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Climate Change Enhances Stability of Wheat-Flowering-Date

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Abstract

The stability of winter wheat-flowering-date is crucial for ensuring consistent and robust crop performance across diverse climatic conditions. However, the impact of climate change on wheat-flowering-dates remains uncertain. This study aims to elucidate the influence of climate change on wheat-flowering-dates, predict how projected future climate conditions will affect flowering date stability, and identify the most stable wheat genotypes in the study region. We applied a multi-locus genotype-based (MLG-based) model for simulating wheat-flowering-dates, which we calibrated and evaluated using observed data from the Northern China winter wheat region (NCWWR). This MLG-based model was employed to project flowering dates under different climate scenarios. The simulated flowering dates were then used to assess the stability of flowering dates under varying allelic combinations in projected climatic conditions. Our MLG-based model effectively simulated flowering dates, with a root mean square error (RMSE) of 2.3 days, explaining approximately 88.5% of the genotypic variation in flowering dates among 100 wheat genotypes. We found that, in comparison to the baseline climate, wheat-flowering-dates are expected to shift earlier within the target sowing window by approximately 11 and 14 days by 2050 under the Representative Concentration Pathways 4.5 (RCP4.5) and RCP8.5 climate scenarios, respectively. Furthermore, our analysis revealed that wheat-flowering-date stability is likely to be further strengthened under projected climate scenarios due to early flowering trends. Ultimately, we demonstrate that the combination of *Vrn* and *Ppd* genes, rather than individual *Vrn* or *Ppd* genes, plays a critical role in wheat-flowering-date stability. Our results suggest that the combination of *Ppd-D1a* with winter genotypes carrying the *vrn-D1* allele significantly contributes to flowering date stability under current and projected climate scenarios. These findings provide valuable insights for wheat breeders and producers under future climatic conditions.

Key words:

Wheat flowering date stability, Crop modelling, Vernalization, Photoperiod, Climate change

1. Introduction

Global food security is dependent on the development of crops that maintain productive through diverse environments, recurrent stresses, and changing climates. Wheat is a crop of particular importance to our food security since it provides 18% of the world's caloric intake and 19% of the protein (Erenstein et al., 2022). The global expansion of bread wheat (*Triticum aestivum* L.) from the Fertile Crescent in the Middle East to the rest of the globe has been facilitated by the development of varieties whose lifecycles and crop phenology have been adapted to their production environments (Haas et al., 2019). Importantly, genetic variability in flowering date has been one of the main determinants driving wheat adaptation across global agrooecosystems (Bogard et al., 2014; Cockram et al., 2007). During the adaptation process, through selective breeding, a stable match between development (i.e. phenology) and the local environment determines the optimal time when the wheat crop can best utilize agricultural ecosystem resources (Reynolds et al., 2009).

Development of wheat varieties capable of producing mature grain within developmental windows through various climates is a common strategy for maximizing yield and helping plants adapt to seasonal heat, cold and drought stress (Chapman et al., 2012). Flowering date stability, defined as the variation in flowering date over a range of sowing dates and different climate conditions, is a prerequisite (Flohr et al., 2018). Reducing flowering date variability is important for buffering against developmental changes that environmental stresses can introduce over a wide range of sowing dates and temperature regimes (Craufurd and Wheeler, 2009; Kamran et al., 2014). Wheat producers and breeders invest substantial resources to manipulate and optimize flowering date to maximize available climatic resources under current climate conditions (Hills and Li, 2016). However, as ambient temperatures have increased globally in recent decades, mismatches between crop phenology and growing conditions have occurred, especially during extreme weather events, such that crops may no longer be adapted to or optimized for their production environments (Ray et al., 2019). Temperature is a main driver of plant development and the rise in temperature due to climate change has been identified as a key driver of earlier flowering date and crop maturity (Wang et al., 2015).

Wheat adaptability to a wide range of climatic conditions is mainly attributed to the allelic diversity within genes controlling vernalization requirements and photoperiod sensitivity (Kamran et al., 2014). The flowering date of wheat is controlled in large part by the responses of three groups of genes: vernalization [*Vrn*], photoperiod [*Ppd*], and earliness *per se* [*Eps*] (Herndl et al., 2008). Adaptability through different agricultural environments is influenced by (*Vrn*) and (*Ppd*) genes through their interactions with new normal temperature regimes (Distelfeld et al., 2009; Gororo et al., 2001; Zikhali and Griffiths, 2015). Numerous studies have explored the effects of *Vrn* and *Ppd* gene families on the phenological growth stages of wheat in different regions of the world (Gomez et al., 2014; Yan et al., 2004) as well as their responses to climate change (Gouache et al., 2015). Additionally, to elucidate the potential impact of climate change on wheat phenology, several studies have explored changes in plant growth and development under warmer temperatures (Asseng et al., 2015; Craufurd and Wheeler, 2009; Zhao et al., 2016). However, the impact of climate change on flowering date stability in wheat remains unclear. Furthermore, although *Vrn* and *Ppd* genes are associated with plant development, reports linking the two groups of genes to wheat flowering stability are lacking in the literature.

Recent studies have revealed the impact of temperature, sowing dates and varieties on wheat phenology through diverse climates at regional scales using multi-locus genotype (MLG) models (Hu et al., 2022; Hu et al., 2021; Zheng et al., 2013). Multi-locus genotypes (MLGs) define the possible combinations of alleles at multiple genetic loci for individual cultivars or accessions. Quantifying the effects of climate change on the different *Vrn* and *Ppd* MLG combinations will enable a better understanding of flowering date stability through rising temperatures and facilitates the development of wheat varieties with greater phenotypic resilience.

This study aims to investigate the impact of climate change on winter wheat-flowering-dates, projected shifts in flowering date stability under different climate scenarios, and identify key genetic factors influencing flowering date stability. Such findings will enhance our understanding of the allelic variation driving wheat-flowering-date stability and provide knowledge to guide breeding selections and the development of wheat production systems with greater resilience to the sustained effects of global warming.

2. Materials and methods

2.1. Field tests, plant materials, and genotyping

A field test for calibrating and evaluating the MLG-based model was performed from

2016 to 2019 at the Beijing Shunyi Experimental Base (40°15′N, 116°55′E) of the Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences. The field-test location was within the NCWWR, and the field experiment was based on a randomized complete-block design with three replicates. The sowing dates were October 17, October 12, and October 14 for the growing season 2016–2017, 2017–2018, and 2018–2019, respectively. The accumulated temperature from sowing dates to flowering dates varied among growing seasons (1126.9 to 1262.0 °C). The plots were 2 m long with 0.25-m spacing between rows, and seeding was at a depth of 5 cm. The seeds were sown in a single-row plot for each wheat variety. After heading, flowering dates were monitored every other day until data from all plots were recorded. Recommended field-management practices for obtaining high yields of wheat, including fertilization and irrigation, were adopted from previous studies (Li et al., 2005; Zhang et al., 2018). Irrigation was applied three times annually (before the sowing, jointing, and grain-filling stages). Fertilizer was applied prior to sowing and during stem elongation. Additionally, pesticides were applied for pest and disease control. Wheat-flowering-dates were observed and recorded based on 50% flowering of the middle spikelet (Pietragalla, 2012).

A total of 100 adapted wheat varieties, including landrace varieties, commercial varieties, and newly bred varieties collected from the NCWWR, were used to characterize the *Vrn* and *Ppd* genes (Supplementary Table 1). The varieties used formed clusters of diverse genetic backgrounds, each with their own sets of allelic combinations of *Vrn* and *Ppd*, which enabled the development of an MLG-based model and investigation of the responses of genotypes with various allele combinations to climate change scenarios. All plant materials used in this study were provided by The National Key Facility for Crop Gene Resources and Genetic Improvement of the Chinese Academy of Agricultural Sciences.

Genotyping experiments were conducted to detect the dominant and recessive expression of *Ppd* and *Vrn* alleles related to flowering date. Leaf DNA from young seedlings was extracted using the high salt and low pH method (Fu et al., 2005; Yan et al., 2006). The vernalization and photoperiod loci were identified using sequence-tagged sites (STSs). Specifically, the alleles *Vrn-A1*, *Vrn-B1*, *Vrn-B3,* and *Vrn-D1* were determined based on studies by Kiss et al. (2014), Muterko and Salina (2019), and Yan et al. (2006). Similarly, the alleles *Ppd-A1*, *Ppd-B1*, and *Ppd-D1* were identified according to research findings by Nishida et al. (2013) and Würschum et al. (2018). Subsequently, the allelic combinations of Vrns and Ppds in each variety were determined based on these analyses.

2.2.Observed weather data and projected climate data

Daily weather data, encompassing sunshine hours, maximum temperature, minimum temperature, and precipitation, recorded at the Beijing Shunyi Experimental Base (40° 15′N, 116°55′E), spanning the years 2016 to 2019 were gathered from the China Meteorological Data Sharing Services System (CMDSSS) accessible at http://cdc.cma.gov.cn/home.do. This weather data were used for calibrating and evaluating the MLG-based model.

To characterize the broader growing region and provide insights into historical climatic conditions in the Northern China winter wheat region, the distribution of monthly accumulated precipitation and air temperature of growing-season at 16 locations of the Northern China Winter Wheat Region (NCWWR) for the period 1961–2015 was collected.

To estimate flowering date stability under climate change by 2050 (2036–2065) of the 16 locations of the Northern China Winter Wheat Region (NCWWR), an ensemble of five climate models (CanESM2, CCSM4, CSIRO-Mk3-6-0, HadGEM2-ES, MIROC-ESM-CHEM) under two greenhouse gas-emissions scenarios [Representative Concentration Pathways (RCPs): RCP4.5 and RCP8.5) were collected (van Vuuren et al., 2011b).

2.3.Modeling of the wheat-flowering-date

The original phenology model of APSIM-Wheat. The APSIM-Wheat module simulates the wheat growth and development in a daily time-step on an area basis that simulates soil water, residue, nutrient dynamics, and the growth and development of more than 30 crops (v.7.6; http://www.apsim.info) (Holzworth et al., 2015). Briefly, phenological development between sowing and maturity in the APSIM-Wheat model has been divided into eight phases. The commencement of each phase, excluding sowing to germination, is determined by the accumulation of the thermal time (*TT*) (target total required thermal time for a specific phenological development phase). In case of flowering date, the target *TT* from floral initiation to flowering (*TTFI, FL*), which is the minimum *TT* requirement when the vernalization and photoperiod requirement are satisfied. The following equation was used for *TT* calculation in

APSIM-Wheat:

$$TT = \sum(\Delta TT \times \min(Fv, Fp)) \tag{1}$$

where ΔTT is calculated from the daily mean temperature using three cardinal temperatures, including 0 °C (base), 26 °C (optimum), and 34 °C (maximum).

The calculation of total *Vrn* (*V*, dimensionless) accumulated by daily ΔV from daily mean crown temperature (T_c), daily maximum air temperature (T_{max}) and minimum air temperature (T_{min}) with crown temperature being daily mean temperature adjusted by snow depth (Ritchie JT, 1988).

$$\Delta V = min\left\{1.4 - 0.0778T_c, 0.5 + 13.44\frac{13.44T_c}{(T_{max} - T_{min} + 3)^2})\right\}$$

$$\text{when } T_{max} < 30\ °\text{C and } T_{min} < 15\ °\text{C}$$

$$\Delta V = 0, \text{ when } T_{max} \geqslant 30\ °\text{C and } T_{min} \geqslant 15\ °\text{C} \tag{2}$$

In APSIM-Wheat, devernalization (V_d) can occur if daily maximum temperature (T_{max}) is above 30 °C and the total *Vrn* (*V*) is less than 10.

$$\Delta V_d = \min(0.5 \times (T_{max} - 30), V \text{ when } T_{max} > 30\ °\text{C and } V < 10 \tag{3}$$

The total *Vrn* (*V*) is calculated by summing daily vernalization and devernalization from emergence to floral initiation.

$$V = \sum(\Delta V - \Delta V_d) \tag{4}$$

The *Vrn* factor (F_v) is calculated from plant emergence to floral initiation and updated daily (Sadras and Monzon, 2006; Zheng et al., 2013).

$$F_v = 1 - (0.0054545 \times R_v + 0.0003) \times (50 - V) \tag{5}$$

where Rv is the sensitivity to vernalization (Zheng et al., 2013). The calculation of total *Vrn* (*V*) accumulated by daily ΔV has been described previously (Zheng et al., 2013).

The *Ppd* factor (F_p) is calculated from plant emergence to flowering and updated daily as follows:

$$F_p = 1 - 0.002 \times R_p \times (20 - L_p)^2 \quad (6)$$

where L_P is the day length plus civil twilight (h) (i.e., the center of the Sun's disc is 6° below the horizon), and R_P is the sensitivity to photoperiod (Zheng et al., 2013).

A modified APSIM-Wheat phenology model (APSIM-Wheat-M). The original APSIM-Wheat phenology model considers only the maximum effect of either vernalization or photoperiod on the accumulation of daily *TT*. However, studies have shown that the observed interactions between vernalization and photoperiod effects could be better accommodated by a multiplicative function, e.g. ARCWHEAT 1 (Weir et al., 1984) and Sirius (Jamieson et al., 1998). Moreover, a physiological study suggested that the developmental rate of wheat is sensitive to photoperiod until flowering (Slafer and Rawson, 1994). Therefore, the APSIM-Wheat phenology model used in our study was changed by: 1) extending photoperiod effects until flowering date, and 2) changing interactions of vernalization and photoperiod from minimum to multiplication (Zheng et al., 2013). The description of the approach used to simulate wheat phenology in APSIM-Wheat-M has been described previously (Hu et al., 2021; Sadras and Monzon, 2006; Zheng et al., 2013). In APSIM-Wheat-M, the *TT* was calculated as follows:

$$TT = \sum(\Delta TT \times Fv \times Fp) \quad (7)$$

A gene-based model of APSIM-Wheat (MLG-based). The MLG-based phenology modules were developed based on the wheat varieties in the NCWWR environments and integrated into the APSIM-Wheat-M model. Some studies have shown different effects among *Vrn* and *Ppd* genes and these effects were allowed to vary in magnitude via a weighting function (Allard et al., 2012; Eagles et al., 2010; González et al., 2005; Loukoianov et al., 2005). Therefore, a multiplicative function has been used to accommodate observed interactions between vernalization and photoperiod effects in some crop models (Jamieson et al., 1998; Weir et al., 1984). Considering there were no polymorphisms identified in the *Vrn-A1*, *Vrn-B3*, or *Ppd-B1* loci, and the *Vrn-B1* locus harbored polymorphism in only one variety, the *Vrn* and *Ppd* genes, *Vrn-D1*, *Ppd-A1*, and *Ppd-D1*, were used to link the physiological processes of vernalization and photoperiod in the modified APSIM-Wheat phenology model (APSIM-Wheat-M). The difference between the APSIM-Wheat-M model and the MLG-based model is that the *Vrn* (R_v) and *Ppd* (R_p) sensitivities [Eqs. (5) and (6)] are related to the number of sensitive alleles of the *Vrn* and *Ppd* genes. Linear functions (weighting functions) were used to simulate the contribution of each *Vrn* locus on vernalization sensitivity and also the effect of *Vrn* locus on photoperiod requirement of target processes:

$$R_v = k_v N_v + b_v \tag{8}$$

$$R_p = k_p N_p + b_p \tag{9}$$

where k_v and k_p are the slopes of varieties for *Vrn* and *Ppd*, respectively, and b_v and b_p are the intercepts of the varieties indicating the unknown effects of the *Vrn* and *Ppd* genes, respectively.

The total weighted numbers of N_v and N_p genes in Eqs. (8) and (9) were calculated by weighting and summing the genotype values of 0 or 1 at each of the *Vrn* and *Ppd* loci:

$$N_v = h_{vd} \times Vrn\text{-}D1 \quad (10)$$

$$N_p = Ppd\text{-}D1 \times Vrn\text{-}D1 \times h_{pd} + Ppd\text{-}A1 \times Vrn\text{-}D1 \times hpa \quad (11)$$

where h_{vd} is the weight of the effect at the *Vrn-D1* locus on vernalization sensitivity, and h_{pd} and *hpa* are the weighted *Vrn* effects on photoperiod requirement. The effects were estimated through removal of vernalization or photoperiod effects based on a previous experiment[33]. The *Ppd* and *Vrn* alleles are represented as zero for spring/insensitive allele and one for winter/sensitive allele. The new parameters in the linear response are estimated using global optimization[33].

2.4. Calibrating and evaluating the MLG-based model

A comprehensive explanation of the MLG-based ecophysiological model can be found in the supplemental material's section on "Modeling the Wheat-Flowering Date". The final MLG-based model included the four gene-specific parameters (k_v, k_p, b_v, and b_p) and one variety-specific parameter ($TT_{FI,\ FL}$). These parameters were fitted simultaneously for all varieties. We generated exhaustive combinations of these parameters across a wide range (from 0 to 3 for k_v, k_p, b_v, and b_p at 0.01 intervals; from 300 to 1300 degree days (°Cd) for $TT_{FI,\ FL}$ at 5 °Cd intervals), and then calculate variety-specific parameters based on gene-specific parameters obtained in our previous study (Zheng et al., 2013) and genotyping information for each variety. These parameter combinations were then used to run simulations to get corresponding wheat-flowering-dates in the calibration year (2016–2018). The final variety-specific allele combinations are shown in Supplementary Table 2. Values were selected according to the minimum

RMSE between the observed and predicted wheat-flowering-dates, and the optimization process is conducted for all varieties. Finally, the performance of MLG-based model was evaluated using an independent dataset from the third growing season (2018–2019, 100 observations including eight missing values). A program was developed in R (v.3.6.2; http://www.R-project.org/) to run the entire phenology algorithm from APSIM-Wheat using customized R scripts implemented across a high-performance computing platform.

Accurate simulation of flowering date using a gene-based model has been accomplished for bean using both varieties and recombinant inbred lines (RILs) (Oliveira et al., 2021) suggesting that dynamic crop simulation models can be transformed into gene-based models by replacing an existing process module with a gene-based module for simulating the same process. In the present study, we link crop genetic architecture to flowering date based on an MLG-based ecophysiological model (Hu et al., 2021). Calibration using variety-specific parameters based on only two years of data may result in multiple plausible model configurations that unreasonably fit observed outcomes, which is known as “equifinality” (Williams et al., 2020). The variety-specific parameters of the MLG-based model was calibrated using the gene-specific parameters. For the MLG-based model calibration, 200 observations (including 16 missing values) were used to estimate 104 parameters and these parameters were fit simultaneously for 100 varieties in one step. Although use of more observations would provide more robust parameter estimation, the calibration process of an MLG-based model facilitates the use of a smaller number of observations, which is one of the major benefits to use an MLG-based method to simulate wheat phenology. The results highlight a notable advancement in our model, which accurately simulated flowering dates. This improvement distinguishes our approach from previous models that simulated wheat-flowering-date without incorporating genetic information (Boote et al., 2001; Wang and Engel, 1998).

2.5. Calculation of stability index of wheat-flowering-date

To assess the impact of climate change on wheat-flowering-date stability, we hypothesized that applying an MLG-based ecophysiological model under projected climate change scenarios would aid investigations on the responses of flowering date stability to allelic combinations more than a matching allele model. The stability index of the flowering dates was calculated based on the predicted flowering dates under a suitable range of sowing dates under different climate scenarios. Here, early sowing dates were set to a range between September 21 and September 29, and the late sowing date was set to October 21. Thus, the sowing date window was 30 days, which is slightly wider than the typical agronomic boundary (i.e., September 25 to October 15). Based on the flowering dates simulated with the described sowing window, the flowering date stability index at year I ($S(i)$) for each location in the NCWWR was calculated as 1 minus the ratio of the thermal-time range for flowering date for each variety ($Fl_{end}(i) - Fl_{start}(i)$) to the thermal-time range for sowing dates for each year ($Sow_{end} - Sow_{start}$).

$$S(i) = 1 - \frac{Fl_{end}(i) - Fl_{start}(i)}{Sow_{end} - Sow_{start}} \tag{12}$$

2.6. Calculation of broad sense heritability

The field-observed flowering date of wheat for calibrating and evaluating the MLG-based model (2016-2019 growing season) at the Beijing Shunyi Experimental Base (40°15′N, 116°55′E) was used to calculate broad sense heritability (H^2). Heritability (H^2) of wheat-flowering-date variance and mean of each MLG was estimated using the repeated measures with variety as a fixed effect using ANOVA. The broad sense heritability was estimated as the ratio of the sum of the additive and epistatic (additive-by-additive) variance to the total phenotypic variance (Jia et al., 2013):

$$H^2 = \frac{V_g}{V_g + V_{gs/s} + V_{gs/s} * V_{e/sr}}$$

(13)

where V_g is the genotypicvariance, V_{gs} is the interactive variance between variety and growing season, V_e is the residual variance, s is the number of growing seasons, and r is the number of replications.

2.7. Statistical analysis

We describe the relationship between stability of the wheat flowering with MLG, climate scenario, location, and their interaction with a linear mixed model (LMM):

$$y = X\beta + Zu + \ \varepsilon,\ u \backsim \ N_q(0, G),\ \varepsilon \ \backsim \ N_n(0, R)$$

(14)

where y is the n×1 response vector, n is the number of observations, β is a p×1 fixed-effects vector, u is the random-effects, X is the $n \times p$ design matrix for the fixed-effects parameters, and Z is the $n \times q$ design matrix for the random-effects, u and ε are independent and $R = \sigma^2 I$. The R package lme4 (Bates et al., 2015) in R version 3.6.2 for Windows (Team, 2020) was used to estimate the stability of the wheat-flowering-date for each MLG, climate scenario, location, and their interaction (fixed effect), whereas the other components (i.e., year and interaction between year and location) were considered random effects. The statistical assumptions of normal distribution and variance homogeneity for the linear mixed models (LMM) were visually checked by inspecting the residual plots. Additionally, the variance components from the LMM were assessed separately to ensure model validity (Kuznetsova et al., 2017). The Type III ANOVA with Satterthwaite's method was used to assess the fixed effects (package lmeTest), and pairwise comparisons were conducted using a Tukey adjustment (function emmeans in package emmeans (Lenth, 2019)). Statistical assumptions (normal distribution and variance homogeneity) for the LMMs were visually checked by inspecting the residual plots.

3. Results

3.1. The Northern China Winter Wheat Region (NCWWR) and Climate Change

The study was conducted in the Northern China winter wheat region (NCWWR), which is located at the northern edge of the autumn sown wheat area (Figure 1a). The area includes Beijing, Tianjin, north central Hebei, southeastern and central Shanxi, northern Shaanxi, and eastern Gansu, which together accounts for ~9% of the total wheat area in China (Li et al., 2019). Climatically, there is a large temperature difference between winter and summer and the precipitation falls mainly in sowing and grain-filling phases. The average temperature and solar radiation during the growing season are 6.5 °C and 12.9 MJ/m^2/day, respectively (Tao et al., 2014). Figure 1b shows the annual average temperature at 16 locations of NCWWR for the 1961–2015 period. Despite variation from year to year, there has been a rapid increase in the average temperature during this period demonstrating that the climate has undergone an overall warming trend in the region. Figure 2 and Figure 3 show the distribution of monthly air temperature and accumulated precipitation of the growing season at the 16 locations of NCWWR for the 1961–2015 period. Overall, there is a large temperature difference between winter and summer and the precipitation mainly occurs during the sowing and grain-filling phases. Winter killing of seedlings (December, January, and February) and high temperature during grain filling (April, May, and June) are major problems (Figure 4) that often cause severe reductions in grain yield (Li et al., 2019). For the preceding climate scenarios, the average temperature of wheat growing season under baseline (1981–2010) and Representative Concentration Pathways 4.5 (RCP4.5) and RCP8.5 scenarios (2036–2065) is 9.3°C, 11.7°C, and 12.6°C, respectively (Figure 1a).

3.2.Multi-locus genotypes (MLGs) of 100 wheat varieties at key Ppd and Vrn genes

To begin our assessment of climate change on wheat flowering, we genotyped a panel of 100 adapted wheat varieties at seven key *Ppd* and *Vrn* genes. The wheat diversity panel includes landrace varieties, commercial varieties, and newly bred varieties, collected from the NCWWR, which require high levels of winter hardiness when sown before winter. Twenty-four landraces, which represent a valuable source of genetic diversity and are specifically adapted to local environmental conditions, were included in our wheat panel. The varieties were clustered into seven possible homozygous MLGs for the three genes in our datasets (*Vrn-D1*, *Ppd-A1*, and *Ppd-D1*; Fig ure 1c). Most varieties were in two MLGs: 58 varieties with *Ppd-A1b+Ppd-D1a+vrn-D1* and 20 for

Ppd-A1b+Ppd-D1b+vrn-D1 (Figure 1c). Within the diversity panel, we were able to identify seven MLGs at multiple *Vrn* and *Ppd* loci. No polymorphisms were identified in the *Vrn-A1*, *Vrn-B3*, or *Ppd-B1* alleles, and allele *Vrn-B1* harbored a polymorphism in only one variety. Therefore, we focused on *Vrn-D1*, *Ppd-A1*, and *Ppd-D1* for our analyses of flowering date stability (Supplementary Table 1). The landraces, primarily containing MLG A4B2 and A3B2 (Figure 1c), were released or distributed before 1950. (Figure 1c). A3B1 and A3B2 MLGs, which harbor the *Ppd*-insensitive allele (*Ppd-D1a*), were dominant in varieties released during and after the 1960s (Figure 1c), indicating that selection in the NCWWR winter wheat breeding programs has favored selection for the *Ppd*-insensitive allele at the major *Ppd-D1* loci, as photoperiod-insensitive genes shape the phenological cycles of vegetative and reproductive growth, thus improving the relationship between sink and source tissues (Pérez Gianmarco et al., 2018).

3.3. Simulation of wheat-flowering-date to generate stability indices under projected climate conditions

To simulate wheat-flowering-date for different allele combinations of *Vrn* (*Vrn-D1*) and *Ppd* (*Ppd-A1*, and *Ppd-D1*) genes under projected climate scenarios, we applied an MLG-based ecophysiological model in the Agricultural Production Systems sIMulator (APSIM) framework (Holzworth et al., 2015). The model incorporates gene allele combinations of *Vrn* and *Ppd* with the physiological processes of vernalization and photoperiod as described in the modified phenology model of APSIM-Wheat (APSIM-Wheat-M) (Zheng et al., 2013). We assumed that all the varieties have the same cardinal temperatures in the present study, while acknowledging that the cardinal temperatures, including the base temperature, optimal temperature, and maximum temperature, may vary across wheat varieties and phenological stages (Porter and Gawith, 1999). This set of cardinal temperatures has been applied to predict wheat phenological stages across wheat environments globally (Hu et al., 2021). The details of the MLG-based ecophysiological model we applied can be found in the Methods. Using both the calibration and validation datasets, the wheat-flowering-date of each genotype was fitted using the MLG-based ecophysiological model.

Overall, there was close agreement (root mean square error [RMSE] = 1.6 days; $y = 0.95x + 11.0$, $R^2 = 0.939$, $p < 0.001$, $N = 184$) between the simulated and observed flowering dates for the calibration dataset based on the 2016–2017 and 2017–2018 growing season at Beijing Shunyi Experimental Base (Figure 5a). Additionally, we compared flowering dates simulated by optimized parameter values with observed flowering dates to evaluate data with an RMSE of 2.3 days ($y = 1.01x - 3.75$, $R^2 = 0.885$, $p < 0.001$, $N = 92$) based on the 2018–2019 growing season at Beijing Shunyi Experimental Base (Figure 5b). All simulations showed close agreement with the observed results, with only a slight deviation from the expected 1:1 relationship (Figure 5).

We then used MLG-based model to predict winter wheat-flowering-date using downscaled climate models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Lobell et al., 2015). To ensure comprehensive coverage of future temperature and rainfall regimes in our study area, we selected five core CMIP5 models (CanESM2, CCSM4, CSIRO-Mk3-6-0, HadGEM2-ES, MIROC-ESM-CHEM) that have demonstrated strong performance for both temperature and precipitation (Wang and Chen, 2014). We considered two greenhouse gas-emissions scenarios, RCP4.5 and RCP8.5 (Van Vuuren et al., 2011a), and used the MLG-based model to predict wheat-flowering-date for each of the 16 locations in the NCWWR under baseline conditions (1981–2010) and future climate scenarios to 2050 (2036–2065). The increases in mean temperatures for vernalization and photoperiod phases are close to the seasonal increases and higher than those of flowering phases (Figure 6). Field-management practices (e.g. irrigation and fertilization) were set as non-water and non-nutrient stress conditions for both the baseline and projected climate conditions, since this research focused on wheat-flowering-date (Hu et al., 2021).

The simulated results predicted flowering dates in response to climate change under different sowing dates. Early sowing dates ranged from September 21st to September 29th (Julian calendar dates of 248 to 272, respectively) and the late sowing date was set as October 21. The model projected average flowering dates for both early and late sowing dates under RCP4.5 and RCP8.5 that were about 11 and 15 days earlier than those under the baseline climate, respectively (Figure 7a). Notably, although the flowering dates differed among climate scenarios, the A1B2, A3B1, and A3B2 were the earliest MLGs under each scenario driven by *Ppd-D1a*. *Ppd-D1a* (except for MLG A1B1) was associated with early flowering in combined analyses across climate scenarios, regardless of MLGs carrying *Vrn-D1* or *vrn-D1* alleles for both early (Figure 7b) and late sowing (e.g., MLGs A1B2 and A3B1) (Figure 7c). *Ppd-D1b* exhibited late flowering, regardless of whether the MLGs carried *Vrn-D1* or *vrn-D1* alleles, excluding the A4B1 allele combination. Under early sowing, the flowering date of allele combinations A1B1 and A4B1 did not differ significantly, whereas they differed significantly if sowing occurred one-month later (Figure 7b and Figure 7c). Even though 14 varieties had *Vrn-D1* (MLG A1B1, A3B1, A4B1), which is dominant over the allele *vrn-D1*, each variety had the recessive *vrn-A1*, *vrn-B1* and *vrn-B3* alleles, and behaved as a winter wheat and not a spring wheat. There also might be other genes within the various genetic backgrounds that result in a winter growth habit, contrary to expectation (Zhang et al., 2008).

The wheat-flowering-date stability is poised to be further reinforced under the projected climate. A higher stability index indicated less change in flowering date for a large range of sowing dates and climate conditions (Flohr et al., 2018). The mean stability indices across the NCWWR including all MLGs were 0.744 (±0.089) for baseline, 0.783 (±0.089) for RCP4.5, and 0.791 (±0.088) for the RCP8.5 climate scenarios. Thus, the ranking of the stability index with increasing ambient temperature was as follows: baseline < RCP4.5 < RCP8.5 (Figure 8a). The baseline scenario showed lower and wider ranges for stability than those in the RCP4.5 and RCP8.5 scenarios, indicating that climate change could be favorable for wheat-flowering-date stability.

3.4. Effect of climate change, MLG, and location on flowering date stability

While MLG-based model simulation showed that the stability index of wheat flowering dates was influenced by MLG, climate change scenarios, and location, we were able to quantify their individual and interactive effects through a generalized linear mixed-effects (GLM) model on the MLG-based simulation results. In light of the diverse range of seven Multi-Locus Genotypes (MLGs) observed among the 100 varieties (Figure 1c), spanning 16 locations and three climate scenarios averaged from five climate models, our analysis of variance for simulated results revealed a notable impact of MLG. Specifically, the MLG factor, contributed 73.4% of the variance ($p < 0.05$, Figure 8b).. Climate scenario also contributed a large component of the variance at 20.5%. The GLM model demonstrated that scenario × location, MLG × location, and scenario × MLG interaction effects were significant ($p < 0.001$), indicating that the projected climate at each location influenced the stability index (Table 1). The significant MLG × scenario interaction effect suggested that the genotypes responded differently to climate (Table 1). Additionally, scenario × location interaction effects were greater than location effects. The best explanation for this is that all locations are located within a similar climatological zone in the NCWWR and highlights the importance of analysis in flowering date stability across different combinations of climates and locations. By contrast, the observation that scenario × MLG × location interaction effects were not significant suggested that the stability index was apparently more strongly a function of MLG and climate than location. This observation is intuitive given the similarity in climatological zone across the study locations.

The MLGs with high flowering date stability under baseline climate were also stable under projected climates and, stability maintained the same order through the climate scenarios. For example, MLGs A1B2, A4B1, and A3B1 were consistently more stable than other MLGs under both the baseline and projected climates ($p<0.05$, Figure 8c), with two of the three MLGs carrying the *Ppd-D1a* gene. Furthermore, the only difference between MLG A3B2 and unstable MLG A4B2 is the *Ppd-D1* locus, further demonstrating the importance of *Ppd-D1a* for wheat-flowering-date stability. Notably, the MLGs including fully early flowering allelic combinations (A1B1) or late flowering allelic combinations (A4B2) with *Vrn* and *Ppd* alleles were unstable across all climate scenarios, whereas allelic combinations with both flowering hastening and late flowering allelic combinations (e.g., A1B2 and A4B1) were more stable MLGs. The long tail on A4B2 also indicates strong variation due to its unstable response to climate variation. Comparison of A1B2 and A1B1 indicated that *vrn-D1* is important for wheat-flowering-date stability when *Ppd* harbors the insensitive alleles *Ppd-D1a* and *Ppd-A1a*.

In comparing flowering date stability to actual flowering dates, the results indicated that MLGs promoting early flowering date also tended to be the MLGs with the high-stability under all climate scenarios. Conversely, MLGs which promoted late flowering such as A1B1, A4B2, and A2B2 tended to have the lowest flowering date stability. Overall, the fact that early flowering MLGs maintain high-stability through climate change scenarios within the NCWWR region is an important result relevant for future breeding activities. However, also important is the finding that A4B1, with *Ppd-A1b*, *Ppd-B1b*, and *Ppd-D1b*, which was within the late flowering group had the second highest stability across the baseline and projected climates – thus, stability is not strictly associated with early flowering.

5. Discussion

We provide a robust assessment to benchmark the effect of climate change on flowering date stability of wheat based on an MLG-based model modeling approach.

As illustrated in our present study, flowering date stability is not always consistent with the flowering date of wheat among MLGs, hence the importance of focusing on stability. While the variation in climate for the calibration dataset used to develop the crop model is smaller than the variation expected under future climate change scenarios, the model can still provide useful insights into how crops might respond to these changes.. This is because crop models are designed to capture the fundamental processes that govern crop growth and development, and can extrapolate beyond the range of environmental conditions observed in the calibration dataset (Jagermeyr et al., 2021). Moreover, quantifying the responses of flowering date stability to climate change has great potential to provide guidelines for the development of phenotypically resilient wheat varieties. The results of the present study suggest that wheat-flowering-date stability is poised to be further reinforced under the projected climate scenarios due to early flowering trends.

Comparisons with baseline climate data revealed that the simulated flowering date under the early sowing window shifted to earlier flowering dates across the NCWWR at an average of 11 days and 14 days sooner for the RCP4.5 and RCP8.5 climate scenarios, by 2050. Thus, in the present study, warmer temperatures were direct contributors to accelerating inflorescence development during early wheat reproductive stages (Craufurd and Wheeler, 2009; Dixon et al., 2018). However, it should be noted that there may also be delays in flowering associated with temperature increases through longer requirements for vernalization (Dixon et al., 2018). The insensitive alleles of *Ppd* genes reportedly have a dominant effect on the nature of accelerated flowering (Gororo et al., 2001). Similar results were observed in our simulated results, where flowering date varied among MLGs carrying *Ppd-A1/D1* allele(s). Although we focused on the simulation of flowering date based on MLGs, the present study also demonstrated the effects of the alleles of each gene and their interactions. The MLGs with photoperiod-insensitive alleles resulted in earlier flowering as compared with photoperiod-sensitive MLGs, which is consistent with results from other studies on winter wheat (Grogan et al., 2016; Worland, 1996).

Key genes controlling the developmental transition to flowering in wheat include *Vrn* and *Ppd* genes and their interactions with temperature during growth (Gororo et al., 2001; Herndl et al., 2008) may not directly link to wheat flowering stability. Allelic combinations of *Ppd* and *Vrn* reportedly result in variations in flowering dates (Cane et al., 2013). However, to date, no study has shown that these are related to wheat-flowering-date stability. Additionally, *Ppd*- and *Vrn*-response genes hasten or delay flowering in response to climate, which also affects wheat-flowering-date stability (Law and Worland, 1997). Therefore, the selection of known allelic combinations and the assessment of their stability in response to projected climate change are crucial for the comprehensive understanding of plant adaptability to future climates in target environments. Although A1B2, A4B1, and A3B1 are among the most stable MLGs under current and projected climates, they achieve the similarity by different means. For example, MLG A1B2 carries photoperiod-insensitive genes (*Ppd-A1a* and *Ppd-D1a*), whereas A4B1 carries photoperiod-sensitive genes (*Ppd-A1b* and *Ppd-D1b*). This is consistent with several studies showing that allelic combinations of *Vrn* and *Ppd* allow for the fine-tuning of phenological events before flowering, without substantial changes to flowering date (Whitechurch et al., 2007). Comparison of the two early flowering and stable MLGs (A1B2 and A3B2) suggests that the *Ppd-A1* locus had a marginal effect on flowering date stability in the presence of the alleles *Ppd-D1a* and *vrn-D1*. Moreover, comparison of the high-stability MLG A3B1 with the low-stability MLG A1B1 revealed that the *Ppd-A1a* allele played an important role in flowering date stability in the presence of the *Vrn-D1* allele. However, this result is tempered by the limited sample size, with only one genotype in A1B1 and seven genotypes in A3B1.

Our results indicate that the allelic combinations of *Vrn* and *Ppd* genes determine wheat-flowering-date stability. For example, MLGs carrying either insensitive (e.g., A1B2 *Ppd-A1a* + *PpD1a*)) or sensitive (e.g., A4B1 *Ppd-A1b* + *Ppd-D1b*) alleles can achieve stability. However, compared to A1B1 and A4B2, MLG A1B2 is more suitable for breeding improved varieties under the projected climate scenarios, not only because of their ability to adapt to a broader environmental range but also because wheat varieties that carry the important photoperiod-insensitive gene *Ppd-D1a* show a prolonged duration of the spike growth period. The prolonged duration of spike growth results in heavier spikes with a larger number of fertile florets, with greater grain number and higher yield (Gonzalez et al., 2011), possibly via increased cumulative spike assimilation (Ghiglione et al., 2008). However, ensuring the highest confidence in recommendations to wheat breeders regarding the optimal allelic combinations of the *Vrn, Ppd*, and *Eps* genes requires further research involving a wider range of genotypes and other factors. For example, although A4B1 is stable MLG under current and projected climates, it only has moderate broad sense heritability (H^2) for wheat-flowering-date (Supplementary Table 3).

In conclusion, the dataset developed from an MLG-based model simulation output allowed us to account for the effects of gene allele combinations, climate, and location, along with their interactions, and facilitates the identification of the most stable genotypes under current and projected climates in the study location. Our findings highlight the potential of introducing allelic combinations of the winter allele *vrn-D1* and photoperiod-insensitive genes (*Ppd-D1a*) into currently cultivated varieties to achieve a more stable flowering date in the NCWWR, especially under future climate change. Furthermore, by linking crop genetic architecture to wheat-flowering-date in our MLG-based physiological model, this study provides novel and useful insights into the responses of allelic combinations of *Vrn* and *Ppd* genes to climate change that could expedite the development of wheat varieties with high stability under increasingly warmer climates. The results and methods presented in this study have implications beyond the NCWWR, considering warming trends across the major wheat producing regions including countries that have similar (or higher) trends of increasing temperatures (Asseng et al., 2015).

6. Limitations of Study

We acknowledge certain limitations in our study. Firstly, we did not consider the potential impacts of extreme weather events, such as drought or storm damage before flowering. Moreover, we assumed that the increased ambient CO_2 concentrations do not influence wheat phenological development (Moot et al., 1996). However, recent study indicate that increased ambient CO_2 concentrations accelerated phenology and resulted in early flowering of wheat (Padhan et al., 2020). Therefore, future modelling approaches should be improved by considering these factors. Consequently, it is imperative that future modeling approaches incorporate these factors to provide a more comprehensive understanding of the system.

The present MLG-based eco-physiological model could be improved further to include up-to-date knowledge of wheat physiology that takes into account genetic variation in base (cardinal) temperature and optimal temperatures for vernalization. Our study revealed no obvious difference of simulated thermal time or flowering date when we introduced hourly temperature into crop growth model for the environment (Figure 9). However, to capture the subtle varietal differences through diverse environments, it might be necessary to explore growth models with other temperature response functions (e.g., Linear, Triangular, Bilinear, Sin, Bell-shaped, non-linear, or Trapezoidal functions). Furthermore, considering wheat yield in simulations could provide more robust guidance for adaptive breeding. However, incorporating this factor would involve a more complex process and require a more comprehensive calibration dataset, including temperature, precipitation, and other climatic factors which play a pivotal role in shaping the ultimate impact on grain yield. his could be investigated in future research when MLG-based models can accommodate a larger number of genes.

Additionally, our genetic analysis revealed no polymorphisms in the *Vrn-A1*, *Vrn-B3*, or *Ppd-B1* alleles, and the presence of a polymorphism in the Vrn-B1 allele was observed in only one variety. Given these outcomes, we focused our analyses of flowering date stability on the *Vrn-D1*, *Ppd-A1*, and *Ppd-D1* alleles, as documented in Supplementary Table 1. It is noteworthy that the earliness *per se* [*Eps*] was not taken into account in our present MLG-based eco-physiological model. These limitations underscore the need for further research and refinement of our modeling approach to encompass a broader range of genetic and environmental factors, ultimately enhancing the accuracy and applicability of our findings.

A noteworthy limitation of our study is the uniformity of sowing dates across the three years of experimentation. Furthermore, while we investigate the impact of warming under climate conditions, it is important to note that our experiment lacks a specific warming treatment. Our study underscores the significance of future research initiatives aimed at examining the influence of diverse sowing dates and simulated warming conditions on winter wheat-flowering-dates. These experiments are essential for generating crucial data to validate and enhance the insights derived from our modeling approach. They will also facilitate a nuanced exploration of the interactions between climatic variables and wheat genotypes under varying climate scenarios.

Declaration of Interests

The authors do not declare any competing interests.

Materials Availability

This study did not generate new unique reagents

Data And Code Availability

The field phenotyping data and genotyping information will be shared by the lead contact upon request. Any other additional data can be provided for reanalysis if requested from the lead contact. The *R* code used for the main analysis in current study is available from the lead contact on reasonable request.

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