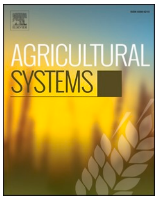
Agricultural Systems 229 (2025) 104430

Contents lists available at ScienceDirect

Agricultural Systems

journal homepage: www.elsevier.com/locate/agsy



Research Paper

A novel approach to accelerate ideotyping using model-aided envirotyping

Brian Collins [a,*], Najeeb Ullah [b], Youhong Song [c], Keith G. Pembleton [a,d]

[a] Centre for Sustainable Agricultural Systems, University of Southern Queensland, Toowoomba, QLD 4350, Australia
[b] Agricultural Research Station, Office of VP for Research & Graduate Studies, Qatar University, 2713 Doha, Qatar
[c] Ministry of Education Key Laboratory of Crop Physiology, Ecology and Genetic Breeding, Jiangxi Agricultural University, Nanchang, Jiangxi 330045, China
[d] School of Agriculture and Environmental Sciences, University of Southern Queensland, Toowoomba, QLD 4350, Australia

HIGHLIGHTS

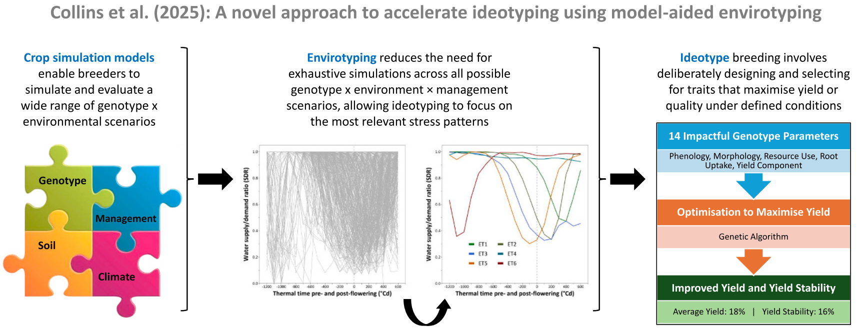
- Envirotyping identified six distinct Australian wheat environment types (ETs).
- Genetic algorithm identified ideotypes by optimising 14 wheat traits for yield improvement.
- Global, targeted at high-stress ETs, and location-specific ideotyping scenarios were assessed.
- Ideotypes boosted average yield (18 %) and yield stability (16 %) across the target population of environments.
- Global and local ideotyping strategies emphasised different traits and their interactions.

ARTICLE INFO

Editor: Zhao Zhang

Keywords:
Climate adaptability
Crop modelling
Envirotyping
Genetic optimisation
Wheat ideotyping

GRAPHICAL ABSTRACT



Collins et al. (2025): A novel approach to accelerate ideotyping using model-aided envirotyping

Crop simulation models enable breeders to simulate and evaluate a wide range of genotype x environmental scenarios

Envirotyping reduces the need for exhaustive simulations across all possible genotype x environment × management scenarios, allowing ideotyping to focus on the most relevant stress patterns

Ideotype breeding involves deliberately designing and selecting for traits that maximise yield or quality under defined conditions

ABSTRACT

CONTEXT: Climate change threatens wheat production by intensifying drought, heat stress, and yield instability. Selecting optimal cultivars is crucial for mitigating climate change impacts. Crop model-assisted ideotyping, i.e., designing and/or selecting for traits that maximise yield or quality under defined conditions, requires exploring a large number of genotype-by-environment (GxE) interactions but is computationally demanding. This is where envirotyping, i.e., categorising environments into a few environment types (ETs), emerges as a promising solution. Integrating envirotyping with ideotyping enhances breeding efficiency and enables targeted trait optimisation. This scalable, data-driven approach supports the development of climate-resilient wheat cultivars suited to diverse and changing environments.

OBJECTIVE: Show how an innovative approach leveraging envirotyping can significantly cut down the computational demands of ideotyping, while still maintaining yield improvements. This approach offers a scalable framework for developing resilient crop cultivars tailored to diverse and changing environments.

METHODS: Using the next generation of Agricultural Production Systems sIMulator (APSIM Next Generation), wheat growth and development was simulated across diverse Australian environments. Four commercial cultivars were simulated under multiple sowing dates to determine optimal sowing windows and highest-yielding cultivars for each location. Cluster analysis of water supply/demand ratios identified six ETs with distinct seasonal drought patterns. A genetic algorithm was used to optimise 14 key cultivar parameters influencing phenology, morphology, resource use, and yield components. Three ideotyping strategies—global, targeted at high-stress ETs, and location-specific—were assessed for their impact on average yield and yield stability.

---

* Corresponding author.
E-mail address: brian.collins@unisq.edu.au (B. Collins).

https://doi.org/10.1016/j.agsy.2025.104430
Received 25 February 2025; Received in revised form 7 June 2025; Accepted 15 June 2025
Available online 18 June 2025
0308-521X/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

RESULTS AND CONCLUSIONS: The ideotyping strategies effectively reduced the occurrence frequency of late-season water stress. The identified ideotypes significantly improved average yield (~18 %) and yield stability (up to 16 % reduction in coefficient of variation). Global and targeted ideotyping strategies outperformed location-specific approaches in enhancing broad adaptability. In these strategies, key traits influencing yield gains included low minimum leaf number, high grain potential size, high radiation use efficiency, low potential root water uptake rate, high stay-green, and high number of grains per gram of stem and spike biomass. Phenological traits and trait interactions were more influential in the location-specific strategy.

SIGNIFICANCE: This study demonstrates the potential of model-assisted envirotyping to improve wheat breeding efficiency by reducing computational demands while maximising average yield and yield stability. Incorporating envirotyping into breeding workflows provides a scalable, data-driven approach that complements traditional GxE testing. Our findings offer valuable insights for developing climate-resilient wheat cultivars and contribute to global food security in the face of increasing climatic variability.

1. Introduction

The global demand for agricultural crop production is projected to nearly double by 2050 due to population growth, increased consumption, and evolving dietary patterns (Gerland et al., 2014; Godfray et al., 2010). This rising demand, compounded by the increasing frequency and intensity of extreme weather events (Collins, 2022; Kornhuber et al., 2023; Ray et al., 2015; Trnka et al., 2019), presents significant challenges. Developing climate-resilient crops (Hammer et al., 2020) and refining agronomic practices tailored to future climatic conditions are crucial for ensuring food security and adapting agricultural systems.

Among staple crops, wheat (*Triticum aestivum* L.) plays an indispensable role in global food security, providing essential nutrients and supporting economies worldwide (Senapati et al., 2022; Shewry and Hey, 2015; Trnka et al., 2019). Australia contributes approximately 10–20 % of global wheat trade, producing an average of ~25 million tonnes annually (Australian Export Grains Innovation Centre, 2025). Australian wheat production faces substantial challenges due to its heavy reliance on rainfed systems, which are highly sensitive to climatic variability, including shifts in rainfall patterns and rising temperatures (Feng et al., 2018; Wang et al., 2015). These climatic shifts have been shown to accelerate crop development, shorten the growing season, and disrupt water availability during critical growth stages (Ababaei and Chenu, 2020; Collins and Chenu, 2021; Watson et al., 2017; Zheng et al., 2012). Furthermore, drought and heat stress have become more frequent (Collins, 2022), amplifying yield reductions and creating a pressing need for adaptive strategies to align the wheat crop cycle with changing water and temperature dynamics. Such climate-induced variability underscores the necessity of developing wheat cultivars that are both resilient to abiotic stresses and capable of maintaining productivity under fluctuating environmental conditions (Semenov and Halford, 2009; Shavrukov et al., 2017). This task is further complicated by the inherent uncertainties in future climate projections and the limited resources available to breeders for identifying and improving key traits (Ghahramani et al., 2015; Parry et al., 2011; Reynolds et al., 2011; Zheng et al., 2012).

Previous research has highlighted the selection of optimal (i.e., "ideal") cultivars as one of the most effective adaptation strategies for mitigating climate change impacts (Loison et al., 2017; Rötter et al., 2015; Tao et al., 2017). The concept of crop ideotypes has gained traction as an innovative approach to enhance breeding efficiency and develop resilient cultivars. Originally introduced by Donald (1968), an ideotype represents an idealised plant type optimised for specific environmental conditions and target traits. Unlike traditional yield selection, which relies heavily on chance, ideotype breeding involves deliberately designing and selecting for traits that maximise yield or quality under defined conditions (Semenov and Stratonovitch, 2013). This strategy offers a systematic framework to address complex challenges in modern agriculture, such as balancing yield with stress tolerance and resource use efficiency (Debaeke and Quilot-Turion, 2014; Rötter et al., 2011).

Donald's early ideotype traits, such as reduced leaf area and shorter plant height, have since been expanded to include physiological characteristics like enhanced photosynthetic efficiency, optimised grain filling, and improved spike fertility (Gracia-Romero et al., 2023; Parry et al., 2011; Semenov and Stratonovitch, 2013, 2015; Tefera et al., 2022; Yadav et al., 2023). These traits collectively support the development of climate-resilient wheat cultivars. Advances in crop simulation models have strengthened the case for ideotyping by providing powerful tools for exploring genotype-by-environment (GxE) interactions and optimising trait combinations (Martre et al., 2015b; Rötter et al., 2015; Semenov and Stratonovitch, 2013, 2015; Webber et al., 2018). Despite their inherent limitations (Rötter et al., 2018; e.g., Webber et al., 2022), crop simulation models have been instrumental in ideotyping, allowing breeders to explore and assess diverse combinations of genotypes and environmental scenarios. These models facilitate the identification of optimal traits for future climatic conditions, allowing researchers to bypass resource-intensive field experiments (Ababaei and Chenu, 2020; Collins et al., 2021; Collins and Chenu, 2021; Deihimfard et al., 2023; Semenov and Halford, 2009; Semenov et al., 2014). For example, Semenov and Stratonovitch (2015) used Sirius to design wheat ideotypes under future climate scenarios.

Despite their utility, crop models face challenges in assisting ideotyping. The vast number of trait-environment combinations that must be tested—along with the need to simulate these interactions under diverse management practices—poses computational challenges. Wang et al. (2019), for instance, explored over 16,000 genotypic parameter combinations to optimise wheat traits under future climate scenarios. Conducting such large-scale simulations is both time- and energy-intensive, necessitating innovative methods to streamline the process (Ababaei and Ullah, 2020).

This is where model-assisted envirotyping emerges as a promising solution. By characterising environments through the analysis of historical and simulated data, envirotyping enables the classification of environmental conditions into manageable clusters, reducing the complexity of G × E interactions (Chapman, 2008; Chenu, 2015; Collins and Chenu, 2021). Envirotyping allows breeders to focus on representative environments, thereby minimising redundant simulations while capturing key stress patterns relevant to breeding targets (Chauhan et al., 2021; Chenu et al., 2011). Clustering-based methods, in particular, offer an effective means of delineating homogeneous stress environments, enhancing the precision and efficiency of crop improvement programs (Chenu et al., 2013). Ababaei and Ullah (2020) demonstrated how clustering-based envirotyping can significantly reduce simulation requirements by focusing on key weather patterns.

Our study aims to highlight the value of envirotyping in model-assisted ideotyping. By integrating crop models with advanced envirotyping techniques, we seek to demonstrate how an innovative approach leveraging envirotyping can significantly cut down the computational demands of ideotyping, while still maintaining yield improvements. This approach not only addresses the computational challenges associated with model-aided ideotyping but also offers a scalable framework to accelerate developing resilient crop cultivars tailored to diverse and changing environments.

2. Material and methods

2.1. Study locations and simulation setup

Australian environments were chosen for this study due to their year-to-year variability in environmental conditions, which provide a wide spectrum of both stressed and non-stressed scenarios that can result in diverse yield outcomes (Wu et al., 2022). Potgieter et al. (2002) categorised the target population of Australian environments into six main types (i.e., mega-environments) using principal component analysis of long-term production variability at the shire scale. This study defines the target population of environments (TPE) as six distinct locations, each representing a specific mega-environment (Table 1).

Four Australian commercial spring wheat cultivars with contrasting maturity habits (Grains Research and Development Corporation, 2023) were selected to represent a broad spectrum of maturity patterns and season durations: Emu Rock (very quick to quick), Scepter (quick to medium), Scout (medium), and Trojan (medium to slow). Phenology parameters were derived from the publicly available the Agricultural Production Systems sIMulator (APSIM; Holzworth et al., 2018, Holzworth et al., 2014) cultivar database, which contains cultivar parameters that have been calibrated and validated (https://github.com/APSIMInitiative/ApsimX; version 2024.12.7641.0).

Historical daily weather data, including maximum and minimum temperatures, solar radiation, and rainfall, were sourced from the SILO patched point dataset (Jeffrey et al., 2001) for the simulation period (1971–2024). At each location, soil characteristics and fertilisation levels were adjusted to reflect local soils and farming practices (Table 1; Wu et al., 2022). For all simulations, soil initial conditions were reset annually, 30 days before the sowing date. Initial nitrogen contents were determined based on Chenu et al. (2013). Initial soil moisture (ISM) was set at either 25 % or 75 % of soil plant available water content (PAWC) to reflect anticipated variability in available soil moisture at sowing. Initial soil nitrogen was assumed to comprise 95 % NO3-N and 5 % NH4-N. A wide range of sowing dates were simulated, from March 15 to July 15 at two-week intervals. Simulation outputs (see below for details) from all the selected sowing dates were used to cluster the seasonal water-deficit patterns into major environment types.

2.2. Identification of environment types

The APSIM-Wheat model calculates a daily water supply/demand ratio index (SDR), which indicates the extent to which the extractable soil water meets the potential transpiration. SDR varies between 1.0 (i.e., no water stress) and 0.0 (i.e., no water available to the crop). For each simulated environment (i.e., a location × year × cultivar × sowing date × ISM), daily SDR values were centred on the flowering stage and averaged over 100 °Cd intervals from 1200 °Cd before flowering to 600 °Cd after flowering. Beyond this period, senescence markedly reduces plant transpiration, leading to a sharp rise in water-deficit stress, while the effects of water stress are predominantly observed as reduced biomass accumulation and resource retranslocation among plant organs (Chenu et al., 2013).

The ‘kmeans’ clustering function in the R programming environment (R Development Core Team, 2024) was utilised to classify the seasonal SDR patterns into major environment types (ETs). Then, an average water-deficit index pattern was calculated to represent each ET. The occurrence frequency (OF) of the identified ETs were analysed across different locations considering optimal plating windows at each location (see below).

2.3. Optimal sowing windows

For each location × cultivar combination, a two-month optimal sowing window (OSW) was identified. Simulations for all location × sowing date × cultivar combinations were used to calculate long-term average yields for every two-month sowing window between 15 March and 15 July. The sowing window with the highest long-term average yield was designated as the OSW for each location × cultivar combination. The highest-yielding cultivar (HYC) at each location was then identified. Subsequent analyses focused on simulations where HYCs were planted at each location within the identified OSWs. This approach ensured that findings were not biased by adopting suboptimal cultivars and/or sowing outside the OSW.

2.4. Designing high-yielding Ideotypes

Fourteen cultivar parameters were selected as promising for improving wheat yield potential and selected for optimisation (Table 2). In APSIM-Wheat, these parameters directly influence phenology, canopy development, morphology, resource use, and yield components and are implemented to model key aspects of wheat growth and development. This set of parameters collectively provide a comprehensive framework to optimise underlying processes to maximise yield across diverse environmental conditions.

2.4.1. Phenology

Optimising phenology is crucial for enhancing crop performance by aligning critical growth stages with favourable environmental conditions. Early or optimal timing of flowering can maximise yield, particularly in dry environments, by avoiding late-season water stress (Herndl et al., 2007; Rezzouk et al., 2022; Richards, 1991), although it might increase the probability of frost damage if early flowering cultivars are planted (Zheng et al., 2015). Yield increases of 30–50 % have been recorded in Australian regions susceptible to post-heading frosts when early flowering cereal crops successfully avoided frost events (Frederiks

Table 1
Study locations along with representative management scenarios and soil initial conditions. Locations are arranged according to latitude. Data from Chenu et al. (2013). PAWC: plant available water capacity (mm). PAW: plant available water (expressed as percentage of PAWC). Initial and applied nitrogen (NRules) are denoted as ‘x-y-z-a’, where x represents initial soil N, uniformly distributed across soil layers at sowing. y refers to N applied at sowing at 50 mm depth as nitrate. z and a denote N applications as nitrate (NO_3-N) at the ‘beginning of stem elongation’ and ‘mid-stem elongation’ stages, respectively.

Location	Lat	Long	PAWC (mm)	Initial PAW (%)	Row Spacing (mm)	Population (plants/m2)	NRules
Dalby	−27.16	151.26	203	25, 75	250	100	30–130–0-0
Dookie	−31.48	118.28	114	25, 76	250	150	50–40-40[d]-40[c]
Dubbo	−32.52	148.52	134	25, 77	250	100	50–50-50[d]-0
Katanning	−33.69	117.61	96	25, 78	250	150	45–20-30-30[a]
Merredin	−35.12	142.00	88	25, 79	250	100	30–20-20-30[a]
Walpeup	−35.91	145.64	134	25, 80	250	100	50–20-30[b]-30[c]

[a] If soil PAW at ‘mid-stem elongation’ exceeds 60 mm.
[b] If rainfall from sowing to ‘beginning of stem elongation’ surpasses 80 mm.
[c] If soil PAW at ‘mid-stem elongation’ is greater than 60 % of PAWC.
[d] If rainfall from sowing to ‘beginning of stem elongation’ exceeds 100 mm.

Table 2
APSIM-Wheat cultivar parameters selected for ideotyping, along with their default values and the ranges used for optimisation (see sections 2.4.1–2.4.3). MinLN: final leaf number (FLN) when fully vernalised before HS1.1 and then grown in long-day conditions; PpLN: Increase in FLN when fully vernalised before HS1.1 then grown at >18oC in short-day conditions; VrnLN: Increase in FLN when un-vernalised and grown in short-day conditions; VxPLN: Change in VrnLN when unvernalised and grown in long-day conditions; Phyll: The thermal time between the emergence of leaf tips; PhyllPpSens: The sensitivity of Phyll to short-day lengthening impact on Phyll; HeadEmergLD: The thermal time for the plant to go from flag leaf ligule appearance in long-day conditions; HeadEmergPpSens: The number of Phyll to go from flag leaf ligule appearance in long-day conditions compared to the number of Phyll for the same phase in short-day conditions; GFDur: The duration of grain-filling phase in thermal time units; RUE: Radiation use efficiency; StayGreen: The modifier of the thermal time that the leaf will remain at maximum area for in the absence of stress; KLModifier: The modifier of the rate of soil moisture extraction by roots, which also affects root biomass demand; GrainPGS: The number of grains per gram of stem and spike biomass; GrainPotSize: The potential size of individual grains.

Parameter Group	Parameter	Default	Lower	Upper	Unit
Phenology	MinLN	8	5	15	leaves
Phenology	PpLN	3.8	0	6	leaves
Phenology	VrnLN	5	0	9	leaves
Phenology	VxPLN	−2	−4	2	leaves
Phenology	Phyll *	120	96	144	^{o}Cd
Phenology	PhyllPpSens *	0.6	0.48	0.72	–
Phenology	HeadEmergLD *	240	192	288	^{o}Cd
Phenology	HeadEmergPpSens	2	1	3	–
Phenology	GFDur *	545	436	654	^{o}Cd
Resource Use	RUE *	1.5	1.2	1.8	g/MJ/d
Resource Use	KLModifier *	1	0.8	1.2	–
Morphology	StayGreen *	1	0.8	1.2	–
Yield Component	GrainPGS *	26	20.8	31.2	grains/g
Yield Component	GrainPotSize *	0.05	0.04	0.06	mg

* The range spans from 80 % to 120 % of the default value.

et al., 2011). On the other hand, adjusting traits such as phyllochron (Phyll, ^{o}Cd) and grain filling duration (GFDur, ^{o}Cd) can improve radiation interception, harvest index, and grain yield (Arnaiz Sánchez et al., 2007; Garg et al., 2013; Gebeyehou et al., 1982), provided crops maintain a green area index until the end of grain filling (Evans and Fisher, 1999; Semenov and Stratonovitch, 2013; Wang et al., 2019). Longer grain filling periods allow for greater biomass translocation and grain weight accumulation, although terminal water and heat stress-induced senescence can reduce yield through interrupting carbon supply (Ababaei and Chenu, 2020; Aggarwal et al., 1997; Borrell et al., 2001; Brisson et al., 2001; Semenov and Halford, 2009). Vernalisation and photoperiod sensitivity also influence yield, with reduced sensitivity enabling earlier flowering and better adaptation to dry or warm environments as it helps to avoid terminal stress (Herndl et al., 2007; Steinfort et al., 2017). Thus, fine-tuning phenological traits is key to improving crop resilience and productivity under diverse environmental conditions.

The selected phenological parameters are crucial for aligning crop growth stages with environmental factors, particularly photoperiod and temperature. In APSIM-Wheat, the CAMP model integrates molecular and physiological representations of flowering time by modelling the expression levels of genes such as *Vrn1*, *Vrn2*, and *Vrn3* based on temperature, photoperiod, and Haun stage progression. MinLN defines the minimum number of leaves under optimal vernalisation and long photoperiods, while PpLN and VrnLN quantify the genotype's sensitivity to photoperiod and vernalisation, respectively. Manipulation of these parameters allows precise adjustments of flowering time under varying conditions (Gouache et al., 2017; Richards, 1991). The parameter VxPLN accounts for the relative contributions of *Vrn2* and *Vrn3* genes, refining crop responses to short-day and long-day conditions. HeadEmergLD (^{o}Cd) refers to the thermal time required for the plant to transition from the emergence of the flag leaf ligule to heading under long-day conditions. HeadEmergPpSens is the factor with which HeadEmergLD is adjusted under short-day conditions. Adjusting these parameters can lead to well-synchronised flowering and grain filling to mitigate the risk of stress during these critical growth stages (Semenov and Stratonovitch, 2013; Steinfort et al., 2017).

2.4.2. *Morphology*

Phyll and PhyllPpSens regulate leaf emergence rates, therefore affect canopy expansion and light interception. In APSIM-Wheat, Phyll determines the thermal time required for the appearance of each leaf, while PhyllPpSens adjusts this rate based on photoperiod. Using these two parameters, optimal canopy expansion can be achieved for light interception during critical growth phases. Similarly, LagDuration and GFDur control the longevity of green leaf area (aka, 'stay-green') and the length (in ^{o}Cd) of grain-filling phase, respectively. By prolonging grain filling and maintaining green leaf area, the interception of radiation and conversion to biomass can be maximised to achieve higher harvest indices (Borrell et al., 2001; Christopher et al., 2016; Wang et al., 2019). HeadEmergLD further enhances crop synchrony by fine-tuning the duration from flag leaf ligule appearance to flowering, ensuring developmental transitions align with environmental cues.

2.4.3. *Resource use and yield components*

Optimising radiation use efficiency (RUE) is critical for improving crop performance, as it directly influences the conversion of intercepted solar radiation into biomass. Increased RUE has been identified as a key driver of yield improvements in wheat and other crops, especially in regions with abundant solar radiation (Semenov and Stratonovitch, 2013; Sylvester-Bradley et al., 2012). Wang et al. (2019) demonstrated that ideotypes with higher RUE and faster potential grain filling rates led to significant yield increases in wet environments. Additionally, improvements in Rubisco specificity for CO_2 over O_2 could enhance carbon assimilation by up to 10 %, further optimising RUE under current atmospheric CO_2 concentrations (Zhu et al., 2004). Although these advancements highlight the significance of optimising RUE for sustainable yield improvements across varying environments, increased photosynthesis can shift the timing and severity of water and nitrogen stress in crops, potentially causing unforeseen seasonal dynamics and yield fluctuations (Wu et al., 2022).

In APSIM-Wheat, potential daily water uptake rate (KL) plays a pivotal role in soil moisture uptake. This parameter is critical for mitigating stress during dry periods, enhancing water use efficiency and yield stability (Manschadi et al., 2006; Rezzouk et al., 2022). APSIM includes a parameter (KLModifier, default value 1) that regulates the daily water uptake rate. In this study, the model was tailored so that any modification to KLModifier is concurrently reflected in the root biomass demand (assuming a higher KL is achieved by a larger root system).

GrainPGS (grains/g) governs the number of grains per gram of stem-and-spike biomass at anthesis, while GrainPotSize (mg) represents the maximum individual grain size. For a constant GFDur, a larger GrainPotSize results in a larger potential grain filling rate. Optimising these traits, as key drivers of yield potential, can help maximise grain number and size under a range of environments (Collins and Chenu, 2021; Ullah and Chenu, 2019; Ullah et al., 2019).

2.5. *Optimisation algorithm*

A scalable optimisation pipeline was developed in the R programming environment using a Genetic Algorithm, aimed to maximise NWAY. Genetic Algorithms are stochastic search methods inspired by the principles of biological evolution and natural selection (Liepins and Hilliard, 1989). These algorithms emulate the evolutionary processes of living organisms, where the fittest individuals prevail through mechanisms such as selection, crossover, and mutation. A customised version of the 'ga' function from the 'GA' package (Scrucca, 2013) was integrated into the optimisation pipeline. The minor customisation allowed the algorithm to run in a vectorised manner to leverage APSIM's multi-core capability and enhance computational performance. The probability of crossover between chromosome pairs ('pcrossover') and the probability of mutation in a parent chromosome ('pmutation') were set to 0.8 and 0.1, respectively. The number of best-fit individuals to survive each generation ('elitism') was set at 2 % of the population. The population size and the maximum number of iterations before halting the search were set to 500 and 400, respectively, resulting in 200,000 simulations conducted under each optimisation scenario.

2.6. Ideotyping scenarios

Three ideotyping scenarios were analysed: (1) 'Optim-Global': optimisation was performed using a single environment (location × year × HYC × ISM) representative of each identified ET, with the occurrence frequencies of ETs serving as weights to estimate average yield (hereafter, 'nominal weighted average yield', NWAY) during optimisation. Representative environments were identified as those with seasonal SDR patterns exhibiting the smallest Euclidean distance from the average pattern of the corresponding ET; (2) 'Optim-ET3+': followed a similar approach to 'Optim-Global' but focused exclusively on high-stress ETs (ET3–6); and (3) 'Optim-Local': optimisation was conducted similarly to 'Optim-Global' but independently for each location, using location-specific ET occurrence frequencies as weights to calculate NWAY. In this context, representative location-specific environments were determined and adopted for optimisation.

After the conclusion of the optimisation process, the optimised values for the selected cultivar parameters were applied to simulations while location-specific OSWs were adopted. Simulation outputs were then compared against benchmark simulations ('Pre-Optim') where the HYCs were planted within the location-specific OSWs.

3. Results

3.1. Global drought environment types

A cluster analysis of simulated crops based on 54-year simulations identified six global drought patterns ('environment types', ETs) within the TPE (Fig. 1) corresponding to varying levels of stress over the growing season. The ETs were sorted based on their corresponding average yield across the TPE (i.e., all combinations of location × year × cultivar × sowing date × ISM; Fig. 2). Without adopting OSWs and HYCs, ET1 aligned with the upper-range average grain yield across the TPE. With their adoption, ET3 achieved the highest average yield, while ET1, ET2, and ET4 exhibited similar yields, albeit with significant variation across study locations. ET5 and ET6 consistently produced the lowest average yields across the TPE, regardless of OSW and HYC adoption.

Approximately 23,200 drought patterns were categorised into six classes. Therefore, each ET encompassed a wide spectrum of water-deficit conditions while collectively explaining 61 % of the total variability. When the OSWs and HYCs were adopted, the most common ET was determined to be ET4 (29 %) followed by ET1 (26 %) and ET2 (19 %). ET3, ET5, and ET6, which represent earlier incidence of mild stress, represent 7, 9, and 11 % of the simulated seasons, respectively (Fig. 1).

Each identified cluster represents a unique temporal pattern of daily SDR. ET1 characterises environments with little to no stress before flowering, followed by mild stress during early to mid-grain filling, which gradually subsides towards maturity. ET2, ET3, and ET5 share a similar trajectory but experience stress accumulation earlier in the season. ET4 generally maintains consistently low stress levels throughout the season that gradually increases towards maturity, whereas ET6 follows a distinct pattern, with mild stress at the onset of the season that diminishes around 500 °Cd before flowering.

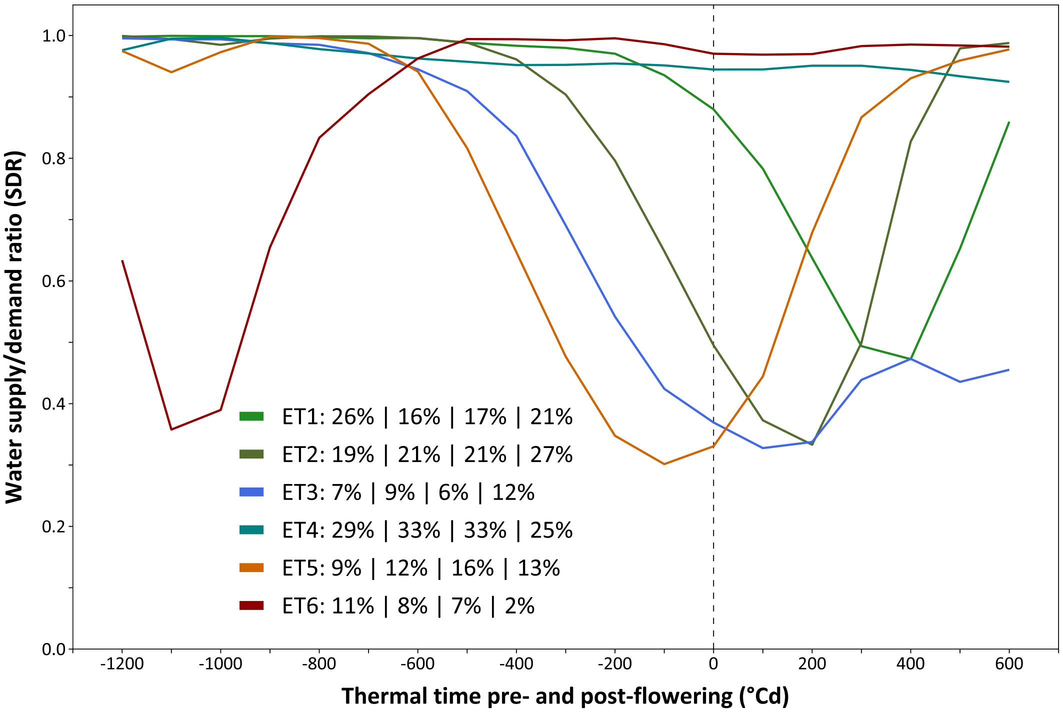


Fig. 1. Water supply/demand ratio (SDR) patterns for the six identified environment types (ET1–6). The lines show the average SDR values across all simulated environments (location × year × cultivar × sowing date × ISM). For each simulated environment, daily SDR values were centred on the flowering stage and averaged over 100 °Cd intervals from 1200 °Cd before flowering to 600 °Cd after flowering. Beyond this period, senescence markedly reduces plant transpiration. In-set numbers (from left to right) indicate the occurrence frequency (OF) of ETs across the target population of environments (TPE) for the benchmark scenario ('Pre-Optim') and the ideotyping scenarios 'Optim-Global', 'Optim-ET3+', and 'Optim-Local', respectively, when optimal sowing windows (OSWs) and highest-yielding cultivars (HYCs) were adopted. Refer to section 2.6 for detailed information on ideotyping scenarios.

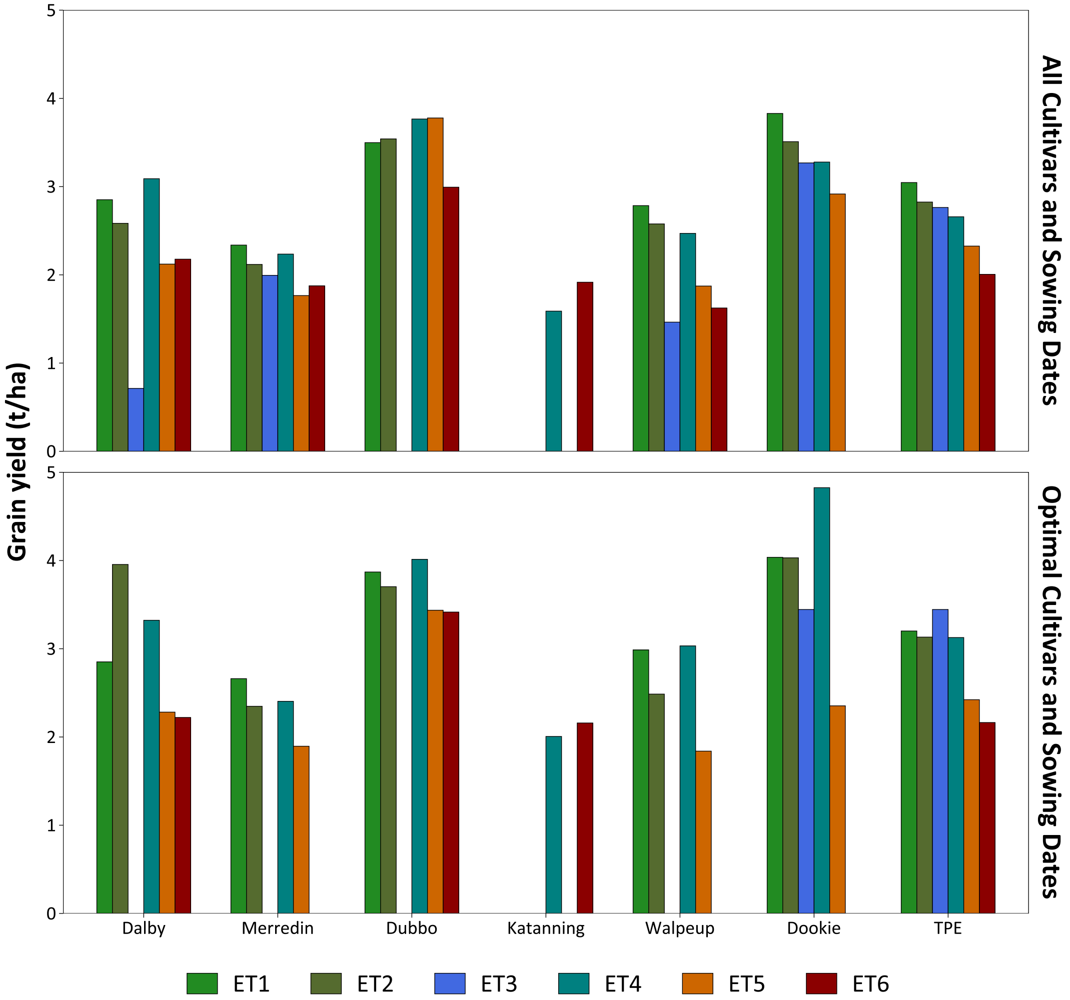


Fig. 2. Average grain yield for the six identified environment types (ET1–6) across the target population of environments (TPE) for the benchmark scenario ('Pre-Optim') with all simulated seasons (top) and when optimal sowing windows (OSWs) and highest-yielding cultivars (HYCs) were adopted (bottom).

3.2. *Ideotyping affects occurrence frequency of ETs*

Ideotyping significantly changes the occurrence frequency (OF) of the identified ETs across the TPE (Fig. 3 and Fig. 4). The OF patterns in the 'Optim-Global' and 'Optim-ET3' ideotyping scenarios followed similar trends, characterised by a substantial 9–10 % point (pp) reduction in ET1's OF, a 4 pp. increase in ET4's OF, a 3–7 pp. rise in ET5's OF, and a slight decrease in ET6's OF. In contrast, the 'Optim-Local' scenario presented a distinct pattern with the most significant increase being in ET2's OF (8 pp), while ET1's OF declined by 5 pp., compared to the 10-

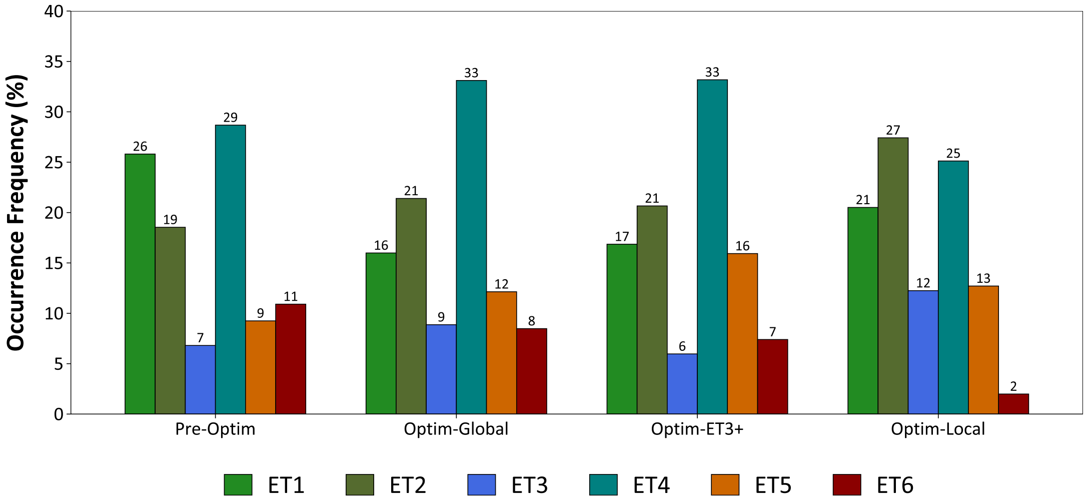


Fig. 3. The occurrence frequency (OF) of the identified environment types (ETs) across the target population of environments (TPE) for the benchmark scenario ('Pre-Optim') and the ideotyping scenarios 'Optim-Global', 'Optim-ET3+', and 'Optim-Local'. Refer to section 2.6 for detailed information on ideotyping scenarios.

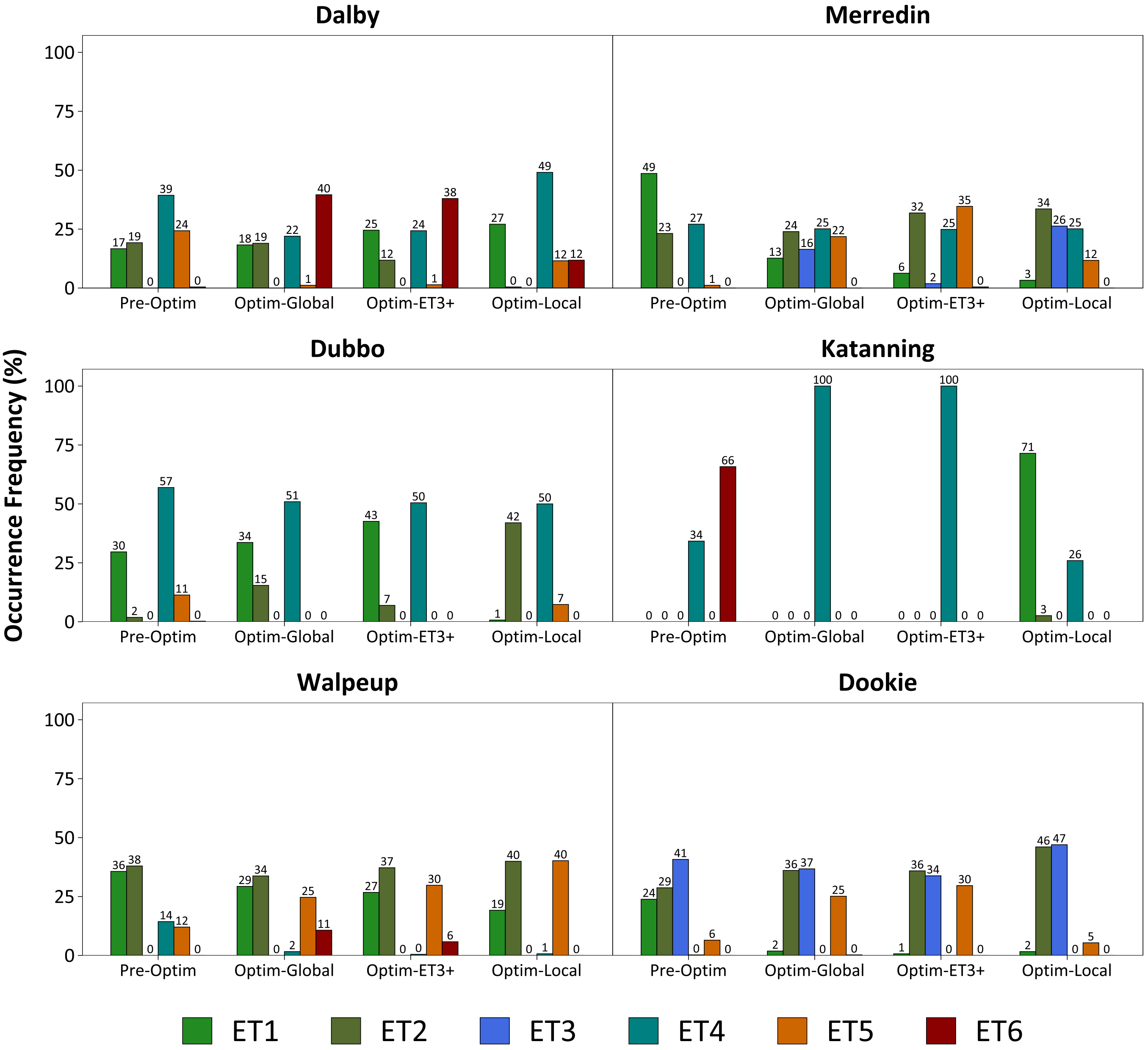


Fig. 4. The occurrence frequency (OF) of the identified environment types (ETs) across the study locations for the benchmark scenario (‘Pre-Optim’) and the ideotyping scenarios ‘Optim-Global’, ‘Optim-ET3+’, and ‘Optim-Local’. Locations are arranged according to latitude. Refer to section 2.6 for detailed information on ideotyping scenarios.

pp drop in the other two scenarios. Compared to the ‘Pre-Optim’ scenario, ET3’s OF rose by 5 pp., offset by a 4 pp. decrease in ET4’s OF. ET5’s OF increased by 4 pp., whereas ET6’s OF dropped sharply from 11 % to just 2 %.

The influence of ideotyping on ETs’ OFs primarily stems from two types of shifts in water-stress dynamics: (1) moving from late-season accumulation (represented by ET1), when grain-filling reaches its peak, to either an earlier onset of water-stress (i.e., pre-flowering) that subsides shortly after flowering (represented by ET2, ET3, and ET5) or low stress levels throughout the seasons (ET4). This transition reduces plant stress during the critical grain-filling phase and provides a more favourable growth environment during this sensitive phase; (2) reduced occurrence of early-season water stress (represented by ET6), which substantially affected canopy expansion and radiation interception throughout the season.

3.3. Ideotyping improved average and stability of yield

Fig. 5 illustrates yield response to different optimisation strategies across the six study locations and all sowing dates when the location-specific HYCs were adopted. In Merredin, Dubbo, ideotyping led to the highest yield improvements when early sowing (March–April) was adopted, where increases exceed 30 % in some cases. However, in Dalby, Walpeup, and Dookie, this benefit was higher with later sowing dates, especially from 01-Jun onwards. These findings reinforce the importance of early sowing and the optimisation objective in different regions.

Notably, yield gains under the ‘Optim-Global’ and ‘Optim-ET3+’ strategies typically exceeded those of the ‘Optim-Local’ strategy when sowing occurred outside the OSWs (except in Katanning). In most cases where the local strategy performed better, sowing occurred within the OSWs. This indicates that global ideotyping strategies offer greater potential for broad adaptability.

The performance of the three optimisation strategies varied by

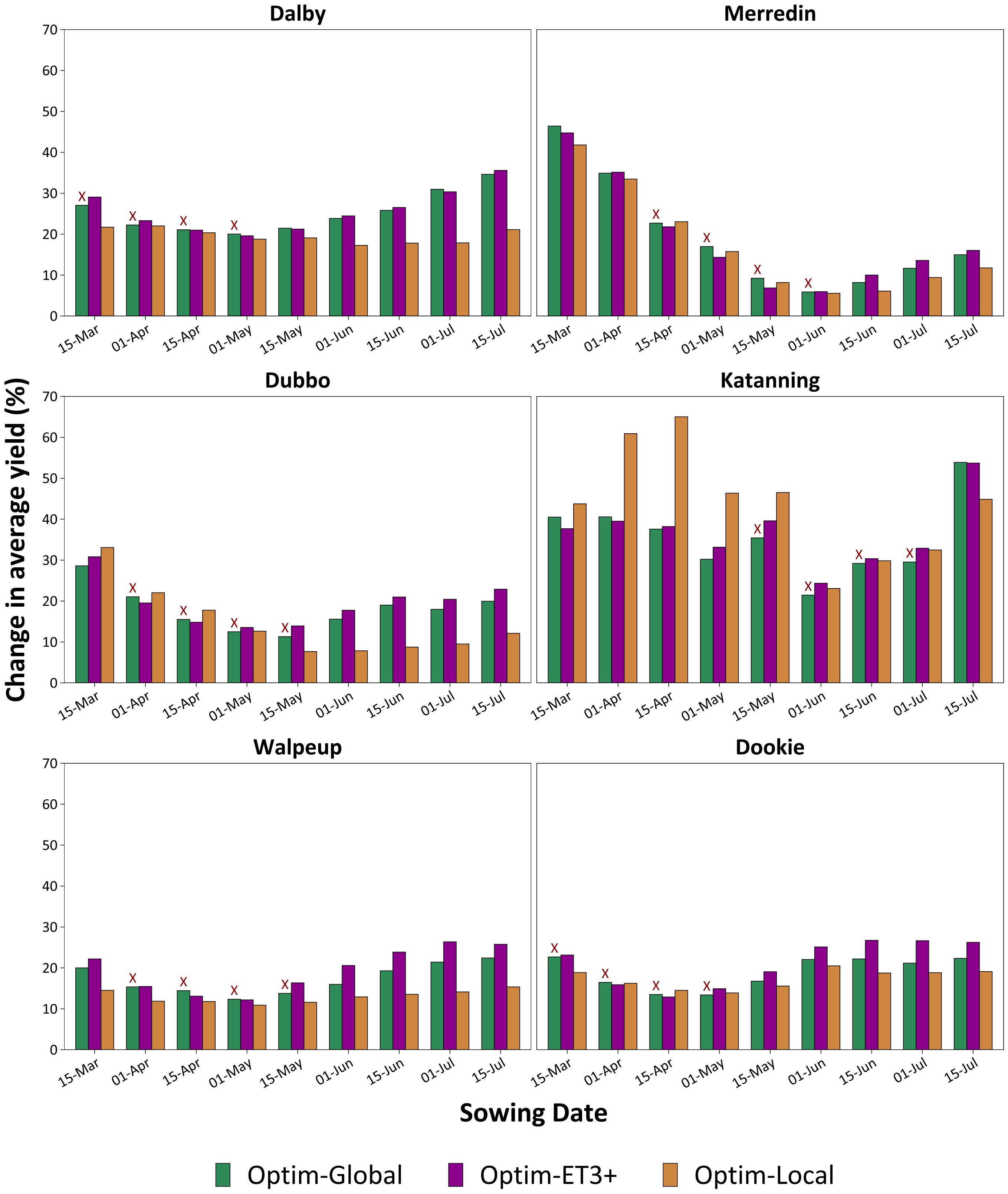


Fig. 5. Change in long-term average yield for the ideotyping scenarios 'Optim-Global', 'Optim-ET3+', and 'Optim-Local' relative to the benchmark scenario ('Pre-Optim') for each simulated sowing date when highest-yielding cultivars (HYCs) were adopted at each location. Locations are arranged according to latitude. Optimal sowing windows (OSWs) are indicated with 'X' symbols. Refer to section 2.6 for detailed information on ideotyping scenarios.

location. 'Optim-ET3+', which focuses on high-stress, low-yielding environments, consistently delivered the highest yield improvements in most location × sowing date combinations. 'Optim-Local' scenarios showed superior performance in Katanning but was less effective in other locations compared to the other two strategies. Meanwhile, 'Optim-Global' provided steady but generally slightly lower improvements than 'Optim-ET3+'.

Fig. 6 summarises the findings presented in Fig. 5 when the OSWs were adopted. The three ideotyping strategies led to ~18 % improvements in grain yield averaged across the TPE. All three strategies led to yield improvements across all study locations, with the highest increases observed in Katanning, where yield gains exceeded 29 %. Dalby and Dookie also experienced notable increases, while Merredin and Walpeup showed relatively smaller improvements. The consistency of yield gains across locations suggests that ideotyping has considerable potential to enhance productivity, though the extent of improvement varied by location and climate. Among the three strategies, 'Optim-Local' achieves the highest yield increases only in Katanning, while 'Optim-ET3+' performs slightly better in Dalby, Dubbo, and Dookie, indicating that localised approach and the approach focusing on high-stress environments may offer region-specific advantages.

In addition to yield improvements, the changes in yield stability (expressed as coefficient of variation, CV) highlight the value of ideotyping strategies. Most locations exhibited a significant reduction in CV, indicating enhanced yield stability when optimised cultivars were adopted. The 'Optim-Global', 'Optim-ET3+', and 'Optim-Local' strategies led to 15.5, 14.8, and 9.1 % reduction in CV, respectively. Katanning, in particular, showed a sharp decrease in CV across all three strategies, with 'Optim-Local' achieving the greatest reduction of over 40 %. This suggests that while this location may benefit the most in terms of average yield, it would also experience a significant reduction in variability, making the yield gains more reliable over the long term. Conversely, Dubbo presents an exception, where 'Optim-Local' resulted in a notable increase in CV, showing increased yield variability despite the improvement in long-term average yield.

The overall trend across the TPE reinforces the idea that ideotyping strategies not only boost yield but also enhance yield stability. The reductions in grain yield CV suggest that ideotyping effectively mitigated risks linked to climate variability. However, the magnitude of these benefits varied by location, which highlights the need for region-specific strategies. While 'Optim-Global' and 'Optim-ET3+' achieved a 6 % greater reduction in CV than 'Optim-Local', the differences among the three approaches across the study locations indicate that no single strategy is universally optimal. Instead, selecting an ideotyping approach should balance yield improvement and stability and be tailored to site-specific conditions.

3.4. Key physiological drivers

Fig. 7 highlights the contributions of cultivar parameters to the variability of NWAY across the three ideotyping strategies and six locations. A high Main Effect (ME) value for a parameter indicates a strong direct effect on yield and small changes in that parameter can significantly alter productivity. Under the 'Optim-Global' and 'Optim-ET3+' strategies, six key parameters—MinLN, GrainPotSize, RUE, KLModifier, StayGreen, and GrainPGS—had the highest Main Effect (ME) values and

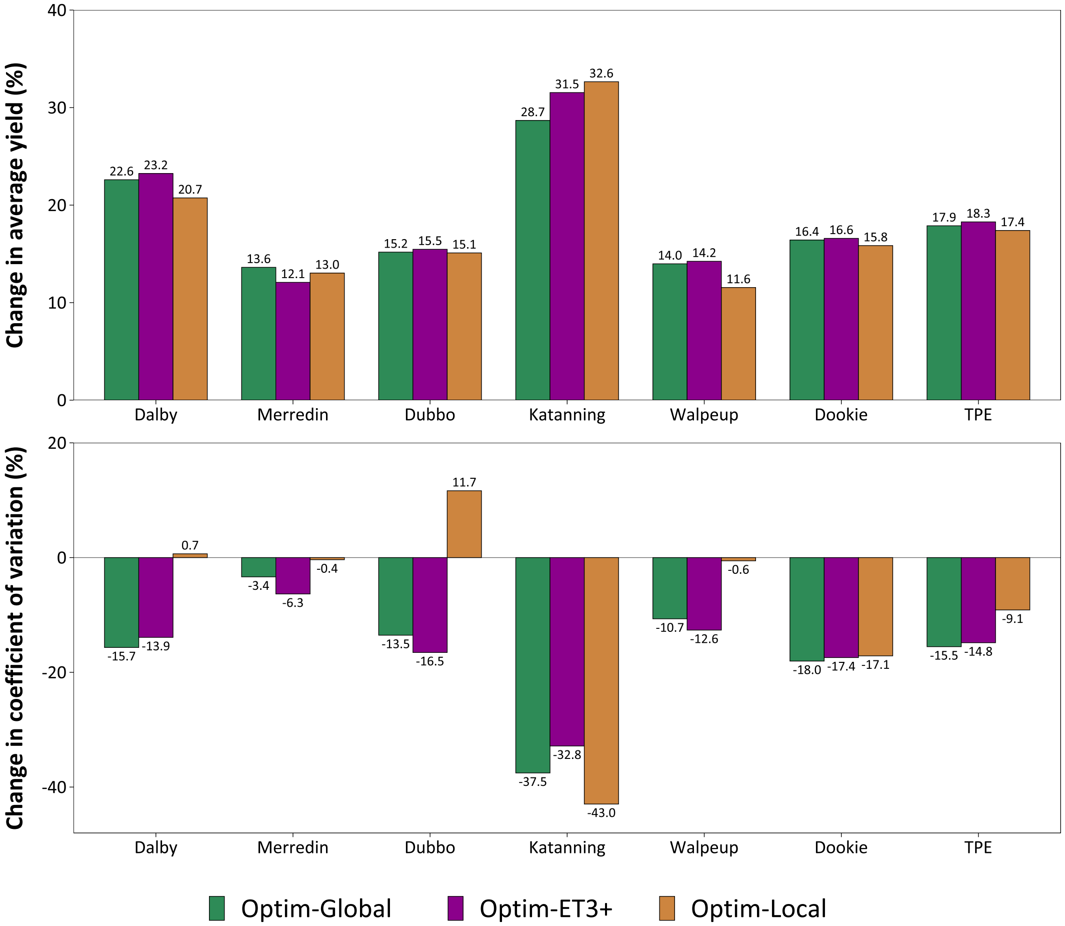


Fig. 6. Change in long-term average yield (top) and change in seasonal yield coefficient of variation (bottom) for the ideotyping scenarios 'Optim-Global', 'Optim-ET3+', and 'Optim-Local' relative to the benchmark scenario ('Pre-Optim') when optimal sowing windows (OSWs) were adopted. Locations are arranged according to latitude. Refer to section 2.6 for detailed information on ideotyping scenarios.

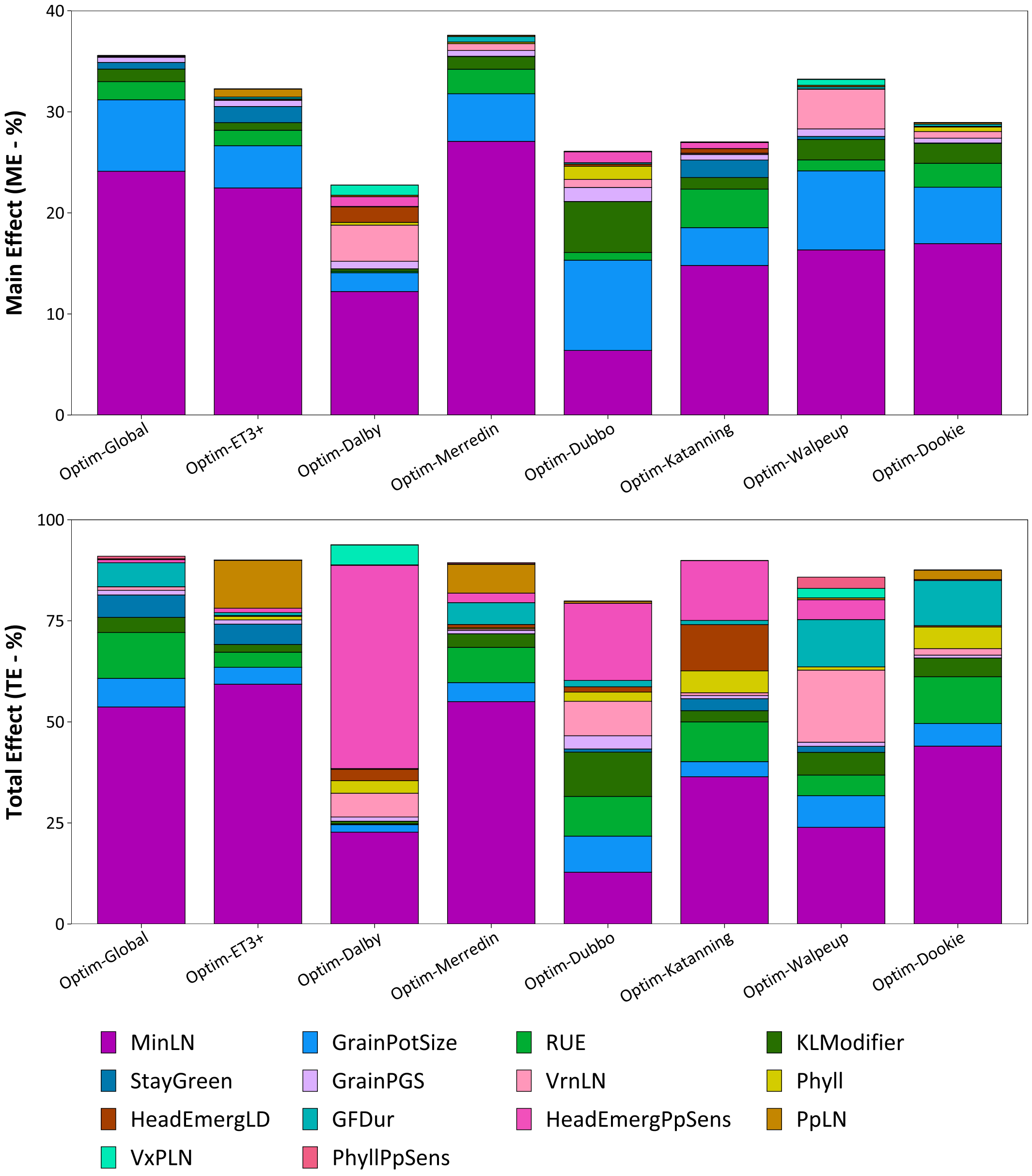


Fig. 7. Main effect (ME) and total effect (TE) of selected cultivar parameters (Table 2) contributing to simulated crop yield variance for the ideotyping scenarios 'Optim-Global', 'Optim-ET3+', and 'Optim-LocationX'. In the 'Optim- LocationX' scenarios, optimisation was conducted separately for each of the six locations. Locations are arranged according to latitude. Cultivar parameters are ranked according to their main effect (ME) in the 'Optim-Global' scenario. The ME of 'Residuals' is not shown. Refer to section 2.6 for detailed information on ideotyping scenarios and to Table 2 for parameter definitions and ranges adopted for optimisation.

exerted the most direct influence on NWAY. Additionally, PpLN became influential under 'Optim-ET3+'. Among these parameters, MinLN consistently showed the highest ME, indicating that variations in minimum leaf number have a substantial direct impact on NWAY. Similarly, GrainPotSize and RUE exhibited relatively high ME values. In contrast, under 'Optim-Local' strategies, the influence of key parameters shifts, with VrnLN, VxPLN, Phyll, and HeadEmergPpSens gaining prominence, particularly in regions like Dalby, Walpeup, and Dubbo. This suggests that local adaptation depends more on phenology-related traits rather than other physiological characteristics such as RUE.

The higher ME values of MinLN, GrainPotSize, RUE, KLModifier, StayGreen, and GrainPGS (as well as PpLN in 'Optim-ET3+') under global strategies suggests that these traits are fundamental to cultivar performance and are largely independent of environmental fluctuations. In contrast, mostly lower ME values in 'Optim-Local' strategies suggest that no single parameter overwhelmingly determines yield. Instead, site-specific optimisation requires a more balanced adjustment of multiple traits rather than a strong reliance on a few dominant ones.

The Total Effect (TE) panel in Fig. 7 reveals the overall influence of parameters, accounting for both direct effects and trait interactions. High TE values under 'Optim-Global' and 'Optim-ET3+' for MinLN, GrainPotSize, RUE, KLModifier, StayGreen, GFDur, and PpLN indicate that these traits do not act in isolation but significantly interact with other parameters to shape crop performance. That is, these traits contribute both individually and through complex interactions and are crucial for broad adaptation strategies. The persistence of high TE values under these global approaches suggests that cultivars optimised for wide adaptability rely on traits that exhibit strong synergistic effects to achieve stable performance across different environments.

Under the 'Optim-Local' strategy, however, TE values for Phyll, HeadEmergLD, HeadEmergPpSens, VrnLN, VxPLN, and GFDur often increased, indicating that in specific environments, their contribution is amplified by interactions with other traits. For example, in Dalby and Dubbo, HeadEmergPpSens showed elevated TE values. This contrast between global and location-specific approaches highlights a fundamental distinction: global ideotyping strategies favoured traits with strong standalone effects and broad adaptability, while site-specific strategies depended more on complex interactions tailored to local conditions. Consequently, 'Optim-Global' and 'Optim-ET3+' are well-suited for generalised breeding efforts, whereas 'Optim-Local' emphasise on targeted genetic improvements aligned with specific climate and agronomic requirements.

Table 3 presents the optimised values for the selected cultivar parameters under various ideotyping scenarios and Fig. 8 illustrates the relationship between parameter values (200,000 parameter values chosen during optimisation) and NWAY (calculated during optimisation) under the 'Optim-Global' scenario. Overall, our findings underscores the complexity of trait interactions in determining yield outcomes, where some parameters benefit from minimisation or maximisation while others require more nuanced adjustments. Across parameters, the highest yields (>95th percentile) were often associated with specific parameter ranges rather than parameter values uniformly distributed across the entire spectrum. For instance, MinLN exhibited a concentration of high-yielding scenarios at the lower end of its range, suggesting that lower minimum leaf number favours increased NWAY across the TPE. Similarly, parameters like KLModifier and GFDur exhibited a tendency for high-yield scenarios when their values remained in the lower to mid-range.

Conversely, increased values of some parameters led to an upward trend in NWAY. GrainPotSize, RUE, StayGreen, and GrainPGS demonstrated a strong positive correlation with yield, with the highest-yielding cases clustering at the upper extremes of their respective ranges. In contrast, most phenology-related parameters, except for MinLN, favoured mid-to-low or mid-to-high values for achieving highest NWAY. While optimal values for VrnLN, Phyll, PpLN, and VxPLN were generally concentrated around the middle of their ranges, those for HeadEmergLD, HeadEmergPpSens, and PhyllPpSens were more widely distributed. On the other hand, GFDur values linked to high yields were predominantly concentrated in the mid-to-lower range. These findings underscore the greater significance of grain-related (i.e., sink) and photosynthesis-related (i.e., source) traits over a majority of phenology-related parameters in maximising yield potential while a global ideotyping strategy is adopted.

4. Discussion

The integration of envirotyping and ideotyping provided a powerful and scalable optimisation framework by leveraging environmental characterisation to guide targeted ideotype development. By classifying drought environments into distinct ETs, envirotyping reduced the need for exhaustive simulations across all possible climate × management scenarios, allowing ideotyping to focus on the most relevant stress patterns. This minimised computational demands by narrowing the solution space and significantly cutting (by a factor of approximately 1/1000 in the 'Optim-Global' strategy and 1 / 1500 in 'Optim-ET3+') the number of genotype × environment (G × E) interactions that needed to be explored. Additionally, by structuring ideotype optimisation around predefined ETs, our approach reduced data volume requirements, as trait optimisation could be performed within clearly defined environmental contexts rather than relying on vast, undifferentiated datasets. The synergy between these methods resulted in a highly efficient optimisation process, enabling robust ideotype design without the computational burden of traditional large-scale simulations, making the approach feasible for widespread application in data-limited and computationally constrained settings.

This study identified six distinct global drought ETs within the TPE for wheat, each representing a unique temporal pattern of water stress (defined by water supply/demand ratio, SDR). These ETs accounted for a significant proportion (61 %) of total yield variability across the TPE. The first four ETs that were identified in this study align with the ETs identified by Chenu et al. (2013), despite that study incorporating a significantly higher number of simulated seasonal drought patterns (185,000 vs 23,200). ET6, though recognised by Chenu et al. (2013) in a single location in South Australia, was ultimately excluded from the final set of global patterns as it occurred infrequently throughout the TPE. This omission may arise from Chenu et al. (2013) adopting (1) different cultivars, (2) a longer simulation period (1889–2011), potentially biasing results towards the cooler conditions crops experienced in the early-mid 20th century, in contrast to the present, warmer climate with more frequent heat and drought events (Collins, 2022), or (3) clustering the TPE based on locally representative sowing dates, whereas the current study considered a broader range of sowing dates (Fig. 5).

The six identified ETs provide an up-to-date, valuable framework for understanding the range of drought conditions affecting wheat crops across Australian cropping systems. The shift in ET distribution following ideotyping implies that optimised cultivars effectively alleviate drought stress during the grain-filling period. This aligns with the established principle that minimising water deficit during this critical stage is essential for maximising yield in dry environments (Collins et al., 2021; Messina et al., 2015; Richards, 1991; Sinclair et al., 2005). The decline in the occurrence of early-season stress (ET6) further underscores the importance of ensuring sufficient canopy development and radiation interception throughout the growing season (Donald, 1968).

The substantial yield improvements achieved through ideotyping, particularly with early sowing (March–April), illustrates the potential of this approach for enhancing wheat productivity. Consistent yield gains across diverse climates suggest that ideotyping can improve resilience

Table 3

Final optimised values of APSIM-Wheat cultivar parameters selected under various ideotyping scenarios. Refer to section 2.6 for detailed information on ideotyping scenarios and to Table 2 for parameter definitions and ranges adopted for optimisation.

	Ideotyping Scenario (Optim-)							
Param	Global	ET3+	Dalby	Merredin	Dubbo	Katanning	Walpeup	Dookie
MinLN	6.14	5.44	5.77	6.32	8.19	7.42	7.39	6.07
GrainPotSize	0.059	0.059	0.059	0.059	0.059	0.058	0.059	0.059
RUE	1.72	1.67	1.55	1.72	1.71	1.71	1.65	1.74
KLModifier	0.87	0.81	0.85	0.82	0.85	0.84	0.84	0.81
StayGreen	1.14	1.13	1.01	1.03	1.08	1.12	1.06	0.99
GrainPGS	30.9	29.5	29.3	28.5	30.2	30.2	29.9	28.3
VrnLN	4.78	4.99	2.11	3.91	3.18	3.53	2.22	3.10
Phyll	119	132	104	122	122	127	123	129
HeadEmergLD	243	240	205	236	222	266	239	229
GFDur	459	439	591	451	497	518	466	478
HeadEmergPpSens	1.91	1.95	1.09	1.96	1.60	2.48	2.08	2.07
PpLN	3.14	1.37	3.93	3.45	2.87	2.95	3.25	2.20
VxPLN	−0.88	−0.54	−2.66	−0.83	−0.81	−1.25	−1.77	−0.81
PhyllPpSens	0.59	0.58	0.62	0.59	0.60	0.62	0.59	0.63

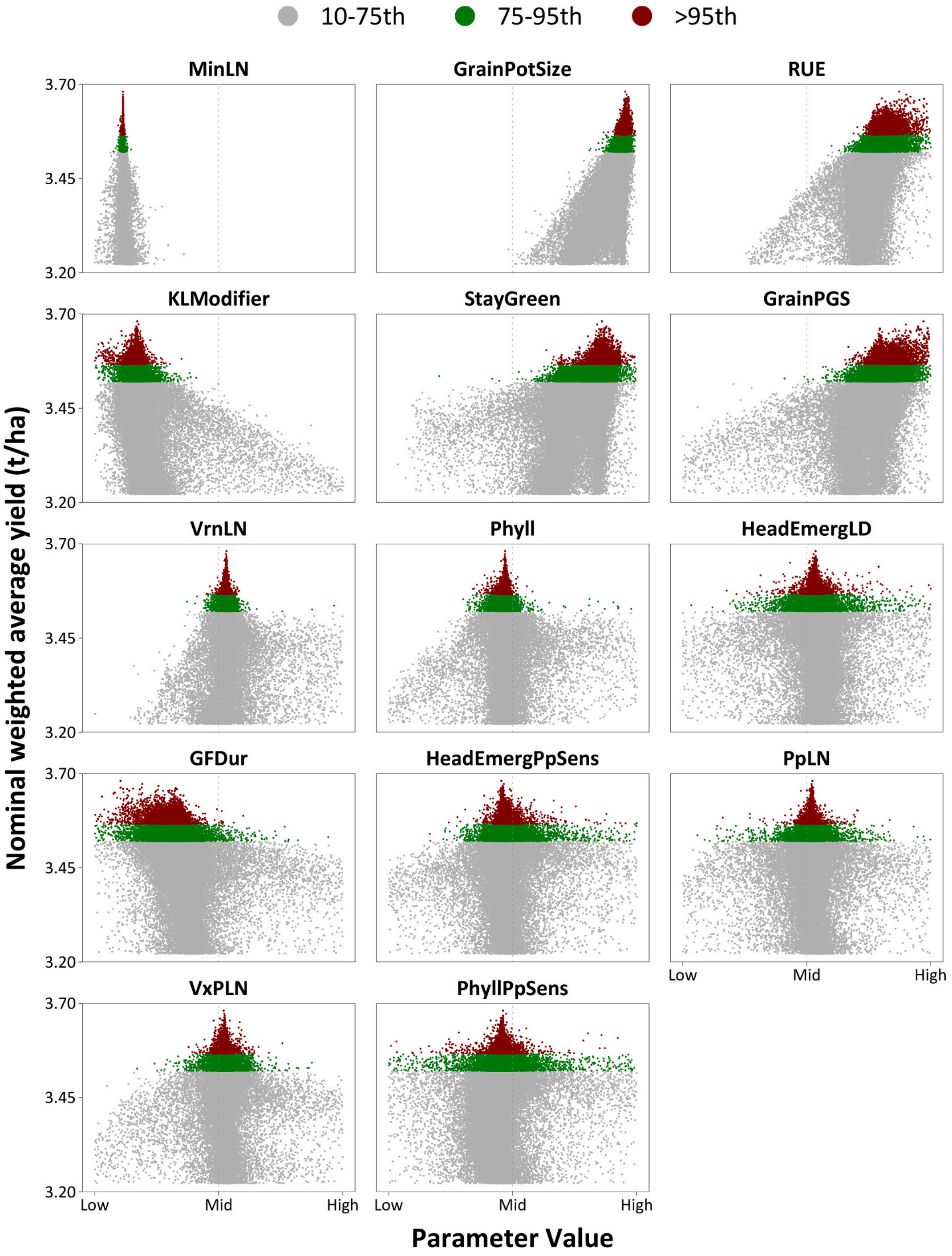


Fig. 8. Values of the selected cultivar parameters vs simulated nominal weighted average yield (NWAY) for the ideotyping scenarios 'Optim-Global'. Each point indicates the value of a corresponding parameter from a single run among 200,000 simulations performed during the optimisation process. Parameter values were normalised using the pre-defined ranges so that they range between 0 and 1, with 0 designated as 'Low', 0.5 as 'Mid', and 1 as 'High'. Cultivar parameters are ranked according to their main effect (ME) in the 'Optim-Global' scenario. Simulated grain yields are categorised into three groups based on yield quantiles: 10-75th, 7595th, and above the 95th quantile. The lowest 10 % of simulated yields are excluded. Refer to section 2.6 for detailed information on ideotyping scenarios and to Table 2 for parameter definitions and ranges adopted for optimisation.

against environmental variability. The varied performance of the three ideotyping strategies ('Optim-Global', 'Optim-ET3+', and 'Optim-Local') underscores the need to tailor ideotype designs to regional conditions. While 'Optim-ET3+' (targeting high-stress environments) generally delivered the greatest yield gains, 'Optim-Local' excelled in specific locations such as Katanning. These findings are in line with those by Wang et al. (2019), who highlighted the importance of matching ideotypes and sowing dates to local environments.

Beyond average yield gains, the significant reduction in yield CV through ideotyping highlights its potential to improve yield stability—an essential factor for mitigating climate-induced risks. However, the magnitude of CV reduction varied across locations, reinforcing the necessity for region-specific ideotyping approaches. Notably, the increased CV in Dubbo under 'Optim-Local' despite yield improvements serves as a reminder that maximising yield should not compromise stability.

The analysis of key physiological drivers revealed distinct trait importance patterns under different ideotyping strategies. Under 'Optim-Global' and 'Optim-ET3+', traits associated with sink capacity (GrainPotSize, GrainPGS), source strength (RUE and KLModifier), and canopy longevity (GFDur and StayGreen) emerged as dominant yield determinants. This confirms the previous findings that these traits are fundamental to crop performance and relatively stable across environments (Semenov and Stratonovitch, 2013; Sylvester-Bradley et al., 2012).

The significance of RUE corroborates the conclusions of Wang et al. (2019) and Sylvester-Bradley et al. (2012), who identified radiation use efficiency as a key driver of yield potential. We used RUE as an aggregate indicator of photosynthetic rate, recognising that direct measurement of its individual components—such as carboxylation efficiency, stomatal conductance, or mesophyll conductance—is often impractical at scale. Despite its complexity and environmental dependence, RUE remains a widely adopted proxy for photosynthetic capacity in crop modelling and ideotyping studies, offering a feasible and scalable means of comparing genotypic performance across diverse environmental conditions. RUE and its equivalent, light use efficiency (LUE), have been employed in previous ideotype design studies to assess yield potential and genotype adaptability under varying environmental conditions—for instance, in wheat (e.g. Martre et al., 2015a), sorghum (e.g. Hammer et al., 2010), and rice (Yin and Struik, 2017).

The influence of GrainPotSize and GrainPGS further underscores the role of grain number and size in determining yield in the context of Australian cropping. Our results align with Wang et al. (2019), who found that ideotypes with larger maximum grain size and a faster potential grain filling rate, when sown at the optimal date, led to an average yield increase of 20–24 % under future climate conditions. They also support Semenov and Stratonovitch (2013) findings, who argued that wheat yield may be limited by both grain number and grain size, suggesting that improving these traits could enhance overall grain yield.

In contrast, under 'Optim-Local', phenology-related traits (VrnLN, VxPLN, Phyll, HeadEmergPpSens) gained prominence, suggesting that local adaptation hinges on optimal developmental timing. This aligns with extensive literature emphasising the role of phenology in environment-specific adaptation (Herndl et al., 2007; Rezzouk et al., 2022; Richards, 1991; Semenov and Stratonovitch, 2013; Zheng et al., 2015). Eliminating the vernalisation requirement in winter crops has been proved a promising strategy for adapting to future warming conditions (Anwar et al., 2015; Wang et al., 2015). Herndl et al. (2007) demonstrated that vernalisation requirement and photoperiod response significantly influenced yield in the North China Plain, with lower sensitivity to these factors linked to higher yields compared to stronger responses. They argued that reduced sensitivity led to earlier maturity, helping crops evade late-season water stress. Calderini et al. (1997) associated increases in wheat yield with shortening of the duration of vegetative development phases. On the other hand, extending the grain filling period has been proposed as a potential trait for enhancing grain yield in wheat (Evans and Fisher, 1999). (Semenov and Stratonovitch, 2013) also demonstrated that at two contrasting European sites, an extended grain-filling period (leading to a higher harvest index) along with optimal phenology, enhances yield only if wheat sustains its green area index until grain filling concludes. Our findings, however, suggest that a balanced sensitivity to vernalisation and photoperiod, coupled with a moderate to short grain-filling duration, slightly higher RUE, and an extended period of maximum leaf area retention under non-stress conditions (i.e., stay-green), could improve yield potential across the Australian grain belt.

Numerous studies have supported Donald's assessment of a wheat ideotype, showing that traits such as reduced leaf area can enhance yield potential (Parry et al., 2011; Srinivasan et al., 2017). In 2011, the Wheat Yield Consortium introduced an updated set of physiological traits aimed at improving yield. These traits include increased photosynthetic efficiency, maximised spike fertility, enhanced grain filling and size, optimised grain partitioning, and improved lodging resistance (Parry et al., 2011; Reynolds et al., 2011). Ullah et al. (2024)demonstrated that under well-watered conditions, natural heatwaves significantly affected grain number when temperatures exceeded 28 °C and individual grain weight beyond 32 °C. With the expected rise in the frequency of such extreme events in Australia (Collins, 2022; Collins and Chenu, 2021; Lobell et al., 2015), enhancing both grain number and size is essential to sustain current yield potential. These studies align with our findings, highlighting the significance of improved photosynthetic efficiency (RUE), enhanced grain filling and size (GrainPotSize and GrainPGS), and reduced leaf area (MinLN) in optimising wheat performance.

The shift in trait importance between global and local ideotyping highlights the distinction between broad and specific adaptation strategies—global approaches favour traits with strong direct effects and broad applicability, while local strategies rely on complex trait interactions tailored to particular conditions. The optimised parameter values (Table 3 and Fig. 8) further illustrate the intricate relationships between traits and yield. The finding that peak yields are associated with narrow ranges for high-impact parameters and more uniformly distributed values for other parameters (Fig. 8) underscores the need to optimise trait combinations rather than isolating individual traits, which aligns well with the potentials of the proposed integration of envirotyping and ideotyping.

While the parameters selected for optimisation in this study provide valuable insights into wheat ideotype design, it is essential to recognise the broader range of traits (beyond phenology, radiation use efficiency, grain components, and stay-green) that can enhance yield outcome. For instance, refining root architecture and function (e.g., specific root length; Rezzouk et al., 2022) is critical for optimising resource acquisition, particularly under water-limited conditions. This also confirms our results that indicated a reduced soil moisture extraction rate (KLModifier; Fig. 8) can be advantageous. Likewise, nitrogen dynamics, including uptake, assimilation, and remobilisation, are key determinants of grain yield. Semenov and Stratonovitch (2013)highlighted the significance of post-anthesis nitrogen uptake and storage, while Rezzouk et al. (2022) underscored the role of nitrogen metabolism efficiency under water-limited conditions. However, a recent study (Liu et al., 2025) showed that model simulations fail to adequately represent the strong correlations between root traits and N losses observed in experiments. Consequently, new functions are required to link root traits with key N-cycling processes. Morphological traits such as height, leaf angle, stem strength, and ear morphology (Donald, 1968), influence light interception, lodging resistance, and grain formation. Additionally, stress tolerance mechanisms extend beyond stay-green; drought resilience through osmotic adjustment and stomatal regulation (Rezzouk et al., 2022; Semenov and Stratonovitch, 2013, 2015; Stratonovitch and Semenov, 2015) and heat tolerance (Semenov and Stratonovitch, 2013; Ullah et al., 2024) are vital for maintaining yield stability in variable climates. Even seemingly minor physiological adjustments, such as optimising the Rubisco specificity factor for present-day CO_2 levels (Wu et al., 2022; Zhu et al., 2004), can enhance photosynthetic efficiency.

Therefore, an effective ideotyping strategy must encompass a broad range of traits while carefully considering their interactions and trade-offs to maximise synergistic gains in wheat performance. This becomes even more complex when accounting for influences beyond physiological traits. For instance, our study did not directly examine the interaction between ideotyping and other adaptation strategies, such as adjusting the sowing date (Collins et al., 2021; Collins and Chenu, 2021; Qin et al., 2018; Wang et al., 2019), which influences the timing and occurrence of plant phenological stages. Furthermore, our study did not evaluate how ideotyping strategies influence other facets of cropping systems, including resource use efficiency and environmental footprints. Hence, adopting a holistic approach that accounts for a broader spectrum of parameters, environments (climate × soil), management scenarios, and performance criteria (in addition to productivity) requires considerable computational power. This requirement can be significantly reduced through the proposed integration of model-assisted ideotyping and envirotyping.

5. Conclusion

This study successfully showcased the potential of model-assisted envirotyping to advance wheat breeding for climate resilience. By clustering simulated water supply/demand ratios, we identified distinct environment types (ETs) based on seasonal water deficit patterns. Optimising key cultivar parameters through a genetic algorithm—using global, high-stress ET, and location-specific strategies—led to substantial improvements in predicted wheat yields and stability across the target population of environments. Our results highlight the power of model-assisted ideotyping in shifting ET occurrence frequencies towards less stressful conditions and enhancing wheat productivity.

These findings carry important implications for plant breeders. The ability to pinpoint and target specific ETs enables a more strategic and efficient breeding process. By identifying key physiological drivers linked to superior performance in different ETs, breeders can prioritise the selection and development of cultivars with optimal trait combinations. This targeted approach can contribute to greater food security by accelerating the creation of climate-resilient cultivars adapted to specific regions and environmental stresses.

CRediT authorship contribution statement

Brian Collins: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Najeeb Ullah:** Writing – review & editing, Methodology. **Youhong Song:** Writing – review & editing, Methodology. **Keith G. Pembleton:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Ethics approval

Not applicable.

Funding

This study was supported by the University of Southern Queensland.

Declaration of competing interest

The authors have no relevant financial or non-financial interests to disclose.

Acknowledgment

We acknowledge the APSIM Initiative for the continued development of APSIM's modelling software, available free for research and development (see www.apsim.info for details).

Data availability

Data will be made available on request.

References

Ababaei, B., Chenu, K., 2020. Heat shocks increasingly impede grain filling but have little effect on grain setting across the Australian wheatbelt. Agric. For. Meteorol. 284, 107889. https://doi.org/10.1016/j.agrformet.2019.107889.

Ababaei, B., Ullah, N., 2020. Detection of major weather patterns reduces number of simulations in climate impact studies. J Agron Crop Sci 206, 376–389. https://doi.org/10.1111/jac.12388.

Aggarwal, P.K., Kropff, M.J., Cassman, K.G., Ten Berge, H.F.M., 1997. Simulating genotypic strategies for increasing rice yield potential in irrigated, tropical environments. Field Crop Res 51, 5–17. https://doi.org/10.1016/S0378-4290(96)01044-1.

Anwar, M.R., Liu, D.L., Farquharson, R., Macadam, I., Abadi, A., Finlayson, J., Wang, B., Ramilan, T., 2015. Climate change impacts on phenology and yields of five broadacre crops at four climatologically distinct locations in Australia. Agr. Syst. 132, 133–144. https://doi.org/10.1016/j.agsy.2014.09.010.

Australian Export Grains Innovation Centre, 2025. Wheat [WWW Document]. URL. https://www.aegic.org.au/grains/wheat. accessed 1.20.25.

Borrell, A., Hammer, G., Van Oosterom, E., 2001. Stay-green: a consequence of the balance between supply and demand for nitrogen during grain filling? Ann. Appl. Biol. 138, 91–95. https://doi.org/10.1111/J.1744-7348.2001.TB00088.X.

Brisson, N., Guevara, E., Meira, S., Maturano, M., Agronomie, G.C., 2001. Response of five wheat cultivars to early drought in the pampas. Science 21, 483–495. https://doi.org/10.1051/agro:2001139ï.

Calderini, D.F., Dreccer, M.F., Slafer, G.A., 1997. Consequences of breeding on biomass, radiation interception and radiation-use efficiency in wheat. Field Crop Res 52, 271–281. https://doi.org/10.1016/S0378-4290(96)03465-X.

Chapman, S.C., 2008. Use of crop models to understand genotype by environment interactions for drought in real-world and simulated plant breeding trials. Euphytica 161, 195–208. https://doi.org/10.1007/S10681-007-9623-Z/FIGURES/9.

Chauhan, Y., Chenu, K., Williams, R., 2021. Using crop modelling to improve chickpea adaptation in variable environments. In: Genetic Enhancement in Major Food Legumes: Advances in Major Food Legumes, 231–254. https://doi.org/10.1007/978-3-030-64500-7_8/FIGURES/5.

Chenu, K., 2015. Characterizing the crop environment - nature, significance and applications. In: Crop Physiology: Applications for Genetic Improvement and Agronomy, Second edition. Elsevier Inc., pp. 321–348. https://doi.org/10.1016/B978-0-12-417104-6.00013-3

Chenu, K., Cooper, M., Hammer, G.L., Mathews, K.L., Dreccer, M.F., Chapman, S.C., 2011. Environment characterization as an aid to wheat improvement: interpreting genotype-environment interactions by modelling water-deficit patterns in north-eastern Australia. J. Exp. Bot. 62, 1743–1755. https://doi.org/10.1093/jxb/erq459.

Chenu, K., Deihimfard, R., Chapman, S.C., 2013. Large-scale characterization of drought pattern: a continent-wide modelling approach applied to the Australian wheatbelt - spatial and temporal trends. New Phytol. https://doi.org/10.1111/nph.12192.

Christopher, J.T., Christopher, M.J., Borrell, A.K., Fletcher, S., Chenu, K., 2016. Stay-green traits to improve wheat adaptation in well-watered and water-limited environments. J. Exp. Bot. 67, 5159–5172. https://doi.org/10.1093/jxb/erw276.

Collins, B., 2022. Frequency of compound hot–dry weather extremes has significantly increased in Australia since 1889. J Agron Crop Sci 208, 941–955. https://doi.org/10.1111/jac.12545.

Collins, B., Chenu, K., 2021. Improving productivity of Australian wheat by adapting sowing date and genotype phenology to future climate. Clim. Risk Manag. 32, 100300. https://doi.org/10.1016/j.crm.2021.100300.

Collins, B., Chapman, S., Hammer, G., Chenu, K., 2021. Limiting transpiration rate in high evaporative demand conditions to improve Australian wheat productivity. In Silico Plants 3. https://doi.org/10.1093/insilicoplants/diab006.

Debaeke, P.P., Quilot-Turion, B., 2014. Conception d'idéotypes de plantes pour une agriculture durable, 254 p. https://doi.org/10.34894/VQ1DJA.

Deihimfard, R., Rahimi-Moghaddam, S., Eyni-Nargeseh, H., Collins, B., 2023. An optimal combination of sowing date and cultivar could mitigate the impact of simultaneous heat and drought on rainfed wheat in arid regions. Eur. J. Agron. 147, 126848. https://doi.org/10.1016/J.EJA.2023.126848.

Donald, C.M., 1968. The breeding of crop ideotypes. Euphytica 17, 385–403. https://doi.org/10.1007/BF00056241.

Evans, L.T., Fisher, R.A., 1999. Yield potential: its definition, measurement, and significance. Crop. Sci. 39, 1544–1551. https://doi.org/10.2135/CROPSCI1999.3961544X.

Feng, P., Wang, B., Liu, D.L., Xing, H., Ji, F., Macadam, I., Ruan, H., Yu, Q., 2018. Impacts of rainfall extremes on wheat yield in semi-arid cropping systems in eastern Australia. Clim. Change 147, 555–569. https://doi.org/10.1007/S10584-018-2170-X/FIGURES/4.

Frederiks, T.M., Christopher, J.T., Fletcher, S.E.H., Borrell, A.K., 2011. Post head-emergence frost resistance of barley genotypes in the northern grain region of Australia. Crop Pasture Sci. 62, 736–745. https://doi.org/10.1071/CP11079.

Garg, D., Sareen, S., Dalal, S., Tiwari, R., Singh, R., 2013. Grain filling duration and temperature pattern influence on the performance of wheat genotypes under late planting. Cereal Res. Commun. 41, 500–507. https://doi.org/10.1556/CRC.2013.0019.

Gebeyehou, G., Knott, D.R., Baker, R.J., 1982. Rate and duration of grain filling in durum wheat Cultivars1. Crop. Sci. 22, 337–340. https://doi.org/10.2135/CROPSCI1982.0011183X002200020033X.

Gerland, P., Raftery, A.E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G.K., Wilmoth, J., 2014. World population stabilization unlikely this century. Science 1979 (346), 234–237. https://doi.org/10.1126/SCIENCE.1257469/SUPPL_FILE/GERLAND.SM.REVISION.1.PDF.

Ghahramani, A., Kokic, P.N., Moore, A.D., Zheng, B., Chapman, S.C., Howden, M.S., Crimp, S.J., 2015. The value of adapting to climate change in Australian wheat farm systems: farm to cross-regional scale. Agric. Ecosyst. Environ. 211, 112–125. https://doi.org/10.1016/j.agee.2015.05.011.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. Science 1979 (327), 812–818. https://doi.org/10.1126/science.1185383.

Gouache, D., Bogard, M., Pegard, M., Thepot, S., Garcia, C., Hourcade, D., Paux, E., Oury, F.X., Rousset, M., Deswarte, J.C., Le Bris, X., 2017. Bridging the gap between ideotype and genotype: challenges and prospects for modelling as exemplified by the case of adapting wheat (Triticum aestivum L.) phenology to climate change in France. Field Crop Res 202, 108–121. https://doi.org/10.1016/J.FCR.2015.12.012.

Gracia-Romero, A., Vatter, T., Kefauver, S.C., Rezzouk, F.Z., Segarra, J., Nieto-Taladriz, M.T., Aparicio, N., Araus, J.L., 2023. Defining durum wheat ideotypes adapted to Mediterranean environments through remote sensing traits. Front. Plant Sci. 14, 1254301. https://doi.org/10.3389/FPLS.2023.1254301/BIBTEX.

Grains Research and Development Corporation, 2023. South Australian Crop Sowing Guide.

Hammer, G.L., Van Oosterom, E., McLean, G., Chapman, S.C., Broad, I., Harland, P., Muchow, R.C., 2010. Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops. J. Exp. Bot. https://doi.org/10.1093/jxb/erq095.

Hammer, G.L., McLean, G., van Oosterom, E., Chapman, S., Zheng, B., Wu, A., Doherty, A., Jordan, D., 2020. Designing crops for adaptation to the drought and high-temperature risks anticipated in future climates. Crop. Sci. 60, 605–621. https://doi.org/10.1002/CSC2.20110.

Herndl, M., Shan, C., Gang Wang, P., Graeff, S., Claupein, W., 2007. A model based Ideotyping approach for wheat under different environmental conditions in North China Plain. Agric. Sci. China 6, 1426–1436. https://doi.org/10.1016/S1671-2927(08)60004-8.

Holzworth, D.P., Huth, N.I., DeVoil, P.G., Zurcher, E.J., Herrmann, N.I., McLean, G., Chenu, K., van Oosterom, E.J., Snow, V., Murphy, C., Moore, A.D., Brown, H., Whish, J.P.M., Verrall, S., Fainges, J., Bell, L.W., Peake, A.S., Poulton, P.L., Hochman, Z., Thorburn, P.J., Gaydon, D.S., Dalgliesh, N.P., Rodriguez, D., Cox, H., Chapman, S., Doherty, A., Teixeira, E., Sharp, J., Cichota, R., Vogeler, I., Li, F.Y., Wang, E., Hammer, G.L., Robertson, M.J., Dimes, J.P., Whitbread, A.M., Hunt, J., van Rees, H., McClelland, T., Carberry, P.S., Hargreaves, J.N.G., MacLeod, N., McDonald, C., Harsdorf, J., Wedgwood, S., Keating, B.A., 2014. APSIM – evolution towards a new generation of agricultural systems simulation. Environ. Model. Software 62, 327–350. https://doi.org/10.1016/j.envsoft.2014.07.009.

Holzworth, D., Huth, N.I., Fainges, J., Brown, H., Zurcher, E., Cichota, R., Verrall, S., Herrmann, N.I., Zheng, B., Snow, V., 2018. APSIM next generation: overcoming challenges in modernising a farming systems model. Environ. Model. Softw. 103, 43–51. https://doi.org/10.1016/j.envsoft.2018.02.002.

Jeffrey, S.J., Carter, J.O., Moodie, K.B., Beswick, A.R., 2001. Using spatial interpolation to construct a comprehensive archive of Australian climate data. Environmental Modelling and Software 16, 309–330. https://doi.org/10.1016/S1364-8152(01)00008-1.

Kornhuber, K., Lesk, C., Schleussner, C.F., Jägermeyr, J., Pfleiderer, P., Horton, R.M., 2023. Risks of synchronized low yields are underestimated in climate and crop model projections. Nature Communications 14:1, 1–10. Doi: https://doi.org/10.1038/s41467-023-38906-7.

Liepins, G.E., Hilliard, M.R., 1989. Genetic algorithms: foundations and applications. Ann. Oper. Res. 21, 31–57. https://doi.org/10.1007/BF02022092/METRICS.

Liu, H., Grant, B., Smith, W., Porter, C., Cammarano, D., Vogeler, I., Hoogenboom, G., Pullens, J.W.M., Olesen, J.E., Bindi, M., Semenov, M.A., Abrahamsen, P., Rötter, R. P., Kumar, U., Abalos, D., 2025. Towards an Improved Representation of the Relationship between Root Traits and Nitrogen Losses in Process-Based Models. https://doi.org/10.2139/SSRN.5129351.

Lobell, D.B., Hammer, G.L., Chenu, K., Zheng, B., McLean, G., Chapman, S.C., 2015. The shifting influence of drought and heat stress for crops in Northeast Australia. Glob. Chang. Biol. 21, 4115–4127. https://doi.org/10.1111/gcb.13022.

Loison, R., Audebert, A., Debaeke, P., Hoogenboom, G., Leroux, L., Oumarou, P., Gérardeaux, E., 2017. Designing cotton ideotypes for the future: reducing risk of crop failure for low input rainfed conditions in northern Cameroon. Eur. J. Agron. 90, 162–173. https://doi.org/10.1016/J.EJA.2017.08.003.

Manschadi, A.M., Christopher, J., deVoil, P., Hammer, G.L., 2006. The role of root architectural traits in adaptation of wheat to water-limited environments. Funct. Plant Biol. 33, 823. https://doi.org/10.1071/FP06055.

Martre, P., He, J., Le Gouis, J., Semenov, M.A., 2015a. In silico system analysis of physiological traits determining grain yield and protein concentration for wheat as influenced by climate and crop management. J. Exp. Bot. 66, 3581–3598. https://doi.org/10.1093/jxb/erv049.

Martre, P., Wallach, D., Asseng, S., Ewert, F., Jones, J.W., Rötter, R.P., Boote, K.J., Ruane, A.C., Thorburn, P.J., Cammarano, D., Hatfield, J.L., Rosenzweig, C., Aggarwal, P.K., Angulo, C., Basso, B., Bertuzzi, P., Biernath, C., Brisson, N., Challinor, A.J., Doltra, J., Gayler, S., Goldberg, R., Grant, R.F., Heng, L., Hooker, J., Hunt, L.A., Ingwersen, J., Izaurralde, R.C., Kersebaum, K.C., Müller, C., Kumar, S.N., Nendel, C., O'leary, G., Olesen, J.E., Osborne, T.M., Palosuo, T., Priesack, E., Ripoche, D., Semenov, M.A., Shcherbak, I., Steduto, P., Stöckle, C.O., Stratonovitch, P., Streck, T., Supit, I., Tao, F., Travasso, M., Waha, K., White, J.W., Wolf, J., 2015b. Multimodel ensembles of wheat growth: many models are better than one. Glob. Chang. Biol. 21, 911–925. https://doi.org/10.1111/GCB.12768.

Messina, C.D., Sinclair, T.R., Hammer, G.L., Curan, D., Thompson, J., Oler, Z., Gho, C., Cooper, M., 2015. Limited-transpiration trait may increase maize drought tolerance in the US corn belt. Agron. J. https://doi.org/10.2134/agronj15.0016.

Parry, M.A.J., Reynolds, M., Salvucci, M.E., Raines, C., Andralojc, P.J., Zhu, X.G., Price, G.D., Condon, A.G., Furbank, R.T., 2011. Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. J. Exp. Bot. 62, 453–467. https://doi.org/10.1093/jxb/erq304.

Potgieter, A.B., Hammer, G.L., Butler, D., 2002. Spatial and temporal patterns in Australian wheat yield and their relationship with ENSO. Aust. J. Agr. Res. 53, 77–89. https://doi.org/10.1071/AR01002.

Qin, W., Zhang, X., Chen, S., Sun, H., Shao, L., 2018. Crop rotation and N application rate affecting the performance of winter wheat under deficit irrigation. Agric Water Manag 210, 330–339. https://doi.org/10.1016/J.AGWAT.2018.08.026.

Ray, D.K., Gerber, J.S., Macdonald, G.K., West, P.C., 2015. Climate variation explains a third of global crop yield variability. Nat. Commun. 6, 5989. https://doi.org/10.1038/ncomms6989.

R Core Team, 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reynolds, M., Bonnett, D., Chapman, S.C., Furbank, R.T., Manés, Y., Mather, D.E., Parry, M.A.J., 2011. Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. J. Exp. Bot. 62, 439–452. https://doi.org/10.1093/JXB/ERQ311.

Rezzouk, F.Z., Gracia-Romero, A., Kefauver, S.C., Nieto-Taladriz, M.T., Serret, M.D., Araus, J.L., 2022. Durum wheat ideotypes in Mediterranean environments differing in water and temperature conditions. Agric Water Manag 259, 107257. https://doi.org/10.1016/J.AGWAT.2021.107257.

Richards, R.A., 1991. Crop improvement for temperate Australia: future opportunities. Field Crop Res 26, 141–169. https://doi.org/10.1016/0378-4290(91)90033-R.

Rötter, R.P., Carter, T.R., Olesen, J.E., Porter, J.R., 2011. Crop–climate models need an overhaul. Nat. Clim. Chang. 1, 175–177. https://doi.org/10.1038/nclimate1152.

Rötter, R.P., Tao, F., Höhn, J.G., Palosuo, T., 2015. Use of crop simulation modelling to aid ideotype design of future cereal cultivars. J. Exp. Bot. https://doi.org/10.1093/jxb/erv098.

Rötter, R.P., Appiah, M., Fichtler, E., Kersebaum, K.C., Trnka, M., Hoffmann, M.P., 2018. Linking modelling and experimentation to better capture crop impacts of agroclimatic extremes—a review. Field Crop Res 221, 142–156. https://doi.org/10.1016/J.FCR.2018.02.023.

Scrucca, L., 2013. GA: a package for genetic algorithms in R. J. Stat. Softw. 53, 1–37. https://doi.org/10.18637/JSS.V053.I04.

Semenov, M.A., Halford, N., 2009. Identifying target traits and molecular mechanisms for wheat breeding under a changing climate. J. Exp. Bot. 60, 2791–2804. https://doi.org/10.1093/jxb/erp164.

Semenov, M., Stratonovitch, P., 2013. Designing high-yielding wheat ideotypes for a changing climate. Food Energy Secur 2, 185–196. https://doi.org/10.1002/fes3.34.

Semenov, M.A., Stratonovitch, P., 2015. Adapting wheat ideotypes for climate change: accounting for uncertainties in CMIP5 climate projections. Climate Res. https://doi.org/10.3354/cr01297.

Semenov, M.A.A., Stratonovitch, P., Alghabari, F., Gooding, M.J.J., 2014. Adapting wheat in Europe for climate change. J. Cereal Sci. 59, 245–256. https://doi.org/10.1016/j.jcs.2014.01.006.

Senapati, N., Semenov, M.A., Halford, N.G., Hawkesford, M.J., Asseng, S., Cooper, M., Ewert, F., van Ittersum, M.K., Martre, P., Olesen, J.E., Reynolds, M., Rötter, R.P., Webber, H., 2022. Global wheat production could benefit from closing the genetic yield gap. Nature Food 3 (7), 532–541. https://doi.org/10.1038/s43016-022-00540-9.

Shavrukov, Y., Kurishbayev, A., Jatayev, S., Shvidchenko, V., Zotova, L., Koekemoer, F., De Groot, S., Soole, K., Langridge, P., 2017. Early flowering as a drought escape mechanism in plants: how can it aid wheat production? Front. Plant Sci. 8, 302418. https://doi.org/10.3389/FPLS.2017.01950/BIBTEX.

Shewry, P.R., Hey, S.J., 2015. The contribution of wheat to human diet and health. Food Energy Secur 4, 178–202. https://doi.org/10.1002/FES3.64.

Sinclair, T.R., Hammer, G.L., Van Oosterom, E.J., 2005. Potential yield and water-use efficiency benefits in sorghum from limited maximum transpiration rate. Funct. Plant Biol. 32, 945–952. https://doi.org/10.1071/FP05047.

Srinivasan, V., Kumar, P., Long, S.P., 2017. Decreasing, not increasing, leaf area will raise crop yields under global atmospheric change. Glob. Chang. Biol. 23, 1626–1635. https://doi.org/10.1111/GCB.13526.

Steinfort, U., Trevaskis, B., Fukai, S., Bell, K.L., Dreccer, M.F., 2017. Vernalisation and photoperiod sensitivity in wheat: impact on canopy development and yield components. Field Crop Res 201, 108–121. https://doi.org/10.1016/J.FCR.2016.10.012.

Stratonovitch, P., Semenov, M.A., 2015. Heat tolerance around flowering in wheat identified as a key trait for increased yield potential in Europe under climate change. J. Exp. Bot. 66, 3599–3609. https://doi.org/10.1093/jxb/erv070.

Sylvester-Bradley, R., Riffkin, P., O'Leary, G., 2012. Designing resource-efficient ideotypes for new cropping conditions: wheat (Triticum aestivum L.) in the high rainfall zone of southern Australia. Field Crop Res 125, 69–82. https://doi.org/10.1016/J.FCR.2011.07.015.

Tao, F., Rötter, R.P., Palosuo, T., Díaz-Ambrona, C.G.H.G.H., Mínguez, M.I., Semenov, M. A., Kersebaum, K.C., Nendel, C., Cammarano, D., Hoffmann, H., Ewert, F., Dambreville, A., Martre, P., Rodríguez, L., Ruiz-Ramos, M., Gaiser, T., Höhn, J.G., Salo, T., Ferrise, R., Bindi, M., Schulman, A.H., 2017. Designing future barley ideotypes using a crop model ensemble. Eur. J. Agron. 82, 144–162. https://doi.org/10.1016/j.eja.2016.10.012.

Tefera, A.T., O'Leary, G.J., Thayalakumaran, T., Rao, S., Silva-Perez, V., Shunmugam, A. S.K., Armstrong, R., Rosewarne, G.M., 2022. Identification of agro-physiological traits of lentil that reduce risks of drought. Front. Plant Sci. 13, 1019491. https://doi.org/10.3389/FPLS.2022.1019491/BIBTEX.

Trnka, M., Feng, S., Semenov, M.A., Olesen, J.E., Kersebaum, K.C., Rötter, R.P., Semerádová, D., Klem, K., Huang, W., Ruiz-Ramos, M., Hlavinka, P., Meitner, J., Balek, J., Havlík, P., Büntgen, U., 2019. Mitigation efforts will not fully alleviate the increase in water scarcity occurrence probability in wheat-producing areas. Sci. Adv. 5. https://doi.org/10.1126/SCIADV.AAU2406/SUPPL_FILE/AAU2406_SM.PDF.

Ullah, N., Chenu, K., 2019. Impact of post-flowering heat stress on stay-green and grain development in wheat. In: Australian Agronomy Conference Wagga. Wagga Wagga, Australia.

Ullah, S., Bramley, H., Mahmood, T., Trethowan, R., 2019. A strategy of ideotype development for heat-tolerant wheat. J. Agron. Crop Sci. https://doi.org/10.1111/jac.12378 jac.12378.

Ullah, N., Collins, B., Christopher, J.T., Frederiks, T., Chenu, K., 2024. Pre- and post-flowering impacts of natural heatwaves on yield components in wheat. Field Crop Res 316, 109489. https://doi.org/10.1016/J.FCR.2024.109489.

Wang, B., Liu, D.L., Asseng, S., Macadam, I., Yu, Q., 2015. Impact of climate change on wheat flowering time in eastern Australia. Agric. For. Meteorol. 209–210, 11–21. https://doi.org/10.1016/j.agrformet.2015.04.028.

Wang, B., Feng, P., Chen, C., Liu, D.L., Waters, C., Yu, Q., 2019. Designing wheat ideotypes to cope with future changing climate in south-eastern Australia. Agr. Syst. 170, 9–18. https://doi.org/10.1016/J.AGSY.2018.12.005.

Watson, J., Zheng, B., Chapman, S., Chenu, K., 2017. Projected impact of future climate on water-stress patterns across the Australian wheatbelt. J. Exp. Bot. 68, 5907–5921. https://doi.org/10.1093/jxb/erx368.

Webber, H., Ewert, F., Olesen, J.E., Müller, C., Fronzek, S., Ruane, A.C., Bourgault, M., Martre, P., Ababaei, B., Bindi, M., Ferrise, R., Finger, R., Fodor, N., Gabaldón-Leal, C., Gaiser, T., Jabloun, M., Kersebaum, K.C., Lizaso, J.I., Lorite, I.J., Manceau, L., Moriondo, M., Nendel, C., Rodríguez, A., Ruiz-Ramos, M., Semenov, M.A., Siebert, S., Stella, T., Stratonovitch, P., Trombi, G., Wallach, D., 2018. Diverging importance of drought stress for maize and winter wheat in Europe. Nat. Commun. 9, 4249. https://doi.org/10.1038/s41467-018-06525-2.

Webber, H., Rezaei, E.E., Ryo, M., Ewert, F., 2022. Framework to guide modeling single and multiple abiotic stresses in arable crops. Agric. Ecosyst. Environ. 340, 108179. https://doi.org/10.1016/J.AGEE.2022.108179.

Wu, A., Brider, J., Busch, F.A., Chen, M., Chenu, K., Clarke, V.C., Collins, B., Ermakova, M., Evans, J.R., Farquhar, G.D., Forster, B., Furbank, R.T., Gorszmann, M., Hernandez, M.A., Long, B.M., Mclean, G., Potgieter, A., Dean Price, G., Sharwood, R.E., Stower, M., van Oosterom, E., von Caemmerer, S., Whitney, S.M., Hammer, G.L., 2022. A cross-scale analysis to understand and quantify effects of photosynthetic enhancement on crop growth and yield across environments. Plant Cell Environ. https://doi.org/10.1111/pce.14453.

Yadav, B., Kumar Nagar, S., Behera, K., Barela, A., 2023. Features and Concepts of Ideotype Breeding for Different Crops.

Yin, X., Struik, P.C., 2017. Can increased leaf photosynthesis be converted into higher crop mass production? A simulation study for rice using the crop model GECROS. J. Exp. Bot. 68, 2345. https://doi.org/10.1093/JXB/ERX085.

Zheng, B., Chenu, K., Fernanda Dreccer, M., Chapman, S.C., 2012. Breeding for the future: what are the potential impacts of future frost and heat events on sowing and flowering time requirements for Australian bread wheat (*Triticum aestivium*) varieties? Glob. Chang. Biol. 18, 2899–2914. https://doi.org/10.1111/j.1365-2486.2012.02724.x.

Zheng, B., Chapman, S.C., Christopher, J.T., Frederiks, T.M., Chenu, K., 2015. Frost trends and their estimated impact on yield in the Australian wheatbelt. J. Exp. Bot. 66, 3611–3623. https://doi.org/10.1093/jxb/erv163.

Zhu, X.G., Portis, A.R., Long, S.P., 2004. Would transformation of C3 crop plants with foreign rubisco increase productivity? A computational analysis extrapolating from kinetic properties to canopy photosynthesis. Plant Cell Environ. 27, 155–165. https://doi.org/10.1046/J.1365-3040.2004.01142.X.