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RESEARCH ARTICLE



Designing high-yielding wheat crops under late sowing: a case study in southern China

Ke Liu^{1,2} • Matthew Tom Harrison² • Bin Wang³ • Rui Yang¹ • Haoliang Yan¹ • Juan Zou⁴ • De Li Liu³ • Holger Meinke⁵ • Xiaohai Tian¹ • Shangyu Ma⁶ • Yunbo Zhang¹ • Jianguo Man⁷ • Xiaoyan Wang¹ • Meixue Zhou²

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Abstract

Cropping of rice and wheat (*Triticum aestivum L.*) in rotation contiguously in the same field is a fundamental pillar of doublecropping systems in southern China. Yields of such cropping systems are increasingly challenged as climate change (CC) drives increases in autumnal rainfall, delaying rice harvesting and subsequent sowing of wheat. Here, our purpose was to identify prospective traits of wheat crops enabling adaptation to later sowing and successively truncated growing seasons caused by CC. To identify traits that maintained or improved yields, we constructed 4,096 hypothetical genotypes underpinned by step-wise variations in parameters regulating phenology, growth and yield components. We then assimilated biophysical response surfaces through genotype (G) by environment (E) by management (M) analyses ($G \times E \times M$) using six locations spread across the breadth of southern China. We showed that later sowing reduced cumulative radiation interception, cumulative thermal time and crop capture of growing season rainfall. The culmination of these factors shortened crop duration and decreased biomass accumulation and retranslocation after anthesis, reducing grain number and penalising yields. Genotypes that had greater radiation use efficiency, longer juvenile phases and greater grain filling rates were more effective in alleviating yield losses with delayed sowing. However, not even the highest yielding genotype × management combination could entirely alleviate yield losses with delayed sowing. Our results suggest that CC and increasingly frequent extreme climatic events may reduce wheat yields in such cropping systems in the absence of other adaptation.

Keywords Wheat yield · Hypothetical genotypes · Late sowing · APSIM-Wheat · Southern China

1 Introduction

Serial rice-wheat (RW) crop rotations in southeastern Asia comprise one of the largest agroecosystems in the world, being practiced on ~10.5 million ha in southern China alone

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(Nadeem and Farooq 2019). Rice and wheat are staple crops for the Chinese, constituting 52% of national grain production (NBSC 2019). While cropping of spring wheat historically predominated the region, the RW double-cropping system was quickly adopted across southern China due to the

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introduction of hyper yielding rice varieties. Such system is a clear example of agricultural intensification, enabling greater food production from the same land area by separating crops in time rather than space. However, wheat yields in the RW system are declining due to progressively higher autumnal rains and earlier autumnal rains driven by climate change (Lu et al., 2021), delaying both the harvesting of rice and subsequent sowing of wheat (Yang et al. 2021; Fig. 1). These trends are expected to continue, with future climate change driving increased frequencies of extreme climatic events such as flash flooding and heat stress, further threatening sustainable food production (Chang-Fung-Martel et al. 2017; Harrison et al. 2012a, 2012b). There is thus a dire need to improve productivity without infringing on natural capital, increasing greenhouse gas emissions, reducing social licence, applying excessive nitrogen or reducing farmer profitability (Harrison et al. 2011; Alcock et al. 2015; Christie et al. 2018).

Rice is prioritised over wheat in southern China as the former is a primary human dietary staple and is more lucrative (CNFSRA 2020). In such regions, rice is traditionally transplanted in early June and harvested in late October. Traditionally, wheat crops were sown in early November and harvested in early- to mid-May (Usman et al. 2010). Recently, farmers in this region have begun adopting later maturing rice genotypes (early to middle November) with longer grain filling periods to improve yields (Wang et al. 2009). However, later rice harvesting pushes back the subsequent sowing of wheat, diminishing wheat yield potential. There is thus a need for the development of new management by considering different genotypes to identify avenues for alleviating yield losses caused by later sowing.

Crop modelling in conjunction with appropriately designed breeding and agronomic packages can help dissect complex and numerous genotype (G) × environment (E) × management (M) interactions (Liu et al. 2020a; Ibrahim et al. 2019; Liu et al. 2021). Several studies have shown that G×E interactions are often the main source of yield variation in rainfed systems (Harrison et al. 2014a, 2014b). Crop models have been used to design ideotypes (Tao et al. 2017; Xiao et al. 2020), optimise flowering times (Flohr et al. 2017; Hunt et al. 2019) and examine whole farm systems adaptations to climate change (Bell et al. 2013; Harrison et al. 2016). Despite this, few studies have explored the extent to which late sowing of wheat in southern China can be alleviated with adoption of new genotypes. To counter high terminal temperature exposure caused by later sowing, promising traits may include higher thermal time and improved radiation use efficiency (RUE) enabling greater growth during winter periods with limited incident radiation (Asseng et al. 2015; Asseng et al. 2004; Asseng et al. 2017; Zhao et al. 2015). However, it remains unknown whether these traits are suitable for late sowing in southern China.

Here, we use a G×E×M paradigm to determine how sowing times of wheat influenced phenology and yield across southern China. We constructed a virtual G×E×M landscape by simulating hypothetical genotypes over multiple sowing dates to identify high-yield combinations over the long term. The aims of this study were to (1) quantify how late sowing affects wheat yield in southern China and (2) identify optimal crop traits that can mitigate yield losses caused by late sowing.

2 Materials and methods

2.1 Genotypes and field site management

Fourteen common commercial Chinese spring wheat genotypes were selected for field experiments in southern China (Table 1). Field experiments were conducted in the Hubei province (at Zaoyang, 32° 12' N, 112° 76' E) from 2016 to 2018, in the Anhui province (at Lujiang, 30° 57' N, 117° 01' E) from 2017 to 2019 and in the Jiangsu province (at Yangzhou, 32° 39' N, 119° 42' E) from 2015 to 2017. At each site, wheat was planted on rice paddy soil in a randomised complete block design with three replications. Fertiliser was drilled at sowing and top-dressed at Zadoks Stage 31 (ZS31). Other agronomic practices and meteorological data are listed in Tables S1 and S2, respectively. Climatic data were obtained from local meteorological bureaus.

Fig. 1 Example of excessive rainfall after rice harvest, which delays wheat sowing date (**a**). Seedling growth status under delayed sowing date (**b**). Photographs: Jianguo Man.



 Table 1
 Genotypic information

 for each province, including year
 of first release and pedigree.

Province	Genotype	Abbreviation	Year of release	Pedigree		
Hubei	Emai170	EM170	2014	Jimai19/Yumai47		
	Emai580	EM580	2012	Taiguhe sterile/957565		
	Emai596	EM596	2009	Zhengmai9023/Emai12/Fengyou7		
	Xiangmai25	XM25	2008	Tai062/Emai19		
	Zhengmai9023	ZM9023	2001	Xiaoyan6/Xinong65		
Jiangsu						
	Ningmai14	NM14	2006	Ningmai9		
	Sumai188	SM188	2012	Yangfumai2		
	Yangmai16	YM16	2004	Yang91F138/Yang90-30		
	Yangmai22	YM22	2012	Yangmai9*3/97033-2		
	Yangmai23	YM23	2014	Yangmai16/Yangfu93-11		
Anhui						
	Annong1124	AN1124	2016	O2P67//Aizao781/Yangmai158		
	Ningmai26	NM26	2016	Ning9531/Ningmai9		
	Ningmai13	NM13	2005	Ningmai9		
	Yangmai25	YM25	2016	Yang17*2/Yang11/Yumai18		

measurements from 30 spikes.

2.2 Phenotyping The number of days to reach half-ear emergence (ZS55) was recorded for each genotype twice per week when over 50% of the plants per plot presented with half-ear emergence. Shoot biomass was harvested from 20 mature plants per pot. Samples were oven-dried at 80°C for \geq 48 h to a constant weight. Plants were selected from a 2-m² harvest area in the middle of each plot to evaluate yield and yield components. One thousand random kernels per harvested grain were weighed to calculate the 1,000-kernel weight. Grain moisture was measured with a grain analyser (InfratecTM 1241; Foss A/S, Hillerød, Denmark). Yield and 1,000 kernel weight were adjusted to 13% moisture.

2.3 Model parameterisation and validation

Simulations were conducted using APSIM-Wheat v7.10 (Holzworth et al. 2014; Keating et al. 2003). Genotypic parameters were defined either by adjusting the parameters of existing genotypes in the APSIM-Wheat XML or by adjusting the base variety when the genotype being parameterised was absent from the default APSIM release.

The average number of kernels per spike was calculated using

Field data obtained at Yangzhou in 2015–2016, Zaoyang in 2016–2017 and Lujiang in 2017–2018 were used for model parameterisation. We first parameterised crop phenology (flowering and maturity date) because the simulation of crop phenology is a fundamental determinant of yield. Thus, matching the phenology of crop varieties to their environments is a critical part of crop design (Hammer et al. 2014; Wallach et al. 2021).

We then parameterised biomass, then finally yield components by adjusting relevant crop parameters reflect the cultivar growth rates (Christie et al. 2018), yield components and grain yield. Heading time control was split into vernalisation requirement, photoperiod sensitivity, and earliness per se (Bogard et al. 2020). These parameters are included in APSIM. For example, phenology is mainly driven in APSIM-Wheat by the parameters of thermal time (tt end of juvenile and tt from start grain filling to maturity), vernalisation (vern sense) and photoperiod (photo sense) (Casadebaig et al. 2016); growth rates in the absence of water stress relate closely to radiation use efficiency, while yield components are mainly governed by kernel number per stem weight at the beginning of grain filling (g), potential daily grain filling rate (g grain⁻¹ day⁻¹) and maximum grain size (g) (Zhao et al. 2015). Parameterisation of those genotypes shown in Table 1 was performed by minimising the sum of squared errors for measured and simulated phenology, biomass, grain number and yield following the automated calibration approach outlined by Harrison et al. (2019).

Field data measured at Yangzhou in 2016–2017, Zaoyang in 2017–2018 and Lujiang in 2018–2019 were then used for validation. We applied evaluation criteria outlined by Harrison et al. (2019), where ideal root mean square error (RMSE) and mean bias (MB) values are represented by 0.0; MB < 0 and MB > 0 represent model underestimation and overestimation of observed data, respectively. For relative root mean square error (RRMSE) values: < 5% = excellent, 5-10% = very good, 10-30% = good and > 30% = poor. The ideal variance ratio (VR) is 1; VR > 1 indicates greater variation in the actual data compared with the simulated data. Model performance and calibrated parameters are shown in Fig. S1 and Table S3.



Parameters	Definition	Unit	HB	AH	GY
X1	Thermal time from sowing to the end of juvenile.	°C day ⁻¹	500	500	500
X2	Thermal time from the start grain filling to maturity	$^{\circ}C \text{ day}^{-1}$	655	655	655
X3	Kernel number per stem weight at the beginning of grain filling	g	25	40	40
X4	Potential daily grain filling rate	g grain ⁻¹ day ⁻¹	0.003	0.003	0.004
X5	Maximum grain size	g	0.041	0.041	0.041
X6	RUE from ZS30 to ZS90	$g MJ^{-1}$	1.24	1.44	1.44

 Table 2.
 Values of different parameters for reference genotypes promulgated in Hubei province (HB), Anhui province (AH) and Jiangsu (GY) province. RUE radiation use efficiency.

2.4 Factorial simulation analyses

Four representative wheat genotypes that were well represented by model simulations (Fig. S1 and Table S1) were used as reference genotypes for each location; values of genetic parameters for hypothetical genotypes (HGs) were generated by systematically modifying values of different parameters for reference genotypes (Table 2). Because growing season temperatures in southern China are relatively higher compared with the North China Plain, many commercial genotypes do not require vernalisation. As well, many wheat genotypes cultivated in southern China are photoperiod insensitive (Han et al. 2016). As such, default photoperiod (3.0) and vernalisation (1.5) values were adopted for all HGs in the present study.

As rainfall during winter in southern China is often sufficient for growth in the majority of years, here, we do not consider improving water use efficiency. Instead, our traits (and parameters therein) were aimed at modifying phenology, biomass production or harvest indices, as these traits are able to be manipulated in current crop breeding experiments (Wang et al. 2019). Six genetic coefficients were used to explore genotypic traits that inhibit yield penalties associated with late sowing (Table 2). For each HG, genotypic parameters were incremented in a step-wise fashion between lower and upper bounds (Table 3). Cumulatively, 196,608 simulations from APSIM (4,096 hypothetical genotypes × 6 sites × 8 sowing dates) were synthesised then evaluated using custom-built codes in R (R-Core-Team 2013).

Table 3. The hypothetical genotypes were analysed using a factorial combination of different steps selected between minimum and maximum value of each parameter. X1, thermal time from sowing to end of juvenile ($^{\circ}C \text{ day}^{-1}$); X2, thermal time from start grain filling to maturity ($^{\circ}C \text{ day}^{-1}$);

Hypothetical genotypes were used to create response surfaces underpinned by the G×E×M, with G representing 4,096 genotypes, E representing environment (soil, climate and year) and M representing management (here, sowing time). Sowing windows were simulated using 7-day increments from 25 October to 13 December each year. Factorial simulations were conducted for each year from 1961 to 2018 at six locations, representing the geographical extent of the RW double-cropping systems across southern China (Fig. 2). Initial soil water in the profile was assumed 100%, as the preceding rice crops were flood irrigated at sowing to stabilise the timing of emergence. The initial soil N (60 kg NO₃ ha⁻¹ and 15 kg NH₄ ha⁻¹) conditions were reset each year to prevent carry-over effects from previous seasons.

2.5 Photothermal quotient

The photothermal quotient (PQ) was calculated following Fischer (1985), where PQ = Rad/TT, with PQ representing the daily photothermal quotient (MJ m⁻² day °C), Rad is the daily solar radiation (MJ m⁻² day) and TT represents thermal time between 300 day °C before flowering and 100 day °C after flowering.

2.6 Yield loss rate

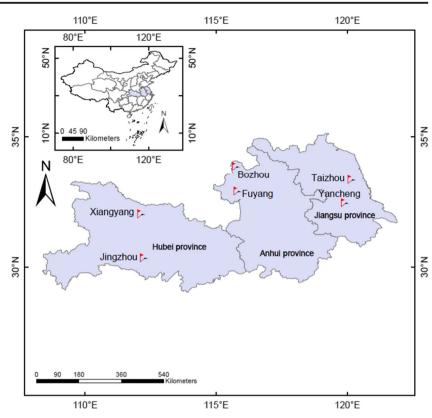
Yield loss (YL, %) caused by delayed sowing was calculated as *YL* (%) = $100 \times (Ymax - Ys)/Ymax$, where *Ymax* is the

X3, kernel number per stem weight at the beginning of grain filling (g); X4, potential daily grain filling rate (g grain⁻¹ day⁻¹); X5, maximum grain size (g); X6, radiation use efficiency (RUE) from ZS30 to ZS90 (g MJ^{-1}).

Parameters	Definition	Lower bound	Upper bound	Step
X1	Thermal time from sowing to the end of juvenile period	300	600	100
X2	Thermal time from the start grain filling to maturity	455	755	100
X3	Kernel number per stem weight at the beginning of grain filling	10	55	15
X4	Potential daily grain filling rate	0.001	0.004	0.001
X5	Maximum grain size	0.031	0.061	0.01
X6	RUE from ZS30 to ZS90	1.04	1.64	0.2



Fig. 2 Six sites in southern China used in this study.



highest long-term averaged yield across sowing dates and *Ys* is the yield associated with each sowing date.

3 Results

3.1 Identifying genotypes with optimal traits for breeding under late sowing

For each site, 4,096 hypothetical genotypes were simulated with eight sowing dates (Fig. 3). Cluster analysis was invoked to ascertain traits enabling high yields under late sowing. Among those clusters, 1,404 hypothetical genotypes were grouped into cluster 2, while cluster 1 comprised the least genotype with only 15% (Table 4). HGs in cluster 1 had the highest long-term average yield $(5,575 \text{ kg ha}^{-1})$, while yield in cluster 3 was the lowest $(1,558 \text{ kg ha}^{-1})$. Hypothetical genotypes in cluster 1 and 2 were characterised by longer juvenile phases, larger maximum grain size and higher RUE. Hypothetical genotypes in cluster 3 and cluster 4 had earlier flowering dates, lower maximum grain size and lower RUE. Potential grain filling rate did not exhibit significant variability across clusters, indicating that selecting for this trait may not result in higher yields compared with other traits examined here.

3.2 Relationships between yield and sowing date across sites

Yield loss caused by late sowing was between 1 and 16%, and the extent to which yield penalty is influenced by late sowing largely depended on genotypes, delay in sowing day and locations (Fig. 4, left panel). Taizhou and Jingzhou suffered the least yield reduction under late sowing while Bozhou and Fuyang suffered the relative higher yield loss under late sowing.

We then simulated the yield gap between local reference genotypes and HGs with optimised traits under different sowing dates for each region (Fig. 4, right panel). Although altering phenological and yield traits would significantly improve yield potential, optimised HGs could not entirely alleviate yield losses with delayed sowing. The yield gap between local reference genotypes and hypothetical genotypes decreased with increased number of days delaying in sowing time.

3.3 Relationships between yield and photothermal quotient across sites

Yield and photothermal quotient decreased with later sowing regardless of genotypes (Fig. 5), mainly due to reduced thermal time and intercepted radiation (Fig. S2). HGs with optimised traits significantly improved simulated yield and



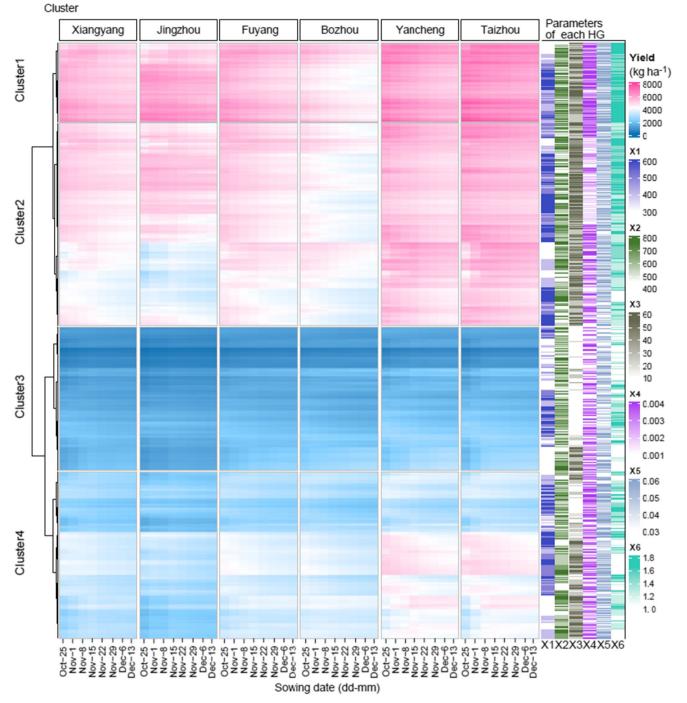


Fig. 3 Cluster analysis of 4,096 hypothetical genotypes (HGs) contrasting phenology, yield components and radiation use efficiency (RUE) based on simulated yields across six sites (Xiangyang, Jingzhou, Fuyang, Bozhou, Yancheng, Taizhou). The main panel (heatmap) shows yield variation across sites with respect to genotypes, sowing dates and

sites; clusters 1 to 4 represent four types of genotypes. Values shown are averaged across years (1961–2018). The corresponding parameters of each HG are shown in the right panel. A detailed description of each parameter can be found in Table 2.

photothermal quotient compared with reference genotypes in Bozhou and Fuyang (Anhui province) and Yancheng and Taizhou (Jiangsu province), but the differences were relatively minor in Xiangyang and Jingzhou (Hubei province). Both reference and hypothetical genotypes in Taizhou and

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Yancheng had the highest yield and photothermal quotient across sowing dates due to higher solar radiation and RUE, while those grown in Xiangyang and Jingzhou had the lowest yields and photothermal quotient as a result of lower solar radiation (Fig. S2).

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Table 4 Mean parameter values and yields for 4,092 hypothetical genotypes (HGs). X1, thermal time from sowing to end of juvenile period ($^{\circ}C$ day⁻¹); X2, thermal time from start grain filling to maturity ($^{\circ}C$ day⁻¹); X3, kernel number per stem weight at the beginning of grain filling (g); X4, potential daily grain filling rate (g grain⁻¹ day⁻¹); X5, maximum grain size (g); X6, radiation use efficiency (RUE) from ZS30 to ZS90 (g MJ⁻¹). Yields (kg ha⁻¹) were computed as averages across hypothetical genotypes in each cluster.

Cluster	No. of HG	X1	X2	X3	X4	X5	X6	Sim yield
1	545	457	634	39.8	0.003	0.048	1.582	5575
2	1404	481	605	42.6	0.002	0.046	1.400	4744
3	993	403	599	16.9	0.002	0.043	1.224	1558
4	1154	449	597	30.1	0.003	0.047	1.252	3276

3.4 Influence of sowing time on maturity biomass and grain number

Later sowing decreased the available time for biomass accumulation in Fig. 6 (left panel). Reference genotypes had higher maturity biomass due to higher solar radiation and RUE in Jiangsu and Anhui compared with genotypes in Hubei. Hypothetical genotypes with optimised traits significantly improved biomass due to higher RUE across sites compared with reference genotypes, especially at sites Xiangyang and Jingzhou (Fig. 6, right panel). Therefore, the breeding efforts should aim to increase biomass (increasing RUE) for Hubei province. Late sowing also decreased grain number regardless of genotypes and sites (Fig. S2).

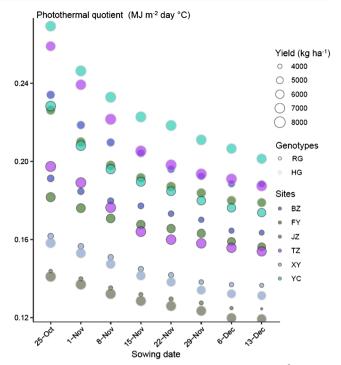
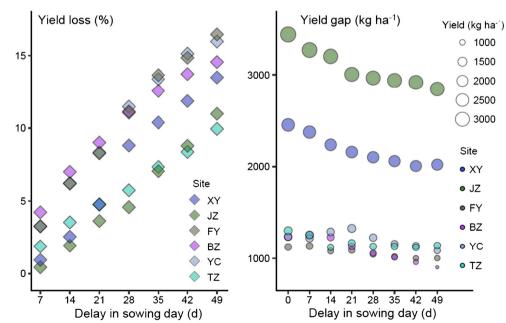


Fig. 5 Relationships between photothermal quotient (MJ m⁻² day °C) and simulated yield (kg ha⁻¹) across genotypes (RG: reference genotypes (circles with solid black border); HG: hypothetical genotypes with optimised traits (circles with solid white border)), sowing dates and sites (XY: Xiangyang; JZ: Jingzhou; FY: Fuyang; BZ: Bozhou; YC: Yancheng; TZ: Taizhou). Values shown are averaged across the 58-year simulations.

4 Discussion

Fig. 4 Left panel: relationship between yield loss and the number of days (d) delaying in sowing time across Hubei province (XY: Xiangyang; JZ: Jingzhou), Anhui province (FY: Fuyang; BZ: Bozhou) and Jiangsu province (YC: Yancheng; TZ: Taizhou). Simulations were conducted for local reference genotypes within each province. Right panel: yield gap between local reference genotypes and hypothetical genotypes with optimised traits under different sowing dates for each site. Values shown are averaged across the 58year simulations.

Delaying sowing time beyond the recommended target date may hinder the realisation of full genetic yield potential of wheat. This study exemplified how crop models can be used





to design wheat ideotypes to cope with the adverse effects of late sowing in southern China. Our methodology (conducted by statistically assimilating 196,608 simulations) revealed that genotypes with higher RUE, longer juvenile phases and greater grain filling rates were more effective in alleviating yield losses with delayed sowing. These results have implications for studies of plant biological responses to environmental stress, breeding programs and crop adaptation to late sowing.

Yield loss caused by late sowing was between 1 and 16%, and the extent to which yield penalty is influenced by late sowing largely depended on genotypes, delay in sowing day and locations (Fig. 4). In this study, the yield loss is less than those observed in previous research (Zhao et al. 2020; Zheng et al. 2020). Relatively lower yield losses in the present study may be explained by the limitation of APSIM-Wheat to simulate abiotic factors. For example, later sowing leads to suboptimal conditions for growth, potentially including greater exposure to high temperature and air humidity during flowering to early grain filling stages, which in practice can increase the risk of pest and disease (e.g. Fusarium head blight) in these regions (Ma et al. 2019). In addition to this, abiotic factors during early growth stages are also not accounted in the default release of the APSIM model, such as low temperature and excessive water stress resulting to poor seed germination, inferior tillering capacity and low plant population (Shah et al. 2020). Therefore, considering pest and disease management simulation in crop models would be another priority as crop yield loss from them is likely to increase with climate change (Peng et al. 2020).

In southern China, temperatures during the flowering months of March and April have risen by 0.8°C over the last 30 years (Table S2). With climate warming, faster crop development due to higher temperatures is one of the main drivers for yield reductions, showing a clear need to maintain flowering times and/or breed genotypes with greater tolerance to heat waves at anthesis. To counter the shortened crop duration caused by higher temperatures, Asseng et al. (2015) suggested that adaptation could be enabled with the use of genotypes with longer maturity and grain filling periods. While such adaptations may be suitable for monocropping systems, longer maturity genotypes are not suitable for double-cropping systems such as the rice-wheat systems examined here, because later maturation pushes back subsequent sowing of next crop, diminishing yield potential. Our results show that a more appropriate adaptation to later sowing may be the use of genotypes with longer juvenile phases and faster grain filling rates (rather than longer grain filling phases). Developing such genotypes might be more appropriate to increase overall crop production under increasingly unfavourable future weather scenarios.

Wheat ideotypes are characterised with early maturity, larger grain size and RUE in Anhui and Jiangsu province, while ideotypes have medium-late maturity, larger grain size and RUE in Hubei province (Table S4). Such differences in ideotypic traits might relate with local environments, especially the cumulative solar radiation during wheat-growing season. Crops grown in Anhui and Jiangsu province usually receive more intercepted photosynthetically active radiation (IPAR) and, thus can produce more biomass compared with crops grown in Hubei province,

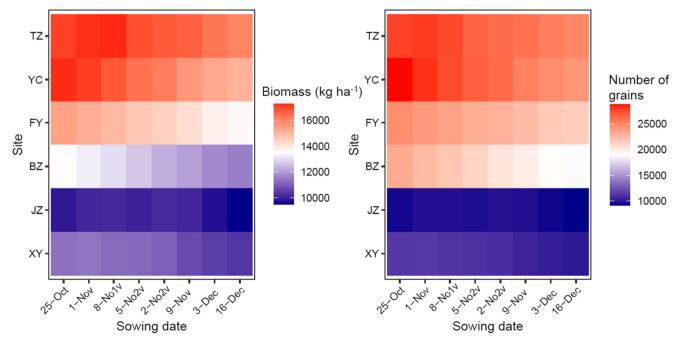


Fig. 6 Left panel: variation in maturity biomass production for reference genotypes across sowing dates and sites (XY: Xiangyang; JZ: Jingzhou; FY: Fuyang; BZ: Bozhou; YC: Yancheng; TZ: Taizhou). Right panel:

simulated biomass for hypothetical genotypes. Values shown are averaged across the 58-year simulations.

although these crops have identical RUE and other yield traits. Further yield improvements are likely to come from more efficient biomass accumulation, while maintaining the current harvest index. Aboveground biomass production in non-stress conditions is mainly determined by RUE. In this case, to further increase yield potential of crops grown in Hubei province, crops need a longer growing season so that they can intercept more IPAR to increase biomass accumulation (Liu et al. 2020c).

In the absence of other stresses, solar radiation has a direct correlation with biomass production (Liu et al. 2020c). Kumagai and Takahashi (2020) reported that late sowing retards canopy development during vegetative and early reproductive growth. These changes may lower radiation interception efficiency and then reducing biomass accumulation. Egli and Bruening (2000) found that latesowing yield reductions are partially explained by the decreases in cumulative intercepted solar radiation around flowering and early pod set. In the present study, cumulative intercepted solar radiation was reduced under late sowing regardless of sites and genotypes (Fig. S2). By using a range of commercial genotypes, we found that yield penalty can be mainly explained by the interactive effects of reduced cumulative radiation interception, less cumulative thermal time and reduced seasonal rainfall due to shortened crop duration.

Indeed, high N input has commonly been considered the reason for the low NUE in China's crop production (IFA 2016). In this study, our focus was on the effects of changing sowing time with different genotypes on wheat yield. Adding N fertilisation levels would complicate and potentially confound our analysis and so was not considered in the present study. However, N management is an important factor in the quest to maximise genetic gains (Guan et al. 2014), which could also lead to higher profitability. Fertilisation using N needs to be evaluated in conjunction with environmental consequences of such high N input, as excessive N is easily leached or lost in gaseous forms, potentially leading to serious environmental problems (Wortman 2016; Christie et al. 2020). Specifically breeding for increased nitrogen-use efficiency (Lammerts van Bueren and Struik, 2017) may also enhance the response of the proposed higher yielding future cultivars.

The soil N status dictated by crop rotations will vary from year to year. This may have implications for subsequent crops (Basso and Martinez-Feria 2019) and add uncertainty to the simulation outputs. To avoid this uncertainty, we simulated wheat crops using the same initial soil N for all years. To evaluate the impact of this assumption, we conducted a sensitivity analysis using three initial N conditions by gauging their relative impact on long-term average yield (Fig. S3). We perturbed initial NO₃ and NH₄ by \pm 30% across sites with three references genotypes sown on 25 Oct during the periods of 1961–2018. For simulated

yield, we found that initial N effects on simulated yield ranged from -18 to 3%; higher sensitivity of initial N effects on simulated yield means there is greater uncertainty in the simulated yields associated with low soil N, and care should be taken with parameterisation. In our study, initial NO₃ was set as 60 kg ha⁻¹, similar to the measured values at our simulated sites (Yang et al. 2021). In addition, we applied 180 kg N ha⁻¹ as the basal fertiliser and 45 kg N ha⁻¹ as the top-dressed fertiliser at ZS31 for all simulations in accordance with local management practices. Given the higher initial soil N in our study, we can justifiably intimate that error propagation implications for yield as a result of initial N are minor.

We have not yet been able to account for waterlogging, which is an important consideration in southern China. We recommend that subsequent studies should investigate how the timing and magnitude of waterlogging stresses will affect wheat yields under climate change. Furthermore, while the simulations are designed to mimic the practiced RW double-cropping system, we did not investigate the combined rice-wheat productivity. Simulating optimum sowing and flowering windows with optimal genotypes for both rice and wheat to cope with climate change should be a focus for future studies.

5 Conclusions

Yield penalties caused by later sowing in this study ranged from 1 to 16% depending on genotype, sowing time and location. Later sowing accelerated development by shortening juvenile and grain filling stages, reducing cumulative intercepted radiation. Together, these factors truncated the vegetative and grain filling periods, reduced biomass production and translocation, reduced grain number and thereby decreased yields. Hypothetical genotypes with higher RUE, longer juvenile phases and greater grain filling rates were more effective in alleviating yield losses with delayed sowing.

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Data availability Simulated data that support the findings of this study are available from the corresponding author upon request.

Code availability The detailed R code for data processing and illustration is available from the corresponding author upon reasonable request.

Declarations

Consent to participate Not applicable

Consent for publication Not applicable

Conflict of interests The authors declare no competing interests.

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