowing conditions (bare, Lucerne, straw) in 1993; (iii) APS26: four N application rates (0, 40, 80, 160 kg ha^{-1}) with two irrigation scenarios (minimal amount for establishment, fully irrigated) in 1995; (iv) APS6: six N application rates (0, 40, 80, 120, 160, 360 kg ha^{-1}) in 1992; (v) GattonRowSpacing: two row spacings (25 and 50 cm) with and without 100 kg ha^{-1} of urea in 2011; (vi) Gatton94: six sowing dates (29 April, 20 May, 10 June, 4 July, 22 July, 15 August) in 1994; (vii) Gatton2009: six sowing dates (10 May, 10 June, 11 July) in 2009.

Figure S3. Average relative impact of the limited transpiration (LTR) trait on selected traits for soils of different plant available water content (PAWC) classes, presented by regions over 1988–2917 for two virtual genotypes with transpiration rate (TR) reduced by 30 % (LTR+) or 100 % (LTR++) for TRs above TR at vapour pressure deficit (VPD) = 1.3 kPa (Fig. 1B). Selected traits are cumulative transpiration (TR_{Mat}), biomass at maturity (DM_{Mat}), transpiration efficiency (TE_{Mat}), water supply-demand ratio for pre- (SDR_{Pre}) and post-anthesis (SDR_{Post}), harvest index (HI) and grain yield (Yield). Environment types (ETs) were characterized for the reference cv. Hartog.

Figure S4. Average relative impact of the limited transpiration (LTR) trait on selected traits for soils of different plant available water content (PAWC) classes, presented by regions drought environment types (ETs) over 1988–2917 for two virtual genotypes with transpiration rate (TR) above TR at vapour pressure deficit (VPD) = 1.3 kPa reduced by 30 % (LTR+) and 100 % (LTR++). Selected traits are cumulative transpiration (TR_{Mat}), biomass at maturity (DM_{Mat}), transpiration efficiency (TE_{Mat}), water supply-demand ratio for pre- (SDR_{Pre}) and post-anthesis (SDR_{Post}), harvest index (HI) and grain yield (Yield). Environment types (ETs) were characterized for the reference cv. Hartog.

Figure S5. Linear correlation coefficient between the relative impact of the limited transpiration (LTR) trait on the selected traits under the current climate for two virtual genotypes with transpiration rate (TR) reduced by 30 % (LTR+) or 100 % (LTR++) for TRs above the TR corresponding to vapour pressure deficit (VPD) = 1.3 kPa (Fig. 1B). Insignificant correlations ($P > 0.05$) are shown in grey. Selected traits are cumulative transpiration (TR_{Mat}), biomass at maturity (DM_{Mat}), transpiration efficiency (TE_{Mat}), water supply-demand ratio for pre- (SDR_{Pre}) and post-anthesis (SDR_{Post}), harvest index (HI) and grain yield (Yield).

Figure S6. Empirical cumulative distribution functions (ECDF) for the relative impact of the limited transpiration (LTR) trait on grain yield in the current (1989–2018) and future (2050) climates across regions for two virtual genotypes with transpiration rate (TR) reduced by 30 % (LTR+; A) or 100 % (LTR++; B) for TRs above the TR corresponding to vapour pressure deficit (VPD) = 1.3 kPa (Fig. 1B).

Figure S7. Probability of positive impact >0 % (A) and >5 % (B) of the limited transpiration (LTR) trait on grain yield across the Australian wheatbelt in the current (1989–2018) and future (2050) climates for two virtual genotypes with transpiration rate (TR) reduced by 30 % (LTR+) or 100 % (LTR++) for TRs above the TR corresponding to vapour pressure deficit (VPD) = 1.3 kPa (Fig. 1B).

Figure S8. Empirical cumulative distribution functions (ECDF) for the maximum diurnal vapour pressure deficit (VPD) in the current (1989–2018) and future (2050) climates across regions. Values on the vertical axis show the proportion of days with a maximum VPD smaller than the values on the horizontal axis. Vertical dashed lines illustrate the three selected VPD thresholds, i.e. 1.1, 1.3 and 2.0 kPa, respectively.

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CONFLICT OF INTEREST

None declared.

CONTRIBUTIONS BY THE AUTHORS

B.C. contributed to the conceptualisation, simulations, data analysis, and writing (original draft). K.C. contributed to the conceptualisation, experimental work (design, data collection and analysis), and writing (review and editing). S.C. and G.H. contributed to the conceptualisation and commented on the manuscript.

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