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Crop Science

ORIGINAL RESEARCH ARTICLE

Crop Breeding & Genetics

Genomic selection of forage agronomic traits in winter wheat

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Abstract

Genomic selection (GS) can improve genetic gain of complex traits in plant breeding. Phenotyping agronomic traits of winter wheat (*Triticum aestivum* L.) for dual-purpose use is expensive and time-consuming. In this study, we compared the prediction accuracies of four GS models (RR-BLUP, GBLUP, GAUSS, and BL) for forage yield (FY), plant height (PH) and heading date (HD) of the hard winter wheat diversity panel ($n = 298$) using random and stratified sampling methods. In addition, we determined the appropriate training population (TP) size and marker density for GS of the traits. Moderate to high prediction accuracies ranging from 0.66 to 0.69 for FY, 0.46 to 0.49 for PH, and 0.71 to 0.74 for HD were observed for the GS models. However, the sampling method had little or no impact on prediction accuracy. The RR-BLUP, GBLUP, and GAUSS models produced slightly greater prediction accuracies than BL for all traits studied. Prediction accuracies increased with increasing TP size and marker density in all the GS models tested. However, increase of prediction accuracy started to plateau at $n_{TP} = 180$ lines and 1,000; 1,500; or 3,000 SNPs suggesting that the minimum TP size and marker density were about 180 lines and 1,000 or more SNPs, depending on the model and trait. The impact of TP size on prediction accuracy was greater for RR-BLUP, GAUSS, and GBLUP than for BL model. This study suggests that RR-BLUP, GBLUP, and GAUSS are viable models for selecting the forage agronomic traits during dual-purpose wheat breeding.

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1 | INTRODUCTION

Winter wheat (*Triticum aestivum* L.) is an important cereal crop grown worldwide. In the southern Great Plains of the United States, winter wheat is the largest crop not only grown for grain, but also for cattle grazing during the autumn and winter seasons when other forage species are dormant or not productive due to cold temperatures (Hossain, Epplin, & Krenzer, 2003; Kim et al., 2016; MacKown, Carver, & Edwards, 2011). When winter wheat is grazed over winter, it is often managed as a dual-purpose crop in which grain is harvested by the end of the season (Maulana, Anderson, Butler, & Ma, 2019a). Although phenotyping forage and other agronomic traits during wheat breeding has been accomplished by using phenotypic selection (PS) over the years, our experience has shown that conventional PS is expensive, tedious, and time consuming. In general, phenotyping forage traits, such as forage yield, is done by growing plant materials in replicated field trials in multiple environments, and then forage samples are manually harvested, dried, and weighed to estimate biomass yield. This phenotypic selection method is a costly activity. Therefore, an efficient selection method is needed during dual-purpose wheat breeding.

Genomic selection (GS) has been shown to be a promising complementary approach to traditional marker-assisted selection (MAS) and conventional PS. Marker-assisted selection is effective for selecting qualitative traits that are governed by major genes, however, most important agronomic traits are polygenic in nature, thus, they are controlled by minor genes with small effects spanning across the genome (Kumar et al., 2019; Riedelsheimer et al., 2012). In general, only the most significant markers explaining large trait phenotypic variance are used with MAS; and as a result, only a small portion of the genetic variance accounting for a complex trait can be captured (Bernardo, 2010). In contrast, with GS genome-wide markers, irrespective of their effects on the phenotype, are included in the prediction model for accuracy prediction (Goddard, 2009). Genomic selection is more effective for complex traits controlled by genes with minor effects that cumulatively contribute to the phenotypic expression of the trait, such as grain yield (Crossa et al., 2010; González-Camacho et al., 2012; Jannink, Lorenz, & Iwata, 2010).

In GS, a training population (TP), composed of lines with both marker and phenotypic information, is used to train the prediction model, which is then used to calculate genomic estimated breeding values (GEBVs) of the selection candidates that have only been genotyped (Meuwissen, Hayes, & Goddard, 2001). In this regard, selection of high-performing individuals is done solely based on GEBVs and the selected individuals are advanced to the next selection cycle, making it less expensive than extensive field phenotyping of a large number of lines, most of which will not be selected in future generations. The prediction accuracy is calculated

Core Ideas

- Genomic selection models were compared for forage agronomic traits of winter wheat.
- Prediction accuracies were estimated by varying TP sizes and marker densities.
- Moderate accuracies were observed for models trained with limited phenotypic data.

based on the correlation between the predicted phenotypic value (GEBV) and the observed phenotypic value (also known as phenotypically estimated breeding value, PEBV).

Studies conducted in the past have shown that GS can complement the conventional PS method (Bernardo & Yu, 2007; Heffner, Sorrells, & Jannink, 2009; Jannink et al., 2010). As a result, GS has attracted attention in both animal and plant breeding programs in recent years because of its potential of increasing genetic gain over time (Beyene et al., 2015; Lorenz & Smith, 2015; Massman, Jung, & Bernardo, 2013; Poland et al., 2012). For example, a previous study done in maize (*Zea mays* L.) showed increased genetic gain for stover yield with GS compared to MAS (Massman et al., 2013). Genomic selection can also increase selection accuracy, reduce phenotyping costs during complex-trait evaluation, and speed up the development of new cultivars (Heffner et al., 2009; Heffner, Lorenz, Jannink, & Sorrells, 2010). In addition, GS can be applied at an early stage of crop growth, or when phenotyping is not feasible, resulting in reduced duration of selection (Rutkoski, Poland, Jannink, & Sorrells, 2013). To date, GS studies have been conducted in a number of crops, such as wheat (Battenfield et al., 2016), maize (Shikha et al., 2017), alfalfa (*Medicago sativa* L.) (Li et al., 2015), oat (*Avena sativa* L.) (Asoro, Newell, Beavis, Scott, & Jannink, 2011), and rice (*Oryza sativa* L.) (Spindel et al., 2015); and these studies have reported different levels of prediction accuracies for agronomic and end-use quality traits.

However, GS studies conducted in different crop species have highlighted factors, such as GS model (Rutkoski et al., 2012), marker-density (Heffner et al., 2009), and TP size (Norman, Taylor, Edwards, & Kuchel, 2018), that affect prediction accuracy. Prediction models of GS influence prediction accuracies because in each model marker effects are estimated under different assumptions. For example, the ridge regression best linear unbiased prediction (RR-BLUP) model assumes that the marker effects have a normal distribution with a common variance (Endelman, 2011; Meuwissen et al., 2001), while genomic best linear unbiased prediction (GBLUP) considers the contribution of markers based on the genomic relationship matrix (VanRaden, 2008). For Bayesian models, such as Bayesian LASSO (BL, where

LASSO stands for least absolute shrinkage and selection operator), the marker effects are assumed not to have a common variance and it also uses a variable selection criterion during analysis (Daetwyler, Pong-Wong, Villanueva, & Woolliams, 2010; Park & Casella, 2008). Increased marker density and TP size can produce greater prediction accuracy than lower densities and TP sizes because of increased chance of capturing larger genetic variance with higher marker density, and improved marker effect estimation with larger TP size (Arruda et al., 2015; Norman et al., 2018). Therefore, these factors need to be considered for cost-efficient, successful implementation of GS in a breeding program.

In the present study, we compared prediction accuracies of four GS models for three key forage agronomic traits of winter wheat. The objectives of the study were to (a) compare prediction accuracies of four GS models using two genotype sampling methods, (b) determine the appropriate TP size, and (c) investigate the appropriate number of single nucleotide polymorphism (SNP) markers to use for predicting forage-related agronomic traits in dual-purpose wheat breeding.

2 | MATERIALS AND METHODS

2.1 | Phenotyping and genotyping

This study used 298 lines of the hard winter wheat diversity panel established by the Triticeae Coordinated Agricultural Project (TCAP) (Guttieri et al., 2015; Guttieri, Frels, Regassa, Waters, & Baenziger, 2017). We used this panel because about 150 lines of the panel are founders of our existing breeding populations. Forage agronomic data of the panel was reported previously (Kim et al., 2016). Phenotypic data used in this study include forage yield (FY) on dry matter basis, plant height (PH), and heading date (HD). Briefly, forage samples were collected during Feekes stage 4–5 or Zadoks 30 as reported previously (Kim et al., 2016). Forage yield was recorded as the weight of samples dried in a forced air oven at 60 °C for at least 72 h. Plant height was measured on a plot basis as the average distance from the soil surface to the tip of the main stem. Heading date was scored on a plot basis using a scale of 1–5, corresponding to heading on 98–102, 103–108, 109–114, 115–120, and 121–127 d after planting, respectively. Phenotypic analysis was done using PROC GLM procedure in SAS. Variance components, including genetic, genotype × environment interaction and residual variances were estimated from the ANOVA.

Broad-sense heritability (H^2) and narrow-sense heritability (h^2) for each trait was estimated on an entry-mean basis across the two environments (Hallauer, Miranda Filho, & Carena, 2010) using the following formulas: $H^2 = \sigma^2_g/(\sigma^2_g + \sigma^2_{ge}/e + \sigma^2_e/er)$ and $h^2 = \sigma_A^2/(\sigma^2_g + \sigma^2_{ge}/e + \sigma^2_e/er)$; where σ_A^2, σ^2_g, σ^2_{ge} and σ^2_e are the additive, genetic, genotype × environ-

ment interaction and residual variance components, respectively, while r and e are numbers of replications and environments, respectively. The h^2 was considered as the expected accuracy of the phenotypic selection, and thus a reference for evaluating GS accuracies.

Genotyping of the panel was performed using the wheat 90K SNP array (Wang et al., 2014) and the marker data was archived in the Triticeae Toolbox (Genotyping experiment TCAP90K_HWWAMP) (Guttieri et al., 2015). Before GS analysis, we filtered out SNP markers with <5% minor allele frequency (MAF) and more than 10% missing data. We removed all monomorphic markers and SNP marker pairs with linkage disequilibrium (LD) > 0.85 using SNPRelate R package (Zheng, 2013) in order to reduce SNP redundancy and computational time. After applying all filtering criteria, a total of 3,484 SNPs remained for GS analysis.

2.2 | Genetic diversity and genomic selection models

Genetic structuring of the panel was performed using a neighbor-joining (NJ) tree with TASSEL 5.14 (Bradbury et al., 2007) and principal component analysis (PCA) in the R program. We compared the performance of four GS models, including RR-BLUP, Gaussian kernel (GAUSS), GBLUP, and BL (De Los Campos et al., 2009; Endelman, 2011; Habier, Fernando, & Dekkers, 2007; Park & Casella, 2008; VanRaden, 2008) on mean values of raw phenotypic data of the three forage agronomic traits. We used mean values instead of best linear unbiased predictions (BLUPs) because the two values were perfectly correlated ($r = 1.0$) for all the three traits. We applied a fivefold cross-validation procedure assigning lines to either a TP or a validation population (VP) using two genotype sampling methods. For cross-validation, the TP was sampled from 298 lines evaluated at two environments and used to predict the GEBVs of the remaining lines evaluated in the same environments. We used genome-wide marker effects estimated from the TP to calculate the GEBVs of the lines assigned to the VP. All R scripts of GS analyses are provided in the Supplemental Material file.

The GS analyses for RR-BLUP, GBLUP, and GAUSS models were performed in R package rrBLUP (Endelman, 2011) with 2,000 iterations and the BL model was implemented with the R package BGLR (Pérez & de Los Campos, 2014). The equations of RR-BLUP, GAUSS, and BL were detailed previously by Maulana et al. (2019b) for forage quality traits of the same population. For GBLUP, the following equation was used (Habier et al., 2007; VanRaden, 2008): $\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\beta_o} + \boldsymbol{\varepsilon}$; where $\mathbf{Y}$ is the vector of the phenotypic data for each trait, $\boldsymbol{\beta}$ is the vector of fixed effects (mean), $\boldsymbol{\beta_o}$ is the vector of random effects and $\boldsymbol{\varepsilon}$ is the vector of residual effects, which is assumed to follow a normal distribution as var (ε) ~ N (0, $I\sigma^2_\varepsilon$), where

σ^2_{ε} is the residual variance and I is the identity matrix. X and Z are the incident matrices of $\boldsymbol{\beta}$ and $\boldsymbol{\beta_o}$.

2.3 | Genomic selection model comparison

The GS model comparison analysis was conducted using a fivefold cross-validation procedure with 238 and 60 lines as the TP and the VP, respectively. The relative performance in prediction accuracies of the GS models was compared in relation to two genotype sampling methods used to assign lines to TP and VP. We tested two genotype sampling methods including random sampling method (RSM) and stratified sampling method (SSM) to assess whether sampling method had effect on predictive ability and prediction accuracy. For RSM, we randomly selected lines from the entire panel without replacement and assigned them to the TP and VP. For SSM, we first clustered the lines into subgroups based on genetic diversities, and from each subgroup we proportionately selected lines and assigned them to the TP and VP.

Predictive ability, $r(\hat{y}, g)$, of the GS model was estimated as the Pearson correlation between the PEBV and the GEBV, $r(\hat{y}, g) = r(\text{GEBV:PEBV})$, where r is the Pearson correlation coefficient between GEBV and PEBV of the VP. Prediction accuracy, $r(\hat{g}, g)$, was estimated by dividing the $r(\hat{y}, g)$ by the square root of H^2 as follows (Dekkers, 2007): $r(\hat{g}, g) = r(\text{GEBV:PEBV})/\sqrt{H^2}$. To account for sampling error, the GS analysis procedure was repeated 2,000 times.

2.4 | Determination of appropriate training population size and marker density of the traits studied

We determined the appropriate TP size for predicting forage agronomic traits of the panel by varying the TP sizes ($n_{\text{TP}} = 60, 120, 180,$ and 238), whereby the wheat lines were assigned to the TP and VP using SSM, when all 3,484 markers were used. On the other hand, the number of SNP markers (marker density) required for optimal prediction accuracy was evaluated by varying marker densities ($n_{\text{SNP}} = 500, 1,000; 1,500; 3,000; 3,484$) for training the GS models.

The SNP marker subsets were selected using two marker sampling strategies (random sampling and even sampling methods). For the random sampling method (RSM), genome-wide SNP markers were selected randomly without replacement to form different SNP marker subsets. With this sampling strategy, the subsets were comprised of markers that were selected without considering the locations of the markers on the chromosomes across the genome. For the even sampling method (ESM), marker subsets were proportionately selected from all the 21 chromosomes across the genome after some SNP markers were filtered out based on LD. To account
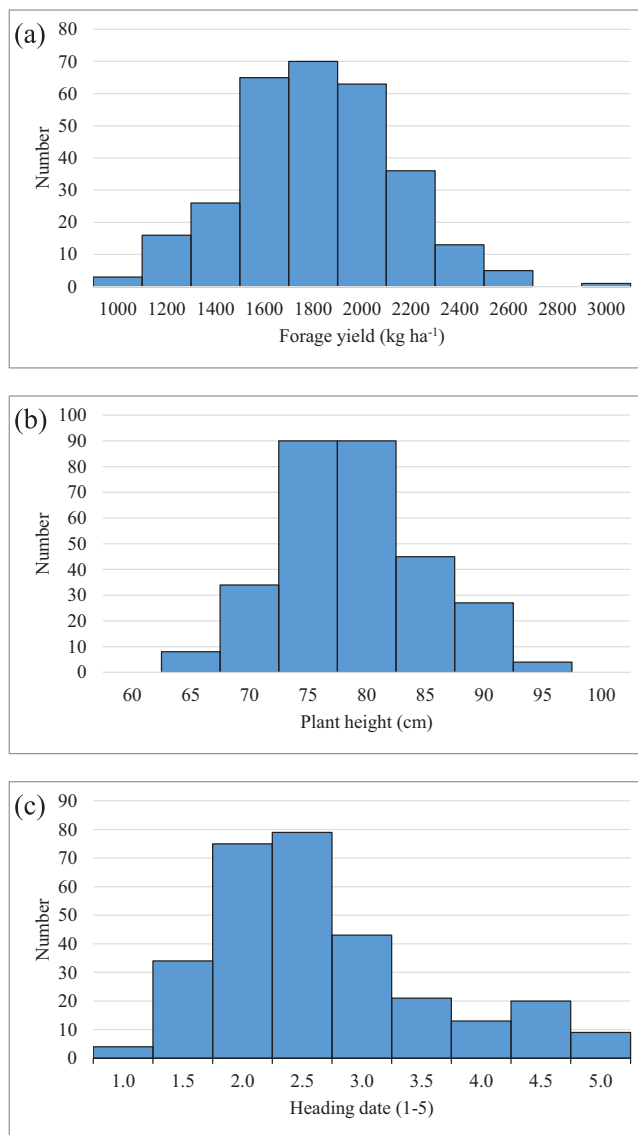

FIGURE 1 Frequency distribution of the three traits in the wheat diversity population. (a) FY, forage yield (kg ha^{-1}); (b) PH, plant height (cm); (c) HD, heading date. The heading dates were recorded on a scale of 1−5, corresponding to heading on 98−102, 103−108, 109−114, 115−120, and 121−127 d after planting, respectively

for sampling error, we repeated the sampling of the markers 2,000 times. We also used 238 and 60 lines as the TP and the VP, respectively, using a fivefold cross-validation scheme.

3 | RESULTS

3.1 | Heritability estimates

Phenotypic variation of the three traits (FY, PH, and HD) was reported previously (Kim et al., 2016), and frequency distributions of the traits are shown in Figure 1. The broad-sense and narrow-sense heritability estimates of the agronomic traits

studied are presented in Table 1. Broad-sense heritability estimates (H^2) of the three agronomic traits ranged from 0.57 for FY to 0.82 for HD, while the narrow-sense heritability estimates (h^2) ranged from 0.19 for FY to 0.56 for HD.

3.2 | Genomic selection model comparison

Predictive abilities, $r(\hat{y}, g)$, and prediction accuracies, $r(\hat{g}, g)$, of the four GS models are presented in Table 1. We have included both predictive abilities and prediction accuracies of the models for facilitating comparison with other GS publications reported with either $r(\hat{y}, g)$ or $r(\hat{g}, g)$. The predictive abilities of the GS models ranged from 0.37 to 0.67 with RSM, while it ranged from 0.37 to 0.66 with SSM (Table 1). However, throughout the paper, we will only present prediction accuracies results in detail.

For all GS models and the two genotype sampling methods (RSM and SSM) tested, prediction accuracies ranged from moderate to high, depending on the trait and model (Table 1). For the RR-BLUP model, prediction accuracies were 0.47 for PH, 0.69 for FY, and 0.73 for HD with RSM, while it was 0.47 for PH, 0.68 for FY, and 0.73 for HD when using SSM. Therefore, the genotype sampling method of assigning lines to TP and VP for cross-validation had little or no effect on prediction accuracies for the RR-BLUP model.

The results of the other three models (GBLUP, GAUSS, and BL) are similar to the RR-BLUP model, but the BL model produced the lowest prediction accuracies in general, with only one exception, for all three traits when using either RSM or SSM. The two genotype sampling methods also had little or no effect on prediction accuracies of these three models. However, regardless of model and genotype sampling method used, all models had the greatest prediction accuracies for HD, followed by FY (Table 1). The PH had consistently the lowest prediction accuracy regardless of the model used. As no difference was seen between the two genotype sampling methods (RSM and SSM), only SSM was used for the rest of the study.

3.3 | Effects of training population size in the traits studied

Prediction accuracies of four GS models for the three agronomic traits (FY, PH, and HD) affected by TP size were estimated by varying TP sizes using SSM according to genetic diversities of the lines when all 3,484 markers were used (Figure 2). In general, an increase in prediction accuracies of the GS models was observed as the number of lines assigned to the TP increased from 60 to 238. For example, prediction accuracy of FY increased from 0.61 ($n_{TP} = 60$) to 0.73 ($n_{TP} = 238$) for RR-BLUP, GAUSS, and GBLUP models, and from 0.60 ($n_{TP} = 60$) to 0.69

TABLE 1 Genomic predictive abilities and prediction accuracies ± standard errors of the four genomic selection models for the three traits[a]

| | | | RR-BLUP | | | | GAUSS | | | | GBLUP | | | | BL | | | |
| | | | RSM | | SSM[b] | | RSM | | SSM | | RSM | | SSM | | RSM | | SSM | |
Traits	h^2	H^2	$r(\hat{y},g)$	$r(\hat{g},g)$	$r(\hat{y},g)$	$r(\hat{g},g)$	$r(\hat{y},g)$	$r(\hat{g},g)$	$r(\hat{y},g)$	$r(\hat{g},g)$	$r(\hat{y},g)$	$r(\hat{g},g)$	$r(\hat{y},g)$	$r(\hat{g},g)$	$r(\hat{y},g)$	$r(\hat{g},g)$	$r(\hat{y},g)$	$r(\hat{g},g)$
FY	0.19	0.57	0.53 ± 0.002	0.69 ± 0.002	0.52 ± 0.002	0.68 ± 0.002	0.53 ± 0.002	0.69 ± 0.002	0.52 ± 0.002	0.68 ± 0.002	0.53 ± 0.002	0.69 ± 0.002	0.52 ± 0.003	0.69 ± 0.003	0.51 ± 0.002	0.67 ± 0.003	0.51 ± 0.002	0.66 ± 0.002
PH	0.43	0.66	0.38 ± 0.003	0.47 ± 0.002	0.38 ± 0.003	0.47 ± 0.002	0.40 ± 0.003	0.49 ± 0.002	0.40 ± 0.003	0.49 ± 0.003	0.37 ± 0.003	0.46 ± 0.003	0.38 ± 0.003	0.47 ± 0.003	0.38 ± 0.003	0.47 ± 0.002	0.37 ± 0.002	0.46 ± 0.002
HD	0.56	0.82	0.66 ± 0.003	0.73 ± 0.003	0.66 ± 0.003	0.73 ± 0.002	0.66 ± 0.003	0.73 ± 0.002	0.66 ± 0.003	0.73 ± 0.002	0.67 ± 0.002	0.74 ± 0.003	0.66 ± 0.003	0.73 ± 0.003	0.65 ± 0.002	0.72 ± 0.002	0.64 ± 0.002	0.71 ± 0.003

Note. h^2, narrow-sense heritability; H^2, broad-sense heritability; RR-BLUP, ridge regression best linear unbiased prediction; GAUSS, Gaussian kernel; GBLUP, genomic best linear unbiased prediction; BL, Bayesian LASSO, where LASSO stands for least absolute shrinkage and selection operator; RSM, random sampling method; SSM, stratified sampling method. Predictive ability, $r(\hat{y}, g)$, is the Pearson correlation between phenotypically estimated breeding value (PEBV) and genomic estimated breeding value (GEBV); Prediction accuracy, $r(\hat{g}, g)$, is the $r(\hat{y}, g)$ divided by the square root of broad-sense heritability estimate of the trait; FY, forage yield (kg ha⁻¹); PH, plant height (cm); HD, heading date.

[a]All genomic selection (GS) analyses were conducted using 3,484 SNP markers.

[b]Sampling of the lines was repeated 2,000 times using 238 lines as a training population and 60 lines as a validation population.
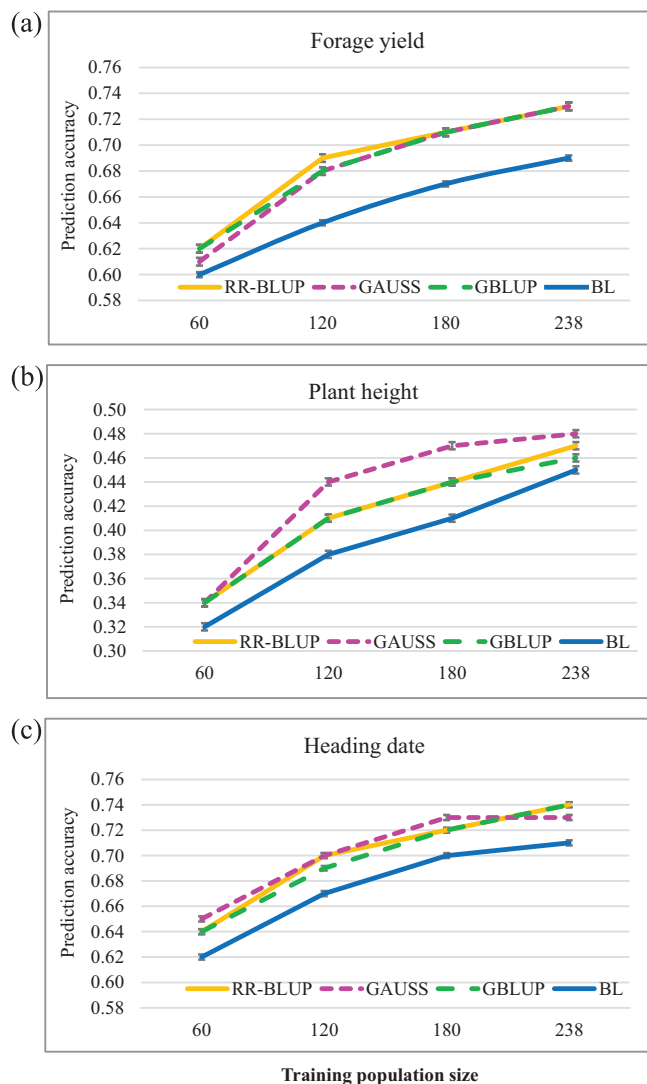
FIGURE 2 Genomic prediction accuracies of the three traits as affected by the training population size. (a) FY, forage yield (kg ha^{-1}); (b) PH, plant height (cm); (c) HD, heading date. RR-BLUP, ridge regression best linear unbiased prediction; GAUSS, Gaussian kernel; GBLUP, genomic best linear unbiased prediction model; BL, Bayesian LASSO, where LASSO stands for least absolute shrinkage and selection operator; Stratified sampling method (SSM) was used to assign genotypes to the TP and the VP in all analyses. Genotype sampling was repeated 2,000 times, and the average prediction accuracy was recorded. All GS analyses were conducted using 3,484 SNP markers

(n_{TP} = 238) for the BL model. Prediction accuracy of PH increased from 0.34 (n_{TP} = 60) to 0.47 (n_{TP} = 238) for the RR-BLUP model, and similar increases were seen for other models tested. Prediction accuracy of HD increased from 0.64 to 0.74 for RR-BLUP, GAUSS, and GBLUP models, and 0.62 to 0.71 for the BL model when increasing the TP size from 60 to 238 lines. Generally, the largest increase in prediction accuracy was observed when the TP size was increased from 60 to 120 or 180, then the increase tended to have less improvement when TP size was further increased

to 238 for the three agronomic traits. This result suggests that the effect of TP size on prediction accuracy for the three traits was greater for RR-BLUP, GBLUP, and GAUSS than for the BL model. Furthermore, the difference in prediction accuracy between traits was more pronounced at smaller TP sizes. For example, the prediction accuracy of GAUSS at n_{TP} = 60 was 0.61 vs. 0.65 for FY vs. HD, representing a 6.6% difference in accuracy, while at n_{TP} = 180, prediction accuracy was 0.71 vs. 0.73 for FY vs. HD, representing only a 2.8% difference in accuracy (Figure 2).

3.4 | Effects of marker density in the traits studied

Results of marker density impact on prediction accuracy of the three forage agronomic traits are presented in Figure 3. We compared prediction accuracies of the four GS models as affected by marker densities selected using two marker sampling methods (RSM and ESM). As expected, prediction accuracy tended to increase with increasing marker density in all models evaluated. Prediction accuracy of FY increased with increasing marker density up to 1,000 SNPs for RR-BLUP model; 3,000 SNPs for GAUSS and GBLUP; and 1,500 SNPs for BL model with both marker sampling methods, RSM and ESM. Prediction accuracy of PH increased with increasing marker densities up to 3,000 SNPs for the four GS models tested except for the GAUSS model. Prediction accuracies of HD for RR-BLUP and GAUSS models increased with increasing marker densities up to 3,000 and 1,500 SNPs, respectively (Figure 3). The greatest prediction accuracy was observed for HD and the lowest for PH, in all four GS models evaluated. The RR-BLUP, GAUSS, and GBLUP models had the same or similar prediction accuracy, and in general, these three models had greater prediction accuracies than the BL model in the three traits with similar marker densities. Overall, prediction accuracies increased up to 1,000; 1,500; or 3,000 SNPs, depending on the model and trait. However, marker sampling method had little or no influence on prediction accuracy in the different models evaluated.

4 | DISCUSSION

Genomic selection is an alternative selection method to PS and MAS, and it can reduce phenotyping costs, increase genetic gain, and accelerate breeding cycle. Genotyping and sequencing costs have been decreasing over the years, however, field phenotyping remains a bottleneck in plant-breeding programs. A more efficient selection method would help to reduce expenses associated with field phenotyping. Genomic selection provides an opportunity to address this limitation, and it can facilitate the selection
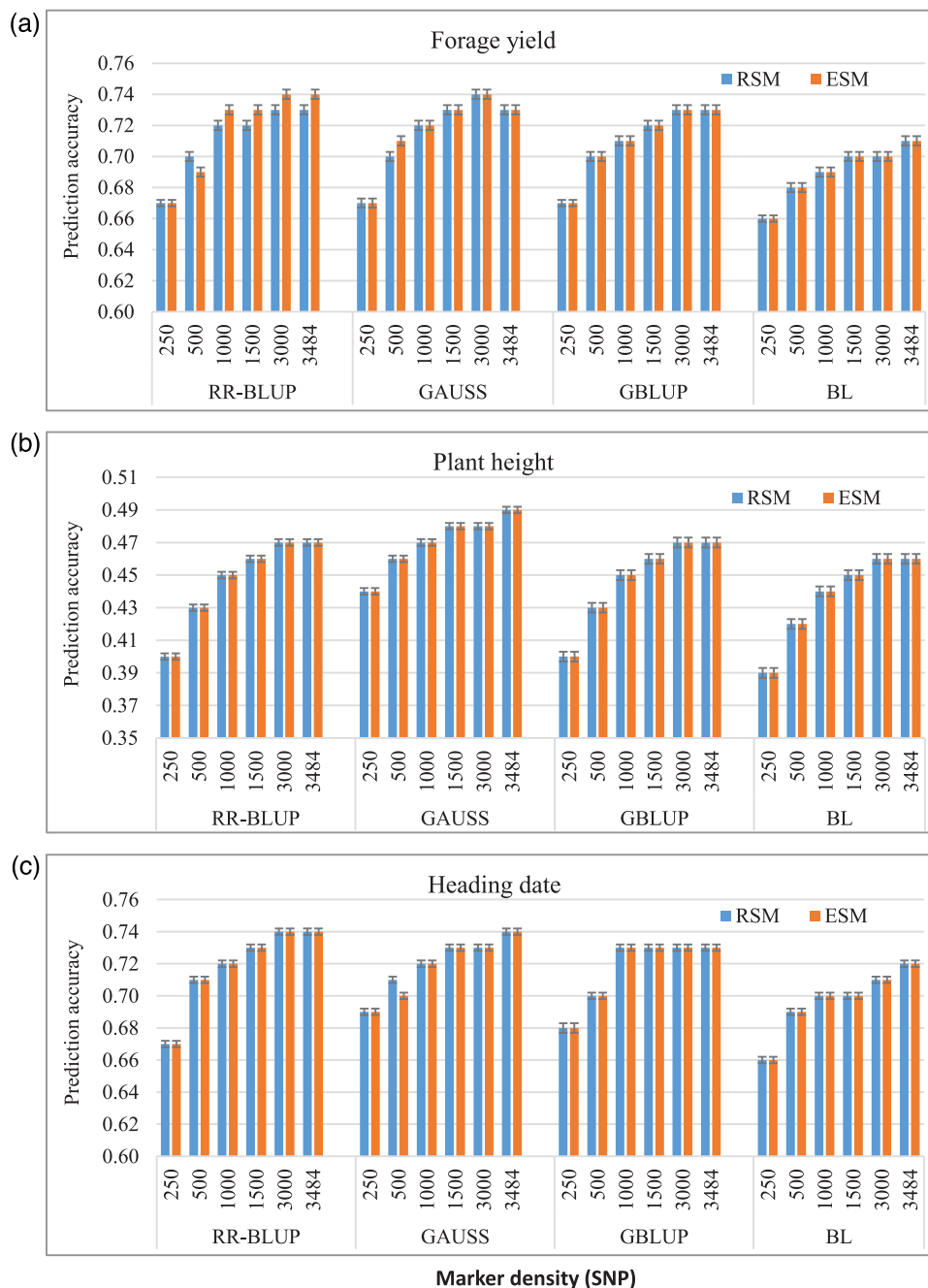
FIGURE 3 Genomic prediction accuracies of the three traits as affected by the marker density. (a) FY, forage yield (kg ha^{-1}); (b) PH, plant height (cm); (c) HD, heading date. RR-BLUP, ridge regression best linear unbiased prediction; GAUSS, Gaussian kernel; GBLUP, genomic best linear unbiased prediction model; BL, Bayesian LASSO, where LASSO stands for least absolute shrinkage and selection operator. RSM, random sampling method; ESM, even sampling method. Sampling of the markers was repeated 2,000 times using 238 lines as a training population and 60 lines as a validation population

of agronomic traits in dual-purpose or forage wheat breeding.

There have been many GS studies conducted for various traits of wheat mainly focusing on grain production (Haile et al., 2018; Saint Pierre et al., 2016; Thavamanikumar, Dolferus, & Thumma, 2015). However, there are few reports to assess the efficacy of deploying GS in forage species

including wheat (Arojju, Cao, Zulfi Jahufer, Barrett, & Faville, 2020; Biazzi et al., 2017; Grinberg et al., 2016; Jia et al., 2018; Maulana et al., 2019b). Successful implementation of GS in plant-breeding programs depends on accurate phenotyping of TP and understanding factors that affect prediction accuracy (Norman et al., 2018; Zhong, Dekkers, Fernando, & Jannink, 2009). Accurate phenotyping of TP for

use in training the prediction model in GS studies can result in producing GEBVs that would be as good as PEBVs. In addition, understanding to what extent those factors such as TP size and marker density affect prediction accuracies helps to determine the appropriate TP size and marker density in practice.

4.1 | Genomic selection model comparison in the traits studied

In the present study, the four GS models (RR-BLUP, GAUSS, GBLUP, and BL) performed similarly with regard to prediction accuracies for the traits studied, except BL which produced numerically lower prediction accuracies across the three traits. These models differ in the way they handle marker information with regard to assumptions related to variance of marker effects. RR-BLUP, GBLUP, and GAUSS assume that all markers have equal variance and all markers are kept in the model, while the BL model uses unequal variance for each marker and makes variable selection by keeping only some markers in the model while assuming other markers having no effect on the trait (Pérez, de los Campos, Crossa, & Gianola, 2010). Therefore, it is not surprising that in our study RR-BLUP performed similarly to GBLUP because both models assume that all markers contribute to trait performance (Habier et al., 2007). Previous simulation and empirical studies have shown that, depending on the genetic architecture of the trait, GS models tend to perform differently. The RR-BLUP model has been shown to be insensitive to the genetic architecture of the trait (i.e., the number of QTL and the distribution of their effects), while the accuracy of BL improves as the number of QTL decreases (Daetwyler et al., 2010). The results observed in this study corroborate a previous study conducted in wheat where it was found that the RR-BLUP outperformed BL for Fusarium head blight (FHB) resistance (Arruda et al., 2016). In another study, BL outperformed RR-BLUP especially for traits governed by fewer genes such as disease resistance (Ornella et al., 2012). Other GS studies have reported similar performance with regard to prediction accuracies of RR-BLUP and BL (Lorenz, Smith, & Jannink, 2012; Rutkoski et al., 2012; Rutkoski et al., 2014). The GAUSS, a model which accounts for both additive and non-additive effects, performed similarly to RR-BLUP, which only accounts for additive effects. Generally, our results are in agreement with the GS study in a barley (*Hordeum vulgare* L.)-breeding population, showing that the GAUSS and the RR-BLUP models produced similar prediction accuracies for Fusarium head blight resistance, yield, and plant height (Sallam, Endelman, Jannink, & Smith, 2015). In another GS wheat study, RR-BLUP was also consistently the best model for processing and end-use quality traits of spring bread wheat (Battenfield et al., 2016).

Overall, our study suggests that RR-BLUP, GAUSS, and GBLUP models can be applied in GS to facilitate the selection of FY, PH, and HD traits during dual-purpose wheat breeding. However, we suggest using RR-BLUP because of its computational time advantage over the other models. Furthermore, we did not see any significant differences in prediction accuracy between the two genotype sampling methods (RSM and SSM) for the traits studied; suggesting that the sampling method of assigning lines to TP and VP had little or no influence on prediction accuracies of all models for the agronomic traits in this study. This result could be attributed to the fact that both sampling methods might have selected representative TP and VP because we used a large number (2,000) of iterations during the GS analysis; hence sampling error was taken into account.

4.2 | Appropriate training population size for genomic selection of the traits studied

Training population size is an important factor that has been shown to influence prediction accuracy and, therefore, over the years its effect has been assessed in many crop species, such as wheat (Arruda et al., 2015; Norman et al., 2018), maize (Crossa et al., 2014), oat (Asoro et al., 2011), and barley (Lorenz et al., 2011). In this study, we compared TP sizes for GS prediction accuracies of forage wheat agronomic traits. With GS, the most costly activity is to develop a TP because it requires both genotyping and phenotyping of the lines contained in the TP. Therefore, the appropriate TP size that can produce high prediction accuracy is important. Our results suggest that phenotyping more than 180 lines of this panel for training the GS model would be unnecessary. These results corroborate findings reported in previous GS studies that found there is a point at which prediction accuracy begins to decline or plateau with increased TP size (Heffner, Jannink, Iwata, Souza, & Sorrells, 2011; Isidro et al., 2015; Norman et al., 2018). Although prediction accuracies of the GS models for various traits were different, the response to TP size was similar in all traits despite their expected differences in genetic complexity. This finding suggests that genetic architecture and complexity of a trait have minor influence on the response of its prediction accuracy to TP size. It also suggests that how representative of the TP in relative to VP is crucial for prediction accuracies of the models. This result corroborates previous GS studies in wheat (Maulana et al., 2019b; Norman et al., 2018).

4.3 | Appropriate marker density for genomic selection of the traits studied

Previous GS studies conducted in different crop species have shown that the number of markers used to train the GS model

has a great impact on prediction accuracy regardless of the model and trait evaluated (Arruda et al., 2015; Lorenzana & Bernardo, 2009; Norman et al., 2018; Zhang et al., 2017). In the present study, the appropriate marker density for predicting forage agronomic traits was assessed by using different marker density subsets with the goal of determining the lowest number of SNP markers that could be used to obtain significant prediction accuracies for each model and trait. Two marker sampling methods (random vs. even sampling) were used to select markers across the genome to form each subset and assess the impact on prediction accuracy. Generally, irrespective of the model used, all traits studied showed some response in prediction accuracy with increasing marker density. Overall, greater prediction accuracies were observed with increasing marker densities in all GS models tested. However, in most cases, prediction accuracy increased with increasing marker density up to a certain point after which diminishing gains were observed due to overfitting the GS models with increased marker density (Heslot, Yang, Sorrells, & Jannink, 2012). Linear increase in prediction accuracy with increasing marker density has been observed in several previous studies conducted in different crops (Arruda et al., 2015; Asoro et al., 2011; Heffner et al., 2011; Lorenzana & Bernardo, 2009; Norman et al., 2018), but upon reaching a certain marker density, diminishing gains in accuracy were observed with no further significant increase.

In this study, it appears that the marker density could be reduced to 1,000; 1,500; or 3,000 genome-wide SNP markers without significantly compromising the prediction accuracy of the wheat agronomic traits depending on the GS model and trait evaluated. These results indicate that at these marker densities (i.e., $n = 1,000, 1,500$ and $3,000$ SNPs) most of the genetic variance accounting for the traits was captured resulting in no significant accuracy increase upon adding more markers. To get high prediction accuracy it is important to sample the markers across the entire genome in order to increase the chance of capturing the markers that are in tight linkage with QTL for the traits of interest (Goddard & Hayes, 2007; Meuwissen et al., 2001). Prediction accuracy, among other factors, is driven by the linkage disequilibrium (LD) between the markers and the quantitative trait loci (QTL) associated with the traits of interest. In our study, markers included in training the GS models should cover most genetic loci contributing to the forage agronomic traits within LD distances because of genome-wide coverage of the SNPs.

4.4 | Prediction of the traits studied

According to the above discussion, we predicted the three traits using a combination of recommended model conditions. We used the RR-BLUP model trained with 180 lines and 3,000 well-distributed SNPs. The scatterplots in Figure 4
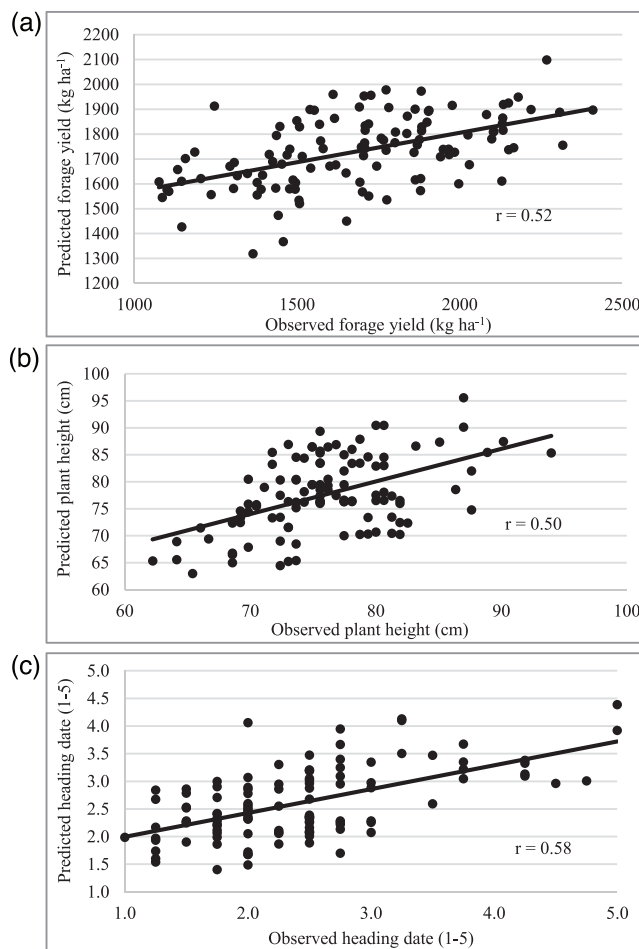

FIGURE 4 Scatterplots showing correlations between the observed values and the predicted values of the three traits when using the RR-BLUP model trained with 180 lines and 3,000 SNPs. (a) FY, forage yield (kg ha^{-1}); (b) PH, plant height (cm); (c) HD, heading date. The heading dates were recorded on a scale of 1−5, corresponding to heading on 98−102, 103−108, 109−114, 115−120, and 121−127 d after planting, respectively

show correlations between GEBVs and PEBVs of the three traits predicted for the remaining 118 lines of the panel. The results indicated that the three forage agronomic traits could be predicted using GS. It is expected that GS predicted the traits with deviation along the trend lines. Since there are only 2 yr of phenotypic data used for training the model, we are encouraged that the predictive abilities of the traits could be further increased if the traits are evaluated in more environmental conditions in practice. This result again suggests that FY, PH, and HD can be predicted using GS in dual-purpose wheat breeding.

5 | CONCLUSION

In this study, moderate-to-high prediction accuracies of four GS models for three agronomic traits were observed.

Generally, RR-BLUP, GBLUP, and GAUSS models slightly outperformed the BL model for most traits studied. The results obtained in this study suggest the potential application of GS for forage agronomic traits in dual-purpose wheat breeding in order to increase genetic gain, reduce phenotyping costs, and more importantly to speed up forage wheat cultivar development. We have shown that greater prediction accuracies of forage agronomic traits of winter wheat can be obtained with small TP sizes and low marker densities depending on the model and trait.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

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REFERENCES

Arojju, S. K., Cao, M., Zulfi Jahufer, M. Z., Barrett, B. A., & Faville, M. J. (2020). Genomic predictive ability for foliar nutritive traits in perennial ryegrass. *G3: Genes, Genomes, Genetics*, *10*, 695–708. https://doi.org/10.1534/g3.119.400880

Arruda, M. P., Brown, P., Brown-Guedira, G., Krill, A. M., Thurber, C., Merrill, K. R., … Kolb, F. L. (2016). Genome-wide association mapping of Fusarium head blight resistance in wheat using genotyping-by-sequencing. *The Plant Genome*, *9*, 1–14. https://doi.org/10.3835/plantgenome2015.04.0028

Arruda, M. P., Brown, P. J., Lipka, A. E., Krill, A. M., Thurber, C., & Kolb, F. L. (2015). Genomic selection for predicting Fusarium head blight resistance in a wheat breeding program. *The Plant Genome*, *8*, 1–12. https://doi.org/10.3835/plantgenome2015.01.0003

Asoro, F. G., Newell, M. A., Beavis, W. D., Scott, M. P., & Jannink, J.-L. (2011). Accuracy and training population design for genomic selection on quantitative traits in elite North American oats. *The Plant Genome*, *4*, 132–144. https://doi.org/10.3835/plantgenome2011.02.0007

Battenfield, S. D., Guzmán, C., Gaynor, R. C., Singh, R. P., Peña, R. J., Dreisigacker, S., … Poland, J. A. (2016). Genomic selection for processing and end-use quality traits in the CIMMYT spring bread wheat breeding program. *The Plant Genome*, *9*, 1–12. https://doi.org/10.3835/plantgenome2016.01.0005

Bernardo, R. (2010). Genome-wide selection with minimal crossing in self-pollinated crops. *Crop Science*, *50*, 624–627. https://doi.org/10.2135/cropsci2009.05.0250

Bernardo, R., & Yu, J. (2007). Prospects for genome-wide selection for quantitative traits in maize. *Crop Science*, *47*, 1082–1090. https://doi.org/10.2135/cropsci2006.11.0690

Beyene, Y., Semagn, K., Mugo, S., Tarekegne, A., Babu, R., Meisel, B., … Oikeh, S. (2015). Genetic gains in grain yield through genomic selection in eight bi-parental maize populations under drought stress. *Crop Science*, *55*, 154–163. https://doi.org/10.2135/cropsci2014.07.0460

Biazzi, E., Nazzicari, N., Pecetti, L., Brummer, E. C., Palmonari, A., Tava, A., & Annicchiarico, P. (2017). Genome-wide association mapping and genomic selection for alfalfa (*Medicago sativa*) forage quality traits. *PLOS ONE*, *12*, e0169234. https://doi.org/10.1371/journal.pone.0169234

Bradbury, P. J., Zhang, Z., Kroon, D. E., Casstevens, T. M., Ramdoss, Y., & Buckler, E. S. (2007). TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics*, *23*, 2633–2635. https://doi.org/10.1093/bioinformatics/btm308

Crossa, J., de Los Campos, G., Pérez, P., Gianola, D., Burgueño, J., Araus, J. L., … Yan, J. (2010). Prediction of genetic values of quantitative traits in plant breeding using pedigree and molecular markers. *Genetics*, *186*, 713–724. https://doi.org/10.1534/genetics.110.118521

Crossa, J., Pérez, P., Hickey, J., Burgueño, J., Ornella, L., Cerón-Rojas, J., … Li, Y. (2014). Genomic prediction in CIMMYT maize and wheat breeding programs. *Heredity*, *112*, 48–60. https://doi.org/10.1038/hdy.2013.16

Daetwyler, H. D., Pong-Wong, R., Villanueva, B., & Woolliams, J. A. (2010). The impact of genetic architecture on genome-wide evaluation methods. *Genetics*, *185*, 1021–1031. https://doi.org/10.1534/genetics.110.116855

De Los Campos, G., Naya, H., Gianola, D., Crossa, J., Legarra, A., Manfredi, E., … Cotes, J. M. (2009). Predicting quantitative traits with regression models for dense molecular markers and pedigree. *Genetics*, *182*, 375–385. https://doi.org/10.1534/genetics.109.101501

Dekkers, J. (2007). Prediction of response to marker-assisted and genomic selection using selection index theory. *Journal of Animal Breeding and Genetics*, *124*, 331–341. https://doi.org/10.1111/j.1439-0388.2007.00701.x

Endelman, J. B. (2011). Ridge regression and other kernels for genomic selection with R package rrBLUP. *The Plant Genome*, *4*, 250–255. https://doi.org/10.3835/plantgenome2011.08.0024

Goddard, M. (2009). Genomic selection: Prediction of accuracy and maximisation of long term response. *Genetica*, *136*, 245–257. https://doi.org/10.1007/s10709-008-9308-0

Goddard, M. E., & Hayes, B. (2007). Genomic selection. *Journal of Animal Breeding and Genetics*, *124*, 323–330. https://doi.org/10.1111/j.1439-0388.2007.00702.x

González-Camacho, J., de Los Campos, G., Pérez, P., Gianola, D., Cairns, J., Mahuku, G., … Crossa, J. (2012). Genome-enabled prediction of genetic values using radial basis function neural networks. *Theoretical and Applied Genetics*, *125*, 759–771. https://doi.org/10.1007/s00122-012-1868-9

Grinberg, N. F., Lovatt, A., Hegarty, M., Lovatt, A., Skøt, K. P., Kelly, R., … Skøt, L. (2016). Implementation of genomic prediction in *Lolium*

perenne (L.) breeding populations. *Frontiers in Plant Science*, *7*, 133–142. https://doi.org/10.3389/fpls.2016.00133

Guttieri, M. J., Baenziger, P. S., Frels, K., Carver, B., Arnall, B., Wang, S., … Waters, B. M. (2015). Prospects for selecting wheat with increased zinc and decreased cadmium concentration in grain. *Crop Science*, *55*, 1712–1728. https://doi.org/10.2135/cropsci2014.08.0559

Guttieri, M. J., Frels, K., Regassa, T., Waters, B. M., & Baenziger, P. S. (2017). Variation for nitrogen use efficiency traits in current and historical Great Plains hard winter wheat. *Euphytica*, *213*, 87–104. https://doi.org/10.1007/s10681-017-1869-5

Habier, D., Fernando, R. L., & Dekkers, J. C. (2007). The impact of genetic relationship information on genome-assisted breeding values. *Genetics*, *177*, 2389–2397. https://doi.org/10.1534/genetics.107.081190

Haile, J. K., N'Diaye, A., Clarke, F., Clarke, J., Knox, R., Rutkoski, J., … Pozniak, C. J. (2018). Genomic selection for grain yield and quality traits in durum wheat. *Molecular Breeding*, *38*, 75–92. https://doi.org/10.1007/s11032-018-0818-x

Hallauer, A. R., Miranda Filho, J., & Carena, M. J. (2010). Germplasm. In M. J. Carena, A. R. Hallauer, & J. B. Miranda Filho (Eds.), *Quantitative genetics in maize breeding* (pp. 531–576). New York: Springer.

Heffner, E. L., Jannink, J.-L., Iwata, H., Souza, E., & Sorrells, M. E. (2011). Genomic selection accuracy for grain quality traits in biparental wheat populations. *Crop Science*, *51*, 2597–2606. https://doi.org/10.2135/cropsci2011.05.0253

Heffner, E. L., Lorenz, A. J., Jannink, J.-L., & Sorrells, M. E. (2010). Plant breeding with genomic selection: Gain per unit time and cost. *Crop Science*, *50*, 1681–1690. https://doi.org/10.2135/cropsci2009.11.0662

Heffner, E. L., Sorrells, M. E., & Jannink, J.-L. (2009). Genomic selection for crop improvement. *Crop Science*, *49*, 1–12. https://doi.org/10.2135/cropsci2008.08.0512

Heslot, N., Yang, H.-P., Sorrells, M. E., & Jannink, J.-L. (2012). Genomic selection in plant breeding: A comparison of models. *Crop Science*, *52*, 146–160. https://doi.org/10.2135/cropsci2011.06.0297

Hossain, I., Epplin, F. M., & Krenzer, E. G. (2003). Planting date influence on dual-purpose winter wheat forage yield, grain yield, and test weight. *Agronomy Journal*, *95*, 1179–1188. https://doi.org/10.2134/agronj2003.1179

Isidro, J., Jannink, J.-L., Akdemir, D., Poland, J., Heslot, N., & Sorrells, M. E. (2015). Training set optimization under population structure in genomic selection. *Theoretical and Applied Genetics*, *128*, 145–158. https://doi.org/10.1007/s00122-014-2418-4

Jannink, J.-L., Lorenz, A. J., & Iwata, H. (2010). Genomic selection in plant breeding: From theory to practice. *Briefings in Functional Genomics*, *9*, 166–177. https://doi.org/10.1093/bfgp/elq001

Jia, C., Zhao, F., Wang, X., Han, J., Zhao, H., Liu, G., & Wang, Z. (2018). Genomic prediction for 25 agronomic and quality traits in alfalfa (*Medicago sativa*). *Frontiers in Plant Science*, *9*, 1220–1220. https://doi.org/10.3389/fpls.2018.01220

Kim, K.-S., Anderson, J. D., Newell, M. A., Grogan, S. M., Byrne, P. F., Baenziger, P. S., & Butler, T. J. (2016). Genetic diversity of great plains hard winter wheat germplasm for forage. *Crop Science*, *56*, 2297–2305. https://doi.org/10.2135/cropsci2015.08.0519

Kumar, A., Mantovani, E. E., Simsek, S., Jain, S., Elias, E. M., & Mergoum, M. (2019). Genome wide genetic dissection of wheat quality and yield related traits and their relationship with grain shape and size

traits in an elite × non-adapted bread wheat cross. *PLOS ONE*, *14*, e0221826. https://doi.org/10.1371/journal.pone.0221826

Li, X., Wei, Y., Acharya, A., Hansen, J. L., Crawford, J. L., Viands, D. R., … Brummer, E. C. (2015). Genomic prediction of biomass yield in two selection cycles of a tetraploid alfalfa breeding population. *The Plant Genome*, *8*, 1–10. https://doi.org/10.3835/plantgenome2014.12.0090

Lorenz, A. J., Chao, S., Asoro, F. G., Heffner, E. L., Hayashi, T., Iwata, H., … Jannink, J.-L. (2011). Genomic selection in plant breeding: Knowledge and prospects. *Advances in Agronomy*, *110*, 77–123. https://doi.org/10.1016/B978-0-12-385531-2.00002-5

Lorenz, A. J., & Smith, K. P. (2015). Adding genetically distant individuals to training populations reduces genomic prediction accuracy in barley. *Crop Science*, *55*, 2657–2667. https://doi.org/10.2135/cropsci2014.12.0827.

Lorenz, A., Smith, K., & Jannink, J.-L. (2012). Potential and optimization of genomic selection for Fusarium head blight resistance in six-row barley. *Crop Science*, *52*, 1609–1621. https://doi.org/10.2135/cropsci2011.09.0503

Lorenzana, R. E., & Bernardo, R. (2009). Accuracy of genotypic value predictions for marker-based selection in biparental plant populations. *Theoretical and Applied Genetics*, *120*, 151–161. https://doi.org/10.1007/s00122-009-1166-3

MacKown, C. T., Carver, B. F., & Edwards, J. T. (2011). Variation in crude protein and in vitro dry matter digestion of wheat forage. *Crop Science*, *51*, 878–891. https://doi.org/10.2135/cropsci2010.06.0319

Massman, J. M., Jung, H.-J. G., & Bernardo, R. (2013). Genome-wide selection versus marker-assisted recurrent selection to improve grain yield and stover-quality traits for cellulosic ethanol in maize. *Crop Science*, *53*, 58–66. https://doi.org/10.2135/cropsci2012.02.0112

Maulana, F., Anderson, J. D., Butler, T. J., & Ma, X.-F. (2019a). Improving dual-purpose winter wheat in the Southern Great Plains of the United States. In F. Shah, Z. Khan, A. Iqbal, M. Turan, & M. Olgun (Eds.), *Recent advances in grain crops research*. London: IntechOpen.

Maulana, F., Kim, K.-S., Anderson, J. D., Sorrells, M. E., Butler, T. J., Liu, S., … Ma, X.-F. (2019b). Genomic selection of forage quality traits in winter wheat. *Crop Science*, *59*, 2473–2483. https://doi.org/10.2135/cropsci2018.10.0655.

Meuwissen, T. H., Hayes, B. J., & Goddard, M. E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics*, *157*, 1819–1829.

Norman, A., Taylor, J., Edwards, J., & Kuchel, H. (2018). Optimising genomic selection in wheat: Effect of marker density, population size and population structure on prediction accuracy. *G3: Genes, Genomes, Genetics*, *8*, 2889–2899. https://doi.org/10.1534/g3.118.200311.

Ornella, L., Singh, S., Perez, P., Burgueño, J., Singh, R., Tapia, E., … Mathews, K. (2012). Genomic prediction of genetic values for resistance to wheat rusts. *The Plant Genome*, *5*, 136–148. https://doi.org/10.3835/plantgenome2012.07.0017.

Park, T., & Casella, G. (2008). The bayesian lasso. *Journal of the American Statistical Association*, *103*, 681–686. https://doi.org/10.1198/016214508000000337.

Pérez, P., & de Los Campos, G. (2014). Genome-wide regression & prediction with the BGLR statistical package. *Genetics: gEnetics*, *114*, 164442.

Pérez, P., de los Campos, G., Crossa, J., & Gianola, D. (2010). Genomic-enabled prediction based on molecular markers and pedigree using the

bayesian linear regression package in R. *The Plant Genome*, *3*, 106–116. https://doi.org/10.3835/plantgenome2010.04.0005.

Poland, J., Endelman, J., Dawson, J., Rutkoski, J., Wu, S., Manes, Y., … Sorrells, M. (2012). Genomic selection in wheat breeding using genotyping-by-sequencing. *The Plant Genome*, *5*, 103–113. https://doi.org/10.3835/plantgenome2012.06.0006.

Riedelsheimer, C., Czedik-Eysenberg, A., Grieder, C., Lisec, J., Technow, F., Sulpice, R., … Melchinger, A. E. (2012). Genomic and metabolic prediction of complex heterotic traits in hybrid maize. *Nature Genetics*, *44*, 217–220. https://doi.org/10.1038/ng.1033

Rutkoski, J., Benson, J., Jia, Y., Brown-Guedira, G., Jannink, J.-L., & Sorrells, M. (2012). Evaluation of genomic prediction methods for Fusarium head blight resistance in wheat. *The Plant Genome*, *5*, 51–61. https://doi.org/10.3835/plantgenome2012.02.0001

Rutkoski, J. E., Poland, J., Jannink, J.-L., & Sorrells, M. E. (2013). Imputation of unordered markers and the impact on genomic selection accuracy. *G3: Genes, Genomes, Genetics*, *3*, 427–439. https://doi.org/10.1534/g3.112.005363

Rutkoski, J. E., Poland, J. A., Singh, R. P., Huerta-Espino, J., Bhavani, S., Barbier, H., … Sorrells, M. E. (2014). Genomic selection for quantitative adult plant stem rust resistance in wheat. *The Plant Genome*, *7*, 1–10. https://doi.org/10.3835/plantgenome2014.02.0006

Saint Pierre, C., Burgueño, J., Crossa, J., Dávila, G. F., López, P. F., Moya, E. S., … Vikram, P. (2016). Genomic prediction models for grain yield of spring bread wheat in diverse agro-ecological zones. *Scientific Reports*, *6*, 27312. https://doi.org/10.1038/srep27312

Sallam, A., Endelman, J., Jannink, J.-L., & Smith, K. (2015). Assessing genomic selection prediction accuracy in a dynamic barley breeding population. *The Plant Genome*, *8*, 1–15. https://doi.org/10.3835/plantgenome2014.05.0020

Shikha, M., Kanika, A., Rao, A. R., Mallikarjuna, M. G., Gupta, H. S., & Nepolean, T. (2017). Genomic selection for drought tolerance using genome-wide SNPs in maize. *Frontiers in Plant Science*, *8*, 550–562. https://doi.org/10.3389/fpls.2017.00550

Spindel, J., Begum, H., Akdemir, D., Virk, P., Collard, B., Redoña, E., … McCouch, S. R. (2015). Genomic selection and association mapping in rice (*Oryza sativa*): Effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding

lines. *Plos Genetics*, *11*, e1004982. https://doi.org/10.1371/journal.pgen.1004982

Thavamanikumar, S., Dolferus, R., & Thumma, B. R. (2015). Comparison of genomic selection models to predict flowering time and spike grain number in two hexaploid wheat doubled haploid populations. *G3: Genes, Genomes, Genetics*, *5*, 1991–1998. https://doi.org/10.1534/g3.115.019745

VanRaden, P. M. (2008). Efficient methods to compute genomic predictions. *Journal of Dairy Science*, *91*, 4414–4423. https://doi.org/10.3168/jds.2007-0980

Wang, S., Wong, D., Forrest, K., Allen, A., Chao, S., Huang, B. E., … Cattivelli, L. (2014). Characterization of polyploid wheat genomic diversity using a high-density 90 000 single nucleotide polymorphism array. *Plant Biotechnology Journal*, *12*, 787–796. https://doi.org/10.1111/pbi.12183

Zhang, A., Wang, H., Beyene, Y., Semagn, K., Liu, Y., Cao, S., … Zhang, X. (2017). Effect of trait heritability, training population size and marker density on genomic prediction accuracy estimation in 22 bi-parental tropical maize populations. *Frontiers in Plant Science*, *8*, 1916–1916. https://doi.org/10.3389/fpls.2017.01916

Zheng, X. (2013). *A tutorial for the R Package SNPRelate* (pp. 1–26). Seattle, WA: University of Washington.

Zhong, S., Dekkers, J. C., Fernando, R. L., & Jannink, J.-L. (2009). Factors affecting accuracy from genomic selection in populations derived from multiple inbred lines: A barley case study. *Genetics*, *182*(1), 355–364. https://doi.org/10.1534/genetics.108.098277

SUPPORTING INFORMATION

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