Selection for yield over five decades favored anisohydric and phenological adaptations to early-season drought in Australian wheat

Faisal Khan · Yupeng Feng · Jairo A. Palta · Yinglong Chen · Victor O. Sadras · Kadambot H. M. Siddique

Received: 23 January 2022 / Accepted: 6 June 2022 / Published online: 10 June 2022 © Crown 2022

Abstract

Background and Aims Climate change in the Mediterranean-climate region of Australia is reducing growing season rainfall and delaying first autumn rain or the onset of ‘autumn break’. We tested the hypothesis that selection for yield and agronomic traits has favored adaptation to early season drought in Australian wheat (Triticum aestivum L.).

Methods Ten wheat varieties released between 1958 and 2012 were grown in a glasshouse. After sowing in dry soil, the equivalent of 25 mm rainfall was supplied, with no subsequent watering provided for 32 days to induce an early season drought treatment (ESD) while a well-watered treatment (WW) was planted on a wet soil that was water-saturated 48 h before sowing. We measured soil and plant water status, gas exchange, shoot and root traits at the end of drought (32 days after sowing) and at anthesis, and grain yield per plant at maturity.

Results Grain yield increased with year of release at 0.43% yr⁻¹ under well-watered conditions and at 0.35% yr⁻¹ under drought. The improved yield under drought was associated with a shorter time to flowering, and a change from isohydric behavior (maintained $\Psi_{\text{leaf}}$, reduced $g_s$, leaf photosynthesis and transpiration rates in response to drought) in older varieties to anisohydric behavior (decreased $\Psi_{\text{leaf}}$ and increased $g_s$, leaf photosynthesis and transpiration in response to drought) in newer varieties that reduced leaf area and maintained higher $g_s$ and higher photosynthesis per unit leaf area.

Conclusions Direct selection for yield and agronomic traits between 1958 and 2012 has improved adaptation to early-season drought. Our collection of varieties is an interesting model to probe for variation in drought tolerance.

Keywords Breeding · Early-season drought · Phenotype · Photosynthesis · Stomata
Introduction

Wheat will remain critical for food security in the foreseeable future, but drought limits its production in major mega-environments worldwide (Shiferaw et al. 2013; Fischer et al. 2014). Adaptive traits need to be tailored to the specific timing, intensity, and duration of water stress (Jordan & Miller 1980; Tardieu 2012), hence the importance of probabilistic, spatial quantification of drought patterns (Chenu 2015). Modeling the seasonal dynamics of water supply and demand using historic climate series and climate projections (2030, 2070) returned four types of drought for wheat in Australia (Chenu et al. 2013; Watson et al. 2017) linked to non-stress condition, extreme drought with an onset at 500°Cd before flowering, and increasing stress as the season progresses. However, modeling water supply, demand and water use at seedling stage, early in the season is unreliable as crop canopies are small, impeding the quantification of early-season drought (K. Chenu, personal communication, March 2021).

Climate change in the Mediterranean-climate region of Australia is increasing maximum temperature, reducing minimum temperature and growing season rainfall, and delaying the onset of ‘autumn break’ or the first good rains of the southern winter cropping season (Pook et al. 2009; Hochman et al. 2017; Cann et al. 2020). In response to the delayed autumn break, many Australian wheat growers are sowing their entire cropping land before the autumn break, further increasing the risk of early season drought (Fletcher et al. 2015, 2016). In Western Australia, wheat crops sown into dry soil germinate and emerge after the first 20–25 mm rainfall, potentially leaving crops vulnerable to 20–23 days drought after emergence in two of four years and 30–32 days drought in one of four years (Chapman and Asseng 2001). While seedlings can survive early season drought, their growth and development are slow, reducing root and shoot biomass at anthesis and grain yield (Armstrong et al. 1996; French and Palta 2014).

Comparisons of varieties in historic collections reveal changes in the crop phenotype associated with selective pressure for yield and agronomic performance (Austin et al. 1980; Slafer 1994; Roche 2015). A collection of wheat varieties adapted to winter-rainfall in Australia showed that five decades of breeding favored (i) a communal phenotype with reduced competitive ability (Sadras and Lawson 2011; Cossani and Sadras 2021), (ii) higher crop photosynthesis associated with more erect canopies that favor light penetration, higher nitrogen uptake and greener leaves (Sadras et al. 2012a; Cossani and Sadras 2021), (iii) higher nitrogen–water co-limitation associated with a higher N uptake per unit of evapotranspiration (Sadras and Lawson 2013; Cossani and Sadras 2019), and (iv) a smaller root system with enhanced nitrogen uptake per unit root length (Aziz et al. 2017). In contrast to the adaptive role of a smaller root system (Aziz et al. 2017), a comparison of three varieties with exceptionally large and small root systems showed that larger root systems associated with late flowering adapted to severe early season drought allowing greater recovery in leaf area and shoot and root biomass by anthesis (Figueroa-Bustos et al. 2019).

Here, we used our historical collection of Australian wheats to test the hypothesis that selection for yield and agronomic traits in winter-rainfall environments has improved early-season drought resistance in Australian wheat varieties selected in the 1958–2012 period. We measured phenological and physiological traits to identify shifts associated with the putative improvement in drought tolerance.

Materials and methods

Plant material and growth conditions

Ten Australian wheat (Triticum aestivum L.) varieties released between 1958 and 2012 and previously phenotyped in field and glasshouse conditions (Aziz et al. 2017; Sadras and Lawson 2011, 2013; Sadras et al. 2012a; Cossani and Sadras 2019, 2021) were used: Heron (released in 1958), Halberd (released in 1969), Condor (released in 1973), Spear (released in 1984), Janz (released in 1989), Frame (released in 1994), Krichauff (released in 1997), Wyalkatchem (released in 2001), Gladius (released in 2007), and Mace (released in 2012). These varieties were selected because of their wide adoption in the winter-rainfall environments of Australia. Plants were grown in an evaporatively-cooled glasshouse at The University of Western Australia, Perth, Australia (31°93’ S, 115°83’ E) from May to November 2018, with an average air temperature of 17 °C (range 7–26 °C), relative humidity of 67%, natural photoperiod from 10.5–13.0 h, and average photosynthetic photon flux density of 935 ± 19 µmol m⁻² s⁻¹ measured at the plant level at 13:00 h.
Plants were grown in 1.0 m deep PVC columns (0.15 m diameter) filled with soil, with 4 cm of gravel at the bottom to facilitate drainage. The soil was a reddish-brown sandy clay loam, Red Calcic Dermosol (Isbell 1993), collected from the top 0–15 cm of soil in a field at Cunderdin (31°64' S, 117°24' E), Western Australia. It comprised 63.5% brown sand, 8.3% silt and 28.3% clay with pH, 6.0 measured in a 1:5 suspension of soil in 0.01 M CaCl2. The soil contained 6 μg g−1 nitrate–N, 4 μg g−1 ammonium-N, 46 μg g−1 Colwell P, and 691 μg g−1 Colwell K. Air-dried soil was sieved to 2 mm and mixed with coarse yellow sand (200–2000 µm particle size) in a 4:1 ratio using a cement mixer for uniformity. The soil was packed slowly into each column from the bottom to the top by sections of 0.20 m length to a bulk density of approximately 1.50 g cm−3. At sowing, the equivalent of 60 kg N ha−1 as urea; 72 kg P ha−1 as amended superphosphate (with Cu, Zn, Mo, S), and 70 kg K ha−1 as potash was mixed into the top 0.1 m of soil in each column. These rates are recommended for wheat on Cunderdin soil (Flower et al. 2012). Four uniform seeds were sown along a center row in each column and thinned to two per column at the two-leaf stage.

Treatments

We established an experiment with 10 varieties and two watering regimes [well-watered (WW) and early season drought (ESD)] in a completely randomized design with four replicates for each variety and treatment. The columns were rotated weekly to minimize spatial variability.

Forty-eight hours before sowing, the well-watered columns were slowly watered by hand to saturation, and the soil surface was covered with aluminum foil to prevent evaporation. From sowing to 32 days after sowing (DAS), the well-watered treatment received 200 mL water per week to maintain the soil water content to 90% field capacity. The columns of the drought treatment were maintained dry until sowing. Immediately after sowing, the ESD columns were watered with the equivalent of 25 mm rainfall (~441 mL water), which wet the top 0.12–0.15 m soil to a volumetric water content~20%; no further water was applied for 32 days. After this time and until physiological maturity (Z91) (Zadoks et al. 1974), both the well-watered and droughted plants were equally watered by hand twice per week to maintain the soil water content close to 90% field capacity and to avoid drainage of excess water.

Phenology, soil water content, leaf water potential, stomatal conductance and leaf photosynthesis

Phenological development was monitored regularly using Zadok’s scale (Zadoks et al. 1974). At 32 DAS for both WW and ESD treatments, before terminating the drought treatment, we measured volumetric soil water content, leaf water potential (Ψleaf), stomatal conductance (gs), and leaf net photosynthetic rate. Volumetric soil water content in the top 0.15 m of the soil profile was measured with a 15 cm soil moisture probe connected to a water content sensor (CS658 HydroSense II Water Content Sensor, Campbell Scientific, Australia). Measurements of Ψleaf, gs, and leaf net photosynthesis rate were made on the last expanded leaf of the main stem on four replicate columns (two plants for each column), between 10:30 and 14:00 on a day with clear sky. Rates of leaf net photosynthesis and gs were measured with a LI-COR gas-exchange system (LI-6400XT, LI-COR Bioscience, Nebraska, USA) with an LED light source on the leaf chamber. The cuvette CO2 concentration was set to 380 µmol \textendash 1 and LED light intensity to 900 µmol m−2 s−1, the average saturation intensity for photosynthesis in wheat (Austin 1990). Immediately after these measurements, Ψleaf was measured using a Scholander pressure chamber (model 1000, PMS Instrument Co., Oregon, USA). The last expanded leaf of the main stem was loosely covered with a plastic sheath before excision and during the measurement to avoid evaporation (Turner 1988).

Shoot traits

We measured leaf area, leaf biomass, specific leaf area (SLA), tiller number, and shoot biomass for each variety and treatment at 32 DAS, before terminating the drought treatment, and at anthesis (Z61), and shoot biomass, yield and yield components at final harvest. At each sampling time, four columns (8 plants) per variety and treatment (4C x 2 T) were harvested and each column (two plants) served as a replicate. Shoots were cut at the crown and leaf area was measured using a portable leaf area meter (LI-3000, Li-COR Biosciences, Lincoln, NE, USA). The number of tillers was recorded, and stems and leaves were dried in an oven at 70 °C for 48 h and then weighed to determine dry weights. Shoot biomass, grain yield and yield components were measured at maturity. Spikes
per plant were counted before separated from shoots, oven-dried at 60 °C for 48 h, and then threshed by hand. The number and weight of grains per plant were recorded. Harvest index (HI) was calculated as the ratio of grain yield to total shoot biomass.

Root traits

We measured total root length, total root biomass, total root length density (root length per unit of soil volume; RLD), and specific root length (SRL, root length per unit of biomass), which is an indirect measure of root thickness. Measurements were made at 32 DAS, just before terminating the drought treatment, and at anthesis (Z61) for each variety. Immediately after harvesting the shoots, the soil profile in each column was sampled from top to bottom. The roots in each column were recovered from the soil by washing and repeated sieving through a 1.4 mm sieve to produce a clean sample as described by Palta and Fillery (1993). After the roots were recovered from a section of the soil profile, they were placed in plastic bags and stored at 4 °C until measurement, often two days later. The root length in each root sample was measured as described by Liao et al. (2004). Briefly, roots were stained for 30 min with 0.1% (w/v) methyl blue prior to analysis, placed in a 0.2×0.3 m glass tray in about 3 mm water, and untangled to avoid any overlap. The glass tray was placed on the scanner, and the roots were scanned at 600 pixels per mm using an Epson scanner (ES2200) connected to a computer. The root material was then dried at 70 °C for 48 h and weighed. The images were analyzed for root length using WinRHIZO 2009 (model Pro, second version, Regent Instruments, Québec, Canada). Total root length density was calculated as the total root length to 1.0 m of the soil profile divided by the soil volume in column (0.0176 m³).

Statistical analysis

The data were analyzed using SPSS 21.0 Statistical Analysis System, Origin Lab 10.0 and Microsoft Excel 2013. Chronological trends of phenotypic traits were tested using least-square regressions of trait deviation vs year of release. Absolute (g plant⁻¹ yr⁻¹) and relative (% yr⁻¹) rates of change for each trait were calculated as the slope of the least-square regression between the trait and year of release. The relative rate was calculated in relation to the newest variety (Fischer et al. 2014). We report p-value as a continuous quantity (Greenland 2019).

We calculated the drought susceptibility index (DSI) (Fischer and Maurer 1978) as follows:

\[
\text{DSI} = \left[ 1 - \left( \frac{Y_d}{Y_w} \right) \right] / D
\]

where \( Y \) is yield, \( d \) and \( w \) are drought and well-watered respectively, and \( D \) is drought intensity = 1 – (mean \( Y_d \) of all varieties/(mean \( Y_w \) of all varieties).

Results

Soil water content, leaf water potential, stomatal conductance and leaf gas-exchange at the end of the drought period

Figure 1 and Table 1 summarize soil water content and water-related traits at 32 DAS, just before terminating the drought treatment. Under well-watered conditions, topsoil (0-0.15 m) volumetric water content was high (14.5–16.2%) and did not vary with year of release of the varieties (Fig. 1a). Consistently, leaf water potential (\( \Psi_{\text{leaf}} \)), stomatal conductance (\( g_s \)), leaf photosynthetic rate and leaf transpiration rate were maintained high under well-watered conditions (Fig. 1b–e, Table 1). While \( \Psi_{\text{leaf}} \) and leaf transpiration rate did not vary with year of release, \( g_s \) and leaf photosynthetic rate varied non-linearly, increasing until mid-80 s with an apparent decline afterwards (Fig. 1c–d).

Under drought, the volumetric soil water content ranged from 7.6–9.0% and decreased with year of release. Newer varieties dried the soil more than their older counterparts (Fig. 1a; Table 1). \( \Psi_{\text{leaf}} \) decreased linearly with the year of release from –1.29 to –1.80 MPa at a rate of –0.008 ± 0.002 MPa yr⁻¹ (Fig. 1b, Table 1). While \( \Psi_{\text{leaf}} \) and leaf transpiration rate did not vary with year of release, \( g_s \) and leaf photosynthetic rate varied non-linearly, increasing until mid-80 s with an apparent decline afterwards (Fig. 1c–d).

Under drought, the volumetric soil water content ranged from 7.6–9.0% and decreased with year of release. Newer varieties dried the soil more than their older counterparts (Fig. 1a; Table 1). \( \Psi_{\text{leaf}} \) decreased linearly with the year of release from –1.29 to –1.80 MPa at a rate of –0.008 ± 0.002 MPa yr⁻¹ (Fig. 1b, Table 1). Stomatal conductance, leaf net photosynthetic rate, and leaf transpiration rate increased linearly with year of release (Fig. 1c,d,e; Table 1).

Leaf area, tiller number, and shoot biomass at the end of the drought period

Under well-watered conditions, leaf area varied non-linearly, increasing initially until 1969, with a subsequent decline until 1990, with an apparent increase afterwards (Fig. 1f, Table 1). Under drought, leaf area decreased linearly with the year of release from 63.2 to 30.6 cm\(^2\)
plant$^{-1}$ at a rate of $0.58 \pm 0.11$ cm$^2$ plant$^{-1}$ yr$^{-1}$ (Fig. 1f; Table 1). Tiller number decreased linearly with year of release from 2.8 to 1.0 tillers plant$^{-1}$ in well-watered plants and 1.12 to 0.30 tillers plant$^{-1}$ under drought (Fig. 1g, Table 1). The rate of decline in tiller number with year of release was 2.8-fold higher under well-watered conditions than under drought (Fig. 1g, Table 1). Under well-watered conditions, shoot biomass decreased with year of release from 0.34 to 0.20 g plant$^{-1}$ yr$^{-1}$ (Fig. 1h; Table 1), while under drought, shoot biomass ranged from 0.15 and 0.20 g plant$^{-1}$, and did not vary with year of release (Fig. 1h, Table 1).

Root traits at the end of the drought period

Figure 2 and Table 1 summarize the variation in root traits under the two watering regimes at the end of the drought treatment. Total root length decreased linearly with year of release under well-watered and drought conditions (Fig. 2a). Under well-watered conditions, total root length decreased from 9.8 m plant$^{-1}$ in Heron, the earliest variety in the series, to 5.1 m plant$^{-1}$ in Mace, the most recent variety, while under drought, total root length decreased from 7.3 to 3.8 m plant$^{-1}$. The rate at which total root length declined with year of release was faster under well-watered conditions than under drought.
Root biomass and root length density similarly declined with year of release under well-watered and drought conditions (ESD) and well-watered conditions (WW). Measurements were made at 32 days after sowing, just before the end of the ESD treatment. Rates and p-values are from the least-square regression between trait and year of release. Relative rate is the percentage of the newest variety.

### Table 1 Absolute and relative rate of change (± s.e.) for traits of Australian wheat varieties released from 1958 to 2012 grown in 1 m deep PVC columns under early season drought (ESD) and well-watered conditions (WW). Measurements were made at 32 days after sowing, just before the end of the ESD treatment. Rates and p-values are from the least-square regression between trait and year of release. Relative rate is the percentage of the newest variety.

| Traits                        | Treatment | Rate of change          | Relative (%) | yr⁻¹ |
|-------------------------------|-----------|-------------------------|--------------|------|
| Volumetric soil water content | WW        | -0.0127 ± 0.010% yr⁻¹   | -0.0847 ± 0.0678 |      |
|                               | ESD       | -0.3085 ± 0.001% yr⁻¹   | -0.3085 ± 0.0209 |      |
| Leaf water potential          | WW        | -0.0005 ± 0.001 MPa yr⁻¹ | -0.0663 ± 0.1742 |      |
|                               | ESD       | -0.0080 ± 0.002 MPa yr⁻¹ | 0.4480 ± 0.1425 |      |
| Stomatal conductance          | WW        | 0.0002 ± 0.0008 mol H₂O m⁻² s⁻¹ yr⁻¹ | 0.0093 ± 0.2281 | 1.3947 ± 0.2405 |
|                               | ESD       | 0.0016 ± 0.0003 mol H₂O m⁻² s⁻¹ yr⁻¹ | 0.0093 ± 0.2281 | 1.3947 ± 0.2405 |
| Leaf net photosynthetic rate  | WW        | 0.0125 ± 0.039 µmol CO₂ m⁻² s⁻¹ yr⁻¹ | 0.1262 ± 0.3335 |      |
|                               | ESD       | 0.0790 ± 0.011 µmol CO₂ m⁻² s⁻¹ yr⁻¹ | 1.0136 ± 0.1507 |      |
| Leaf transpiration rate       | WW        | 0.0216 ± 0.017 mmol H₂O m⁻² s⁻¹ yr⁻¹ | 0.4512 ± 0.3539 |      |
|                               | ESD       | 0.0323 ± 0.095 mmol H₂O m⁻² s⁻¹ yr⁻¹ | 0.9485 ± 0.1900 |      |
| Leaf area                     | WW        | -0.583 ± 0.114 cm² plant⁻¹ yr⁻¹ | -1.9181 ± 0.3881 |      |
|                               | ESD       | 0.312 ± 0.029 cm² plant⁻¹ yr⁻¹ | 0.825 ± 0.2221 |      |
| Tiller number                 | WW        | -0.033 ± 0.004 plant⁻¹ yr⁻¹ | -3.4154 ± 0.4105 |      |
|                               | ESD       | -0.012 ± 0.003 plant⁻¹ yr⁻¹ | -2.3816 ± 0.6297 |      |
| Shoot biomass                 | WW        | -0.0020 ± 0.0006 g plant⁻¹ yr⁻¹ | -1.021 ± 0.293 |      |
|                               | ESD       | -0.0002 ± 0.0002 g plant⁻¹ yr⁻¹ | -0.1106 ± 0.1897 |      |
| Root length                   | WW        | -0.0849 ± 0.008 m plant⁻¹ yr⁻¹ | -1.6306 ± 0.1697 |      |
|                               | ESD       | -0.0591 ± 0.005 m plant⁻¹ yr⁻¹ | -1.5270 ± 0.1402 |      |
| Root biomass                  | WW        | -0.0005 ± 0.00006 g plant⁻¹ yr⁻¹ | -1.8145 ± 0.2103 |      |
|                               | ESD       | -0.0004 ± 0.00003 g plant⁻¹ yr⁻¹ | -1.3254 ± 0.1009 |      |
| Root length density           | WW        | -0.0024 ± 0.0002 cm³ plant⁻¹ yr⁻¹ | -1.6306 ± 0.1697 |      |
|                               | ESD       | -0.0017 ± 0.0002 cm³ plant⁻¹ yr⁻¹ | -1.5270 ± 0.1402 |      |
| Root: shoot ratio             | WW        | -0.0006 ± 0.0003 yr⁻¹ | -1.321 ± 0.2213 |      |
|                               | ESD       | -0.0020 ± 0.0004 yr⁻¹ | -0.4242 ± 0.2455 |      |

(Table 1). Root biomass and root length density similarly declined with year of release under well-watered and drought conditions (Fig. 2b, c). The decline in RLD with year of release was greater under well-watered conditions than under drought (Table 1). The root: shoot ratio declined linearly with year of release under drought from 0.28 in Heron to 0.17 in Mace (Fig. 2d; Table 1). Under well-watered conditions the root: shoot ratio showed no trend (Fig. 2d, Table 1).

### Shoot and root traits at anthesis

At anthesis of each variety, leaf area declined linearly with year of release in well-watered and droughted plants (Fig. 3a). Leaf area of well-watered plants declined from 826 cm² plant⁻¹ in Heron to 655 cm² plant⁻¹ in Mace at a rate of 3.9 ± 0.62 cm² plant⁻¹ yr⁻¹. Leaf area of droughted plants declined from 476 to 332 cm² plant⁻¹ at a rate of 2.9 ± 0.49 cm² plant⁻¹ yr⁻¹ (Table 2). The number of tillers and shoot biomass similarly declined linearly with year of release in well-watered and droughted plants (Fig. 3b; Table 2). The decline could be associated with the fact that modern genotypes showed an early anthesis time respect to the older ones. The decline in tiller number with year of release was sharper in well-watered plants than droughted plants (Table 2).

Total root length, root biomass, root length density, and the root: shoot ratio at anthesis declined...
linearly with year of release in both well-watered and droughted plants (Fig. 3d–g, Table 2).

**Phenology**

Wheat varieties released between 1958 and 2012 emerged at 7–10 DAS under both watering regimes, with 1–3 d difference among the varieties. Time to 50% anthesis declined linearly with year of release in well-watered and droughted plants (Fig. 4a). Time to anthesis in well-watered plants decreased by 23 days, from 103 d in Heron to 80 d in Mace, while in droughted plants declined from 91 to 77 d. The rate at which time to anthesis declined was faster in well-watered than in droughted plants (Table 3). Time to physiological maturity (Z91) declined with year of release at similar rates in both watering regimes (Fig. 4b, Table 3). Duration of grain filling did not vary with year of release in well-watered plants but ranged from 39 d in Condor to 42 d in Krichauff. In droughted plants, duration of grain filling decreased linearly with year of release from 42 to 33 d at a rate of $0.13 \pm 0.009$ d yr$^{-1}$ (Fig. 4c; Table 3).

**Grain yield and yield components**

Grain yield increased with year of release under both well-watered and early season droughted conditions (Fig. 5a). The rate of increasing grain yield with year of release was faster under well-watered conditions than under drought (Table 3). Shoot biomass at final harvest showed no trend with year of release under both watering regimes (Fig. 5b; Table 3). Harvest index increased linearly with year of release at similar rates for well-watered and droughted plants (Fig. 5c, Table 3). Ear number, grain number, and grain weight did not vary with year of release irrespective of watering regime.
There was a strong correlation between the mean grain yield of nine of the ten cultivars used in this study, measured in field plots in three sites in South Australia (Sadras and Lawson 2011) and the grain yield from plants grown in 1.0 m deep PVC columns under early season drought (ESD) and well-watered (WW) conditions in the glasshouse in this study (Fig. 5g).

Relative rates of change for traits of Australian wheat varieties released from 1958 to 2012 are presented in Tables 1, 2, and 3, together with the absolute rates of change with year of release of the varieties. While the absolute rates of change are the regression coefficients, which have agronomy relevance, the relative rates involve the analysis of change relative to the latest cultivar released, which have physiological importance. The relative rate is a standardized measure of trait change that allows the performance of cultivars to be compared on an impartial basis.
## Discussion

Wheat breeding focuses primarily on yield, agronomic adaptation, grain quality, and disease resistance (Richards et al. 2014). This selective pressure leads to predictable changes in phenotype, such as increased HI (Slafer et al. 2021), and some unexpected changes, such as reduction in root biomass compensated by increased nitrogen uptake per unit root length (Aziz et al. 2016). In our study, the phenotyping of a collection of wheat cultivars representing breeding efforts from 1958 to 2012 showed improved grain yield with year of release in plants under early season drought associated with shifts in stomatal conductance, leaf net photosynthesis and transpiration rate and phenological development. Grain yield in this study was measured in 8 plants per variety and treatment (4 pots of two plants each) grown in 1.0 m deep PVC columns in a glasshouse. Although these growing conditions may have resulted in a more severe early season drought than for field crops (Turner 2019), the mean grain yield of nine of ten varieties grown in this study positively and strongly correlated with that of the same varieties grown in the field at three sites in South Australia (SADRAS and LAWSON 2011). Despite the different growing conditions, the correlation confirms an improved grain yield in wheat varieties released between 1958 and 2007 in Australia (SADRAS and LAWSON 2011).

Selection for yield favored an anisohydric phenotype. The response to early season drought revealed a change in the continuum from isohydric to anisohydric phenotypes (TARDIEU and SIMONEAU 1998; BLUM 2015). Under the early season drought, the increase in soil water use at the top 0.12–0.15 m soil surface with the year of release, decreased $\Psi$ leaf and increased $g_s$, leaf photosynthesis and transpiration rates (anisohydric behavior), but shoot biomass was unchanged with the year of release. Old and modern cultivars in the series have almost similar shoot biomass despite it was expected modern cultivars to have higher shoot biomass as their leaf photosynthesis was higher (Henson et al 1989; Jensen et al 1989) than the older ones. However, leaf area and tiller number, two contributors to shoot biomass, decreased with year of release and likely the benefit in the modern cultivars of having a higher leaf photosynthesis rate for gaining shoot biomass was offset by the reduction in leaf area and tiller number. Despite the reduction in leaf area and tiller number with the year of release, the relative reduction of shoot biomass in recently released cultivars (drought/well irrigated) was smaller than in old cultivars, indicating that high leaf photosynthesis rate with high stomatal conductance and transpiration rate would contribute to maintenance of shoot biomass under early season drought in recently released cultivars.

### Table 2 Absolute and relative rates of change for traits of Australian wheat varieties released from 1958 to 2012 grown in 1 m deep PVC columns under early season drought (ESD) and well-watered conditions (WW). Measurements were made at 50% anthesis of each cultivar. Rates and $p$-values are from the least-square regression between trait and year of release. Relative rate is the percentage of the newest variety.

| Traits               | Treatment | Rates of change | Absolute           | Relative (yr$^{-1}$) |
|----------------------|-----------|-----------------|--------------------|----------------------|
|                      |           |                 | $p$-values         |                      |
| Leaf area WW         | -3.91 ± 0.62 cm$^2$ plant$^{-1}$ yr$^{-1}$ | -0.7531 ± 0.2579  |                     |
| ESD                  | -2.97 ± 0.49 cm$^2$ plant$^{-1}$ yr$^{-1}$ | -0.8919 ± 0.3454  |                     |
| Tiller number WW     | -0.085 ± 0.011 plant$^{-1}$ yr$^{-1}$    | -2.1836 ± 0.2993  |                     |
| ESD                  | -0.059 ± 0.049 plant$^{-1}$ yr$^{-1}$    | -2.4325 ± 0.2037  |                     |
| Shoot biomass WW     | -0.042 ± 0.012 g plant$^{-1}$ yr$^{-1}$  | -0.9169 ± 0.2418  |                     |
| ESD                  | -0.040 ± 0.010 g plant$^{-1}$ yr$^{-1}$  | -1.1328 ± 0.2433  |                     |
| Root length WW       | -0.506 ± 0.075 m plant$^{-1}$ yr$^{-1}$  | -1.0034 ± 0.1503  |                     |
| ESD                  | -0.244 ± 0.033 m plant$^{-1}$ yr$^{-1}$  | -1.4769 ± 0.1999  |                     |
| Root biomass WW      | -0.013 ± 0.002 g plant$^{-1}$ yr$^{-1}$  | -2.2122 ± 0.3795  |                     |
| ESD                  | -0.007 ± 0.0009 g plant$^{-1}$ yr$^{-1}$ | -3.0177 ± 0.3596  |                     |
| Root length density  | -0.006 ± 0.0009 cm cm$^{-3}$ yr$^{-1}$   | -1.0034 ± 0.1503  |                     |
| ESD                  | -0.003 ± 0.0004 cm cm$^{-3}$ yr$^{-1}$   | -1.4769 ± 0.1999  |                     |
| Root: Shoot ratio WW | -0.001 ± 0.0002 yr$^{-1}$               | -1.0294 ± 0.2456  |                     |
| ESD                  | -0.0009 ± 0.0002 yr$^{-1}$              | -1.5635 ± 0.2977  |                     |
Older phenotypes reduced $g_s$ and maintained $\Psi_{leaf}$ at the expense of leaf photosynthesis and transpiration per unit leaf area (isohydric behavior) and did not reduce leaf area and tiller number, maintaining shoot biomass. Newer phenotypes featured a more anisohydric behavior maintaining $g_s$, leaf photosynthesis and transpiration per unit leaf area at the expense of $\Psi_{leaf}$. Similarly, Pima cotton ($Gossypium barbadense$ L.) bred for higher yield potential had higher $g_s$ and smaller leaf area than earlier lines (Lu et al. 1994).

We did not measure osmotic adjustment but hypothesize that osmotic adjustment might have contributed to the maintenance of $g_s$ and leaf photosynthesis under decreasing $\Psi_{leaf}$ in newer phenotypes. Osmotic adjustment, which results from an active accumulation of solutes in response to decreasing $\Psi_{leaf}$ under water deficit (Turner and Jones 1980), varies among wheat genotypes (Morgan and Condon 1986; Morgan et al. 1986; Blum et al. 1999; Moinuddin et al. 2005). However, the marked reduction in leaf area of newer phenotypes under drought is evidence against superior osmoregulation (Blum 1989; Nio et al. 2011, 2018). Further experiments that measure osmotic potential are needed to solve these questions. The higher $g_s$ of newer varieties under drought is a widespread response of crops to selection for yield (Roche 2015). In some crop-environment settings, high $g_s$ has been interpreted as an adaptation to elevated temperature at the expense of water use efficiency (Radin et al. 1994; Lu et al. 1994; Sadras et al. 2012b; Galat Giorgi et al. 2020).

Selection for yield favored smaller root system

Consistent with Aziz et al. (2016), we found a decline in root length, root biomass, and root length density with year of release in well-watered plants and it is likely that the decline is a consequence of shorter time to anthesis in modern cultivars. However, early season drought reduced root traits more markedly in older varieties than newer ones. Since drying soil often triggers seminal root growth that favors water uptake in some wheat genotypes (Palta and Gregory 1997; Whitmore and Whalley 2009; Hodgkinson et al. 2017), it is likely that, seminal roots of recent released varieties grew deeper in dry topsoil and slowed the decreasing rate with year of release. This is consistent with the early idea that phenotype must match the environment, and drought adaptation is associated with smaller root systems (Jordan and Miller 1980; Tardieu 2013).

Although plants exposed to early-season drought were well-watered after 32 DAS, the recovery of root length, root biomass and RLD at anthesis was unremarkable for all varieties. This was likely because
root system growth, which usually peaks at flowering (Gregory and Atwell 1991; Gregory et al. 1995; Palta and Gregory 1997), run-off time as time to anthesis shortened. Moreover, wheat genotypes with longer time to anthesis have larger root growth (total root length and root biomass) at maturity than those with shorter time to anthesis (Motzo et al., 1993; Aziz et al. 2016; Figueroa-Bustos et al. 2019, 2020).

Selection for yield reduced phenological response to drought

Early field studies with a similar collection of varieties revealed no trend in time to flowering with year of release (Sadras and Lawson 2011, 2013). In contrast, our glasshouse study showed earlier flowering in newer varieties in the well-watered treatment. The regressions between time to flowering and year of release converged between well-watered and droughted plants. Older varieties had a marked shortening of time to flowering in response to drought, whereas newer varieties were less responsive, despite being more stressed. In contrast, two independent studies under field and glasshouse conditions have reported delayed anthesis of wheat in response to early-season drought (French and Palta 2014; Figueroa-Bustos et al. 2019). The non-linear response of wheat phenology to water stress could explain these contradictory responses. Angus and Moncur (1977) found that time from flower initiation to anthesis shortened under mild water stress ($\Psi_{\text{leaf}} - 1.5 \text{ MPa}$) and delayed with severe stress ($\Psi_{\text{leaf}} - 2.5 \text{ MPa}$). In our study, a mild stress ($\Psi_{\text{leaf}} - 1.8$) shortened time to flowering, whereas more severe stress ($\Psi_{\text{leaf}} - 2.5 \text{ MPa}$) delayed flowering in Figueroa-Bustos et al. (2019). Our findings highlight the need for simulation modeling to account for genotype-dependent phenological response to water deficit (Chauhan et al. 2019; McMaster et al. 2013) because mainstream crop models do not (Wallach et al. 2021). Overlooking the effect of plant water status on phenology can therefore bias predictions of crop adaptation to future climates, including early-season drought.

Interesting, shoot biomass at maturity did not change with year of release, but grain yield increased with year of release and the increase was associated to HI. The ratio of shoot biomass under well-watered to early season droughted was similar ($\sim 0.66$) regardless

---

**Table 3** Absolute and relative rates of change for traits of Australian wheat varieties released from 1958 to 2012 grown in 1 m deep PVC columns under early-season drought (ESD) and well-watered conditions (WW). Measurements were made at final harvest. Rates and $p$-values are from the least-square regression between trait and year of release. Relative rate is the percentage of the newest variety.

| Traits               | Treatment | Rates of change          | Absolute     | Relative (% yr$^{-1}$) |
|----------------------|-----------|--------------------------|--------------|------------------------|
|                      |           |                          | WW           | ESD                    |
| Grain yield          | WW        | 0.031 ± 0.007 g plant$^{-1}$ yr$^{-1}$ | 0.4300 ± 0.0787 |
|                      | ESD       | 0.026 ± 0.005 g plant$^{-1}$ yr$^{-1}$ | 0.3594 ± 0.0829 |
| Shoot biomass        | WW        | -0.0158 ± 0.0234 g plant$^{-1}$ yr$^{-1}$ | -0.0752 ± 0.1180 |
|                      | ESD       | -0.0184 ± 0.0264 g plant$^{-1}$ yr$^{-1}$ | -0.0752 ± 0.1180 |
| Harvest index        | WW        | 0.190 ± 0.034% yr$^{-1}$ | 0.4358 ± 0.0784 |
|                      | ESD       | 0.231 ± 0.027% yr$^{-1}$ | 0.5469 ± 0.0637 |
| Ear number           | WW        | 0.008 ± 0.021 plant$^{-1}$ yr$^{-1}$ | 0.2064 ± 0.5508 |
|                      | ESD       | 0.001 ± 0.019 plant$^{-1}$ yr$^{-1}$ | 0.0206 ± 0.3791 |
| Grain number         | WW        | 0.585 ± 0.491 plant$^{-1}$ yr$^{-1}$ | 0.3233 ± 0.2713 |
|                      | ESD       | 0.616 ± 0.372 plant$^{-1}$ yr$^{-1}$ | 0.4083 ± 0.2465 |
| 1000-grain weight    | WW        | 0.033 ± 0.087 mg yr$^{-1}$ | 0.0693 ± 0.1797 |
|                      | ESD       | 0.022 ± 0.061 mg yr$^{-1}$ | 0.0532 ± 0.1456 |
| Time to anthesis     | WW        | -0.457 ± 0.067 days yr$^{-1}$ | -0.5905 ± 0.0764 |
|                      | ESD       | -0.289 ± 0.026 days yr$^{-1}$ | -0.3755 ± 0.0352 |
| Time to physiol. maturity | WW   | -0.4792 ± 0.022 days yr$^{-1}$ | -0.3941 ± 0.0401 |
|                      | ESD       | -0.4240 ± 0.019 days yr$^{-1}$ | -0.3820 ± 0.0206 |
| Duration grain filling | WW     | 0.0038 ± 0.0170 days yr$^{-1}$ | 0.0096 ± 0.0427 |
|                      | ESD       | -0.1325 ± 0.009 days yr$^{-1}$ | -0.3980 ± 0.0560 |
| Drought susceptible index | WW | -0.003 ± 0.0003 yr$^{-1}$ | -1.1062 ± 0.1082 |
of year of released, likely indicating that an increase in the potential yield through an increase in grain number in the recent released cultivars was a reason of high yielding even if they experienced early season drought. The shortening of grain filling with drought often reduces HI and yield (Kobata et al. 1992; He and Rajaram 1993; Wheeler et al. 1996). In our experiment, plants exposed to early season drought, maintained duration of grain filling in older varieties, but shortened it in newer ones. Drought did not affect HI since the proportional reduction in grain yield and shoot biomass was similar under well-watered and drought conditions. Modern cultivars had higher grain yield associated with higher HI than the old cultivars, presumably because of a higher amount of reserve carbohydrates and/or faster rates of remobilization to the grain in newer varieties (Kobata et al., 1992; Palta et al. 1994).

As reported in Aziz et al. (2017), the root system of wheat varieties released in Australia between 1958 and 2012 progressively reduced their root length, root biomass, and RLD with year of release. The rate of
A decrease was 0.059 ± 0.005 m pl⁻¹ yr⁻¹ for total root length and 0.0017 ± 0.0002 cm cm⁻³ yr⁻¹ for RLD. The reduction in root length, root biomass, and RLD with year of release was likely associated with the reduction in time to anthesis in the modern cultivars compared to the older ones. However, early season drought slowed down the rate of decline in these root traits. Since drying soil often triggers seminal root growth in some wheat genotypes (Palta and Gregory 1997; Whitmore and Whalley 2009; Hodgkinson et al. 2017), seminal root tips of recent varieties likely grew deeper than older varieties with decreasing soil water content in the topsoil layer, and this additional root growth slow down the rate of declining in root length, root biomass and RLD with year of release.

Early season drought reduced root length, root biomass, and RLD; less so in the varieties released after 1997 (Wyalkatchem, Gladius, Mace) than earlier varieties (Heron, Halberd, and Condor). This was likely because the recent varieties kept leaf photosynthesis and transpiration rate and reduced leaf area during early drought, with more available carbon assimilates for root growth, when the demand of daily carbon assimilates for wheat root system growth and proliferation was high (Gregory and Atwell 1991; Palta and Gregory 1997).

Under early drought, the recent released varieties had a higher capacity to maintain shoot biomass than older varieties, despite their shoot biomass potentiality decreased. It is unknown whether the higher capacity to maintain shoot biomass came from the high capacity of gs and leaf photosynthesis rate, as leaf area, one of factors determining whole plant photosynthesis decreased. It is likely that root biomass and length did not contribute to the high capacity to maintain shoot biomass, despite it is thought that a low root biomass gives a source for an increase in shoot biomass. At anthesis shoot biomass, root biomass and root length in plants exposed to early season drought was lower in recent released varieties than in older ones, associated with the differences in time to anthesis between recent and older released varieties (Aziz et al. 2017).

Under early season drought, the root: shoot ratio decreased linearly with year of release, and it is likely that the change in root: shoot ratio from high in the older cultivars to low in the recent released ones, increased the transpiration rate in recent released cultivars. This is because a high root: shoot ratio can decrease transpiration rate as a large root system provides more water to the plant while a less large shoot will provide less evaporation. A low root: shoot ratio could increase transpiration rate as the supply of water through the root system will be not enough due to increased evaporation by a larger shoot system (Saidi et al. 2010; Vadez et al. 2021). Indeed, the linear decrease in root: shoot ratio with year of release under early season drought was consistent with the linear increase in leaf transpiration rate with year of release. Under drought the root: shoot ratio of old varieties was higher as shoot biomass was more negatively affected than root biomass. This trend was different at anthesis as the root: shoot ratio decreased similarly in both modern and old varieties with the year of release and at similar rate under drought ad well-watered conditions.

Terminal drought or drought after anthesis often occurs in the Mediterranean climate zone of Australia. An interesting question is what the contributions from the performance under early season drought are to yield in the case terminal drought occurs? Clearly this question cannot be answer with the results from this study, but the less effect of early season drought in shoot biomass at anthesis is likely to give a benefit on the yield under terminal drought. There is no unique and obvious answer to this question, as the contributions from the performance under early season drought to yield depends on the time, intensity and rate of development of the terminal drought. This can be only speculated that grain yield might be reduced if duration of grain filling is further reduced in the recent released cultivars, but if there is not room for further reductions in duration of grain filling, grain yield might be maintained. We may also speculate that grain yield under terminal drought could be less affected if biomass accumulation between the end of the early season drought and anthesis is high.

Conclusions

Wheat varieties released in Australia between 1958 and 2012, exposed to early-season drought after leaf emergence, progressively increased grain yield with year of release. The decreasing susceptibility index to early season drought with year of release was associated with a change from isohydric to anisohydric
phenotypes and distinct phenological adaptation to early season drought. The higher $g_s$ and leaf photosynthesis rate of anisohydric varieties contributed to the increased grain yield with year of release since the early water deficit was moderate with $\Psi_{\text{leaf}}$ down to $-1.8$ (Alvarez et al. 2007; Sade et al. 2009). Selection for grain yield and agronomic adaptation has favored traits for early season drought tolerance in Australian wheat. The wheat collection used in this study is a suitable model to further investigate the phenotypic response to drought, including the dual role of labile carbohydrates in osmoregulation and as a buffer for grain fill and its genetic basis.

Acknowledgements We thank Mr. Robert Creasy and Mr. Bill Piasini for technical assistance in the glasshouse experiment, and Prof. Neil C Turner for discussion on the data. This research was supported by The University of Western Australia (UWA). The Higher Education Commission of Pakistan and the China Scholarship Council provided financial support to Mr. Faisal Khan and Mr. Yupeng Feng, respectively, for their training visits to UWA.

References

Alvarez E, Scheiber SM, Beeson RC Jr, Sandrock DR (2007) Drought tolerance responses of purple Lovegrass and 'Adagio'maiden grass. Hort Sci 42:1695–1699

Angus JF, Moncur MW (1977) Water stress and phenology in wheat. Aust J Agric Res 28:177–181

Armstrong LJ, Abrecht DG, Anderson WK, Belford RK (1996) The effect of non-lethal water deficits during establishment on the growth of wheat crops. Proceedings of the 8th Australian Agronomy Conference, Toowoomba, Queensland, Australia, 30 January-2 February, 1996. Australian Society of Agronomy Inc., Toowoomba, Australia

Austin RB, Bingham J, Blackwell RD, Evans LT, Ford MA, Morgan CL, Taylor M (1980) Genetic improvements in winter wheat yields since 1900 and associated changes. J Agricul Sci 94:675–689

Austin RB (1990) Prospects for genetically increasing the photosynthetic capacity of crops In: Zelith Y (ed) Perspectives in biochemical and genetic regulation of photosynthesis. Alan R. Liss, New York, vol. 1, pp. 395–409

Aziz MM, Palta JA, Siddique KHM, Sadras VO (2017) Five decades of selection for yield reduced root length density and increased nitrogen uptake per unit root length in Australian wheat varieties. Plant Soil 413(1–2):181–192

Blum A (1989) Osmotic adjustment and growth of barley genotypes under drought stress. Crop Sci 29:230–233

Blum A, Zhang J, Nguyen HT (1999) Consistent differences among wheat cultivars in osmotic adjustment and their relationship. Field Crops Res 64:287–291

Blum A (2015) Towards a conceptual ABA ideotype in plant breeding for water limited environments. Funct Plant Biol 42:502–513

Cann DJ, Schillinger WF, Hunt JR, Porker KD, Harris FAJ (2020) Agroecological Advantages of early-sown winter wheat in semi-arid environments: a comparative case study from southern Australia and pacific northwest United States. Front Plant Sci 11:568

Chapman R, Asseng S (2001) An analysis of the frequency and timing of false break events in the Mediterranean region of Western Australia. Aust J Agricul Res 52(3):367–376

Chauhan YS, Ryan M, Chandra S et al (2019) Accounting for soil moisture improves prediction of flowering time in chickpea and wheat. Sci Rep 9:7510. https://doi.org/10.1038/s41598-019-43848-6

Chenu K, Dehirmfard R, Chapman SC (2013) Large-scale characterization of drought pattern: a continent-wide modeling approach applied to the Australian wheatbelt – spatial and temporal trends. New Phytol 198:801–820

Chenu K (2015) Characterising the crop environment - nature, significance and applications. In: SadrasD VO, Calde-rini F (eds) Crop physiology: Applications for genetic improvement and agronomy. Academic Press, San Diego, pp 321–348

Cossani CM, Sadas VO (2019) Increasing co-limitation of water and nitrogen drives genetic yield gain in Australian wheat. Europ J Agron 106:23–29

Cossani CM, Sadas VO (2021) Symmetric response to competition in binary mixtures of cultivars associates with genetic gain in wheat yield. Evol Appl 14:2064–2078

Figueroa-Bustos VF, Palta JA, Chen Y, Siddique KHM (2019) Early season drought largely reduces grain yield in wheat cultivars with smaller root systems. Plants 8(9):1–15. https://doi.org/10.3390/plants8090305

Figueroa-Bustos V, Palta JA, Chen Y, Stefanova K, Siddique KHM (2020) Contrasting root system size wheat genotypes responded differently to terminal drought. Front Plant Sci. https://doi.org/10.3389/fpls.2020.01285

Fischer R, Maurer R (1978) Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust J Agric Res 29:897–912. https://doi.org/10.1071/AR9780897

Fischer RA, Byerlee D, Edmeades GO (2014) Crop yields and global food security. Will yield increase continue to feed the world? ACIAR, Canberra

Fletcher A, Lawes R, Weeks C (2016) Crop area increases drive earlier and dry sowing in Western Australia: implications for farming systems. Crop Pasture Sci 67:1268–1280. https://doi.org/10.1071/CP16200

Fletcher AL, Robertson MJ, Abrecht DG, Sharma DL, Holzworth DP (2015) Dry sowing increases farm level wheat yields but not production risks in a Mediterranean environment. Agric Syst 136:114–124. https://doi.org/10.1016/j.agsy.2015.03.004

Flower KC, Cordingly N, Ward PR, Weeks C (2012) Nitrogen, weed management and economics with cover crops in conservation agriculture in a Mediterranean climate. Field Crops Res 132:63–75. https://doi.org/10.1016/j.fcr.2011.09.011

French B, Palta JA (2014) Early vigour avoids drought stress. GRDC Ground Cover 112:71–74
Galat Giorgi E, Keller M, Sadras V, Roig FA, Perez Peña J (2020) High temperature during the budswell phase of grapevines increases shoot water transport capacity. Agric Forest Meteorol 295:108173

Greenland S (2019) Valid P-values behave exactly as they should: Some misleading criticisms of P-values and their resolution with S-values. Am Statist 73:106–114

Gregory PJ, Atwell BJ (1991) The fate of carbon in pulse-labelled crops of barley and wheat. Plant Soil 136:205–213. https://doi.org/10.1007/BF02150051

Gregory PJ, Palta JA, Battas GR (1995) Root systems and root:mass ratio-carbon allocation under current and projected atmospheric conditions in arable crops. Plant Soil 187:221–228. https://doi.org/10.1007/BF00170889

He Z, Rajaram S (1993) Differential responses of bread wheat characters to high temperature. Euphytica 72:197–203. https://doi.org/10.1007/BF00034145

Henson IE, Jensen CR, Turner NC (1989) Leaf gas exchange and water relations of lupins and wheat. I. Shoot responses to soil water deficits. Funct Plant Biol 16:401–413

Hochman Z, Gobbert DL, Horan H (2017) Climate trends account for stalled wheat yields in Australia since 1990. Glob Chang Biol 23:2071–2081. https://doi.org/10.1111/gcb.13604

Hodgkinson L, Dodd IC, Binley A, Ashton RW, White RP, Watts CW, Whalley WR (2017) Root growth in field-grown winter wheat: Some effects of soil conditions, season and genotype. Europ J Agron 91:74–83

Isbell RF (1993) A classification system for Australian soils (third approximation). Technical Report 2/1993 Australia, CSIRO

Jensen CR, Henson IE, Turner NC (1989) Leaf gas exchange and water relations of lupins and wheat 11 Root and shoot water relations of lupin during drought-induced stomatal closure. Aust J Plant Physiol 16:415–28

Jordan WR, Miller MR (1980) Genetic variability in sorghum root system: Implications for drought tolerance. In: Turner NC, Kramer J (eds) Adaptation of plants to water and root:mass ratio-carbon allocation under current and projected atmospheric conditions in arable crops. Plant Soil 187:221–228. https://doi.org/10.1007/BF00170889

Kobata T, Palta JA, Turner NC, Fillery IR (1994) Remobilization of Carbon and Nitrogen in Wheat as Influenced by Postanthesis Water Deficits. Crop Science 34(1):118–124. https://doi.org/10.2135/cropsci1994.0011183X0034000010021x

Pook M, Lisson S, Risbey J, Unmenhofer CC, McIntosh P, Rebbeck M (2009) The autumn break for cropping in southeast Australia: trends, synopticinfluences and impacts on wheat yield. Int J Climatol 29:2012–2026

Radin JW, Lu Z, Percy RG, Zeiger E (1994) Genetic variability for stomatal conductance in Pima cotton and its relation to improvements of heat adaptation. Proc Natl Acad Sci USA 91:7217–7221

Richards RA, Hards RA, Hunt JR, Kirkegaard JA, Passioura JB (2014) Yield improvement and adaptation of wheat to water-limited environments in Australia—a case study. Crop Pasture Sci 65:676–689

Roche D (2015) Stomatal conductance is essential for higher yield potential of C3 crops. Crit Rev Plant Sci 34:429–453

Sadras VO, Lawson C, Montoro A (2012a) Photosynthetic traits of Australian wheat varieties released between 1958 and 2007. Field Crops Res 134:19–29

Sadras VO, Montoro A, Moran MA, Aphalo PJ (2012b) Elevated temperature altered the reaction norms of stomatal conductance in field-grown grapevine. Agric For Meteorol 165:35–42

Sadras VO, Lawson C (2013) Nitrogen and water-use efficiency of Australian wheat varieties released between 1958 and 2007. Europ J Agron 46:34–41

Saidi A, Ookawa T, Hirasawa T (2010) Responses of root growth to moderate soil water deficit in wheat seedlings.
Shiferaw B, Smale M, Braun H-J, Duveiller E, Reynolds M, Muricho G (2013) Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Security 5(3):291–317

Slafer GA (1994) Genetic improvement of field crops. Marcel Dekker Inc, New York

Slafer GA, Savin R, Pinochet D, Calderini D (2021) Wheat. Crop Physiology: Case Histories for Major Crops. Academic Press, pp 99–163

Tardieu F, Simonneau T (1998) Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. J Exp Bot 49:419–432. https://doi.org/10.1093/jxb/49

Tardieu F (2012) Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario. J Exp Bot 63(1):25–31

Tardieu F (2013) Plant response to environmental conditions: assessing potential production, water demand, and negative effects of water deficit. Front Physiol 4:17

Turner NC, Jones MM (1980) Turgor maintenance by osmotic adjustment: a review and evaluation. In: Turner NC, Kramer PJ (eds) Adaptation of plants to water and high temperature stress. Wiley, New York, pp 87–103

Turner NC (1988) Measurement of plant water status by the pressure chamber technique. Irrigation Sci 9:289–308

Turner NC (2019) Imposing and maintaining soil water deficits in drought studies in pots. Plant Soil 439:45–55. https://doi.org/10.1007/s11104-018-3893-1

Vadez V, Choudhary S, Kholová J, Hash CT, Srivastava R, Kumar AA, Prandavada A, Anjaiah M (2021) Transpiration efficiency: insights from comparisons of C4 cereal species. J Exp Bot 72:221–5234. https://doi.org/10.1093/jxb/erab251

Wallach D, Palosuo T, Thorburn P, Gourdain E, Asseng S, Basso B, Buis S, Crout N, Dibari C, Dumont B, Ferriere R (2021) How well do crop modeling groups predict wheat phenology, given calibration data from the target population? Europ J Agron 124:126195. https://doi.org/10.1016/j.eja.2020.126195

Watson J, Zheng BY, Chapman S, Chenu K (2017) Projected impact of future climate on water-stress patterns across the australian wheatbelt. J Exp Bot 68(21–22):5907–5921

Wheeler TR, Hong TD, Ellis RH, Batts GR, Morison JIL, Hadley P (1996) The duration and rate of grain growth, and harvest index, of wheat (Triticum aestivum L.) in response to temperature and CO2. J Exp Bot 47:623–630

Whitmore AP, Whalley WR (2009) Physical effects of soil drying on roots and crop growth. J Exp Bot 60(10):2845–2857. https://doi.org/10.1093/jxb/erp200

Zadoks JC, Chang TTK, Konzak CF (1974) A decimal code for the growth stages of cereals. Weed Res 14:415–421

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.