# Regression with Variable Selection Priors for the Prediction of Breeding Values in Spring Wheat

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Background

Plant breeding is the process of selecting individuals with superior traits and removing those with undesirable characteristics from a population. This process dates back thousands of years to the domestication of teosinte that had only a handful of grains per plant into modern maize with ears that can grow up to a foot long, wild apples the size of cherries into modern Honeycrisp apples, or the crossing of several wild grasses into modern bread or pasta wheats (Bernardo 2014). Plant breeders are tasked with the simultaneous improvement of multiple, normally uncorrelated, traits in their breeding programs. In spring wheat these primary traits of importance include yield, height, maturity, percent grain protein content, and test weight of the grain. These traits can only be measured effectively from plants grown in the field with large enough plot sizes to remove edge effects and uneven weed pressures from comparisons between wheat lines. This means that the process of evaluating several traits in the field for thousands of wheat lines is expensive, time consuming, and slow. The traditional approach of evaluating traits of interest in the field is dubbed phenotypic selection.

Quantitative traits are traits that are expressed in degree rather than in kind (Falconer and Mackay 1996). An example trait would be yield of wheat plants; a histogram of wheat yields from hundreds of lines grown in a field season roughly approximates a normal distribution. The variance of a quantitative trait in a population reflects the underlying genetic differences in that population. Historically, quantitative traits were understood through Fisher's Infinitesimal Model in which hundreds, or thousands, of causal genes with small effects explained differences in performance. Under this model, the improvement of quantitative traits relies on selecting and mating individuals with beneficial genes and removing those with detrimental genes (Falconer and Mackay 1996).
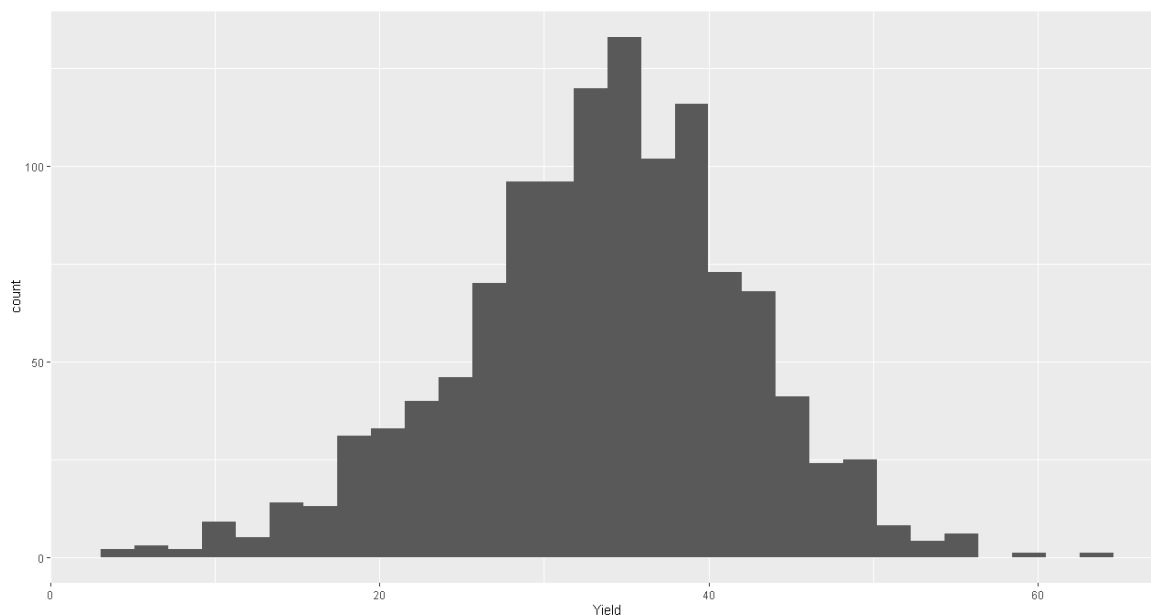
Any quantitative trait expressed in a wheat line reflects both the environment and underlying genetic background of a wheat line. Genetic variance is split into three portions of additive variance, epistatic variance, and dominance variance. Additive variance is the individual genetic effect of a gene. For example, having two copies of gene A gives a two bushel per acre yield boost, having one copy gives one bushel per acre boost, and having no copies offers no improvement. Epistatic variance is the interaction between genes that are not in physical linkage. Dominance variance is viewed as heterozygote overperformance relative to the minor allele homozygous state. Additive variance is the prime driver for genetic improvement in spring wheat as epistatic variance is difficult to advance between generations due to lack of linkage and dominance variance is irrelevant to self-pollinated, inbred crops like spring wheat (Bernardo 2014).

An alternative approach to classical phenotypic selection is to discover and select for individual genes in breeding populations that have large, additive effects on a trait. This approach has proven unsuccessful in the improvement of most quantitative traits due to the overestimation of gene effects (Zuk et al. 2012). This phenomenon, known as the Beavis effect, is the result of attempting to measure the effect of a gene in isolation from all other genes present in a breeding population (Xu 2006). Instead, animal and plant breeders have explored methods that measure the effect of all genes in a population simultaneously to give estimates of additive breeding values for individuals. These methods belong to two general approaches. One classical approach is the use of a kinship matrix calculated originally with pedigree information but know with molecular marker information to predict performance of future individuals based on relatedness. A more modern approach is the use of predictive models that apply shrinkage to regression coefficients or variable selection methods to predict additive genetic value (Meuwissen 2011). Lines are evaluated for traits of interest, genotyped, a model is created to assign coefficients to markers. Going forward, a breeder can then genotype plants in a greenhouse, predict performance, and make selections before growing these lines in the field. As the cost of field research has grown while cost of genetic sequencing has fallen, the use of predictive methods to estimate additive genetic merit has become vital to the breeding process.

Objectives

Prediction of additive breeding values can be accomplished through use of regression models. These regression methods should reflect the underlying genetic architecture explaining a trait's variance in a breeding population (Morgante et al. 2018). Traits that have fewer, more impactful genes would benefit in prediction accuracy from models that allow for several predictors to have greater regression coefficients compared with models that fit predictors with less extreme coefficient distributions. Bayesian Lasso fits parameters to independent double-exponential prior distribution (Park and Casella 2008). Bayesian Lasso also has a regularizing effect in reducing the size of prediction coefficients compared to use of a normal prior with no regularization.

$$\beta \sim DoubleExponential(0, 1)$$

The Regularized Horseshoe Prior provides another option of variable selection and regularization in linear regression (Piironen and Vehtari 2017). The prior accomplishes sparsity by having two shrinkage effects, a global and local shrinkage effect. A global shrinkage parameter regularizes all parameters towards zero. There is then a local shrinkage parameter that allows relatively important

predictors to escape this shrinkage to zero. The Regularized Horseshoe provides the benefit over the classic horseshoe of being able to provide additional regularization on predictors that escape variable removal. These hyperparameters can be further tuned to increase sparsity through variable removal or increase regularization of the non-removed predictors (Piironen and Vehtari 2017). If regularization of non-removed predictors is minimized, the prior instead resembles a non-regularized Horseshoe Prior (Carvalho et al. 2009). Models fit using a Horseshoe prior will have fewer, larger effect predictors compared to use of a normal prior or Lasso prior.

$$\beta | \lambda, \tau, c \sim N(0, \tau^2, \overline{\lambda^2})$$
$$\overline{\lambda^2} = \frac{c^2 \lambda^2}{c^2 + \tau^2 \lambda^2}$$
$$\lambda \sim C^+(0, 1)$$

Equations for Regularized Horseshoe Prior

Plant height and maturity are thought to have fewer, larger effect genes compared to traits like yield, test weight, and protein content. Theoretically, this means that the extreme sparsity and lesser regularization supplied by a Horseshoe prior compared to Bayesian Lasso could be beneficial to the prediction of height and maturity. The inverse should be true of prediction of yield, test weight, and protein instead benefitting from lesser variable selection and greater regularization provided by Bayesian Lasso compared to the Horseshoe prior. I will test the prediction accuracy of variable selection priors for plant height, maturity, yield, protein content, and test weight in spring wheat. Fivefold cross validation accuracy based on Pearson correlation coefficient, root mean square error, and mean error absolute for the expected versus fitted values will be the main metrics of predictive accuracy. Fitted values will also be extracted and compared to observed to calculate a correlation value for a model that has all datapoints included to give a measure of training accuracy.

$$Mean\,Error\,Absolute = \frac{sum_1^n |y - \hat{y}|}{n}$$

Equations for the three loss values

$$R^2 = \frac{sum_1^n (y - \hat{y})^2}{sum_1^n (y - \bar{y})^2}$$

$$Root\,Mean\,Square\,Error = \sqrt{\frac{sum_1^n (y - \hat{y})^2}{n}}$$

Secondary quantitative traits can be used to aid in the prediction of primary traits (Rutkoski et al. 2017). Plant yield is difficult to predict accurately compared to traits like protein content. Secondary traits that are correlated to primary traits can be included in prediction models to boost predictive accuracy. Secondary traits sourced from remote sensing imagery of wheat fields can be predictive of yield. Examples include normalized difference vegetative index, NDVI, calculated as a ratio of red pixels versus near infrared pixels over pictures taken of a wheat plot, are related to photosynthetic efficiency and crop productivity. Models with secondary traits included as predictors should have higher accuracy

measured through root mean square error in cross validation testing. By evaluating the posterior of secondary traits in prediction models relative to the very flat posteriors of individual genetic markers in the same prediction model, I can confirm the increased stability of predictions that result from including secondary traits.

Breeders are interested in furthering their understanding of advanced breeding populations. Understanding population level genetic correlations between breeding traits could be valuable for future breeding decisions (Bernardo 2014). If many genes that positively impact one trait have a negative impact on another trait, it could mean that improving both traits simultaneously will be difficult. If such relationships exist, breeders may be interested in introducing new genetic resources into their breeding germplasm to attempt and break this relationship. I will examine the coefficients of impactful genes between prediction models of different traits to find correlations between traits.

Data

This project will be working with data from a spring wheat breeding population grown in Pullman, Washington during the 2021 drought. Roughly 1,145 wheat lines were grown at Spillman Agronomy Farm with standard agronomic practices. The wheat lines were split into two separate experiments grown in proximity. Most lines were grown in the soft wheat preliminary yield trials while the remaining lines were grown in the hard preliminary yield trials. Soft wheats belong to a market class that demands lower protein content relative to the hard wheat market class. All wheat lines had their plot yield measured in bushels per acre, seed protein content measured by NIR spectroscopy as a percentage, seed test weight measured by weighing a standardized volume of seed, plant height measured by meter stick, and maturity notes taken by recording when pollination was occurring. Summary statistics for these traits are shown below.

Trait	Mean	Standard Deviation
Yield	33.37	8.68
Maturity	164.01	4.17
Height	26.46	3.63
Test Weight	58.17	3.38
Protein	12.28	1.61

Leaf tissue was sampled for each wheat line for DNA extraction. Extracted DNA was sent to North Carolina State Small Grains Genotyping Laboratory for genotyping by sequencing. Genotyping results were aligned to Chinese Spring Wheat Reference Genome Version One using Bridget-Wheeler Alignment. Marker variant calling was done using the TASSEL GBS Pipeline (Bradbury et al. 2007). Quality filtering on 10% missingness, 5% Minor Allele Frequency, and Mean Read Depth of 3 was done using VCF Tools. Redundant markers in close physical position were removed using TASSEL (Wang and Zhang 2021). The final VCF genotyping file was converted to Numerical format using GAPIT3 with a final 3,000 genetic markers included in prediction models.

A DJI Inspire-2 drone equipped with a Sentara Multispectral camera was flown over the experiments at peak maturity. The camera was able to capture narrowband Red, Green, Blue, Near Infrared, Red Edge, and two Far Infrared Edge bands. Reflectance information can be combined through several equations to yield unitless values that are indictive of plant health and performance. Secondary

traits calculated from these images include NDVI, NDRE1, NWI1, and NWI2. Summary statistics for these secondary traits and their correlation with yield is shown below.

Secondary Trait	Mean	Standard Deviation	Correlation to Yield
NDVI	0.476	0.049	0.119
NDRE1	-0.094	0.018	0.202
NWI1	-0.037	0.014	0.182
NWI2	0.013	0.015	0.088

Modeling

Models were implemented using the BRMS R Package (Bürkner 2017). BRMS users write code in R that is similar in syntax to other linear modeling packages. BRMS translates the model into Stan code and the NUTS sampler can be used to fit the model (Gelman et al. 2015). Long run times were experienced in modeling due to the highly dimensional nature of the data and within-chain threading was implemented to reduced run time. The reduce sum function implemented in Stan is responsible for speedup achieved by within chain threading (Stan User's Guide 26.1). Models were fit with two chains of 10,000 iterations and a 5,000 sample warmup period. For all models, information from all lines was used once to fit a main model which later had coefficients extracted. Five-fold cross validation was then implemented by randomly dividing the wheat lines into groups. Five new models were then fit with reduced datasets and the hold out lines were used as testers for model accuracy. Mean error absolute and root mean square error were measured on the testing groups by comparing against their observed trait values.

Two main priors were tested in this study, the double exponential for Bayesian Lasso and mixture distributions for Regularized Horseshoe Prior. Each prior was tested with several different prior specifications. For Bayesian Lasso, different degrees of freedom were tested and their impact on prediction accuracy recorded. Greater degrees of freedom should reduce shrinkage of coefficients. For the Horseshoe Prior in BRMS, users can specify an expected ratio of non-zero predictors through the par ratio parameter. Working with this method of expected ratio of non-zero predictors impact the global shrinkage parameter. The expected numbers of non-zero predictors specified for the Regularized Horseshoe does not force the final model to have this number of impactful predictors. The final posterior of every marker is still a product of the likelihood and prior specifications. Additionally, slab width can be modified which controls the amount of regularization on non-zero predictors. Different par ratio and slab width values were tested and the impact on predictions recorded as well.

Genotypic data is worked with in numerical format. This means minor allele homozygous genetic markers are 0 values, heterozygous markers are 1 values, and major allele homozygous markers are 2 values. The same three thousand genetic markers were used for every model. For models with secondary traits as predictors, all values must be scaled and centered for shrinkage priors to impact all parameters with equal effectiveness. The scale or secondary traits like NWI1 are normally in the negative .1 to .3 range while NDVI is normally on a positive scale between .3 and .6. A sample of

numerical genotypic data is shown in the table below. The taxa columns contain a wheat line's identifier name and each column represents one genetic marker.

taxa	S1A_1158055	S1A_1236236	S1A_1236254	S1A_1236317	S1A_1238021
SW17127-11	0	0	0	2	2
HR17076-6	0	0	0	2	2
HR17030-5	2	2	2	1	0
HR17030-3	2	2	2	0	0
HR17030-2	0	0	0	2	2
HR17030-1	2	2	2	0	0

Results

The chart below shows several loss values for cross validations of the two different Bayesian priors. For all five traits, there is better model fit with the Bayesian Lasso prior, shown by the Fitted R2 value, compared to Horseshoe prior. The greatest differences between the two priors in fitted values are for Maturity, Test Weight, and Yield. However, the differences between the two priors are not nearly as dramatic with cross validation prediction accuracies. Based on any of the three calculated loss values, there are no biologically meaningful differences in the predictive abilities for the two priors in predicting plant height or grain protein content. It is possible there is a slight advantage for Bayesian Lasso in predicting Test Weight over use of a Horseshoe prior. There is also possible a slight benefit to use of a Horseshoe prior in predicting yield over use of the Bayesian Lasso prior.

Looking at prediction accuracy metrics coming from cross validation, protein content had the highest prediction accuracy while plant height had the lowest. Protein content is a trait with much less environmental impact in its expression compared to plant height. The difficulty in predicting plant height could be caused by the extreme drought in the 2021 field season. Instead of differences in genetics explaining a large portion of the variance in height within the breeding population, instead a moisture gradient across the field could be more impactful.

| Maturity	Lasso DF1	Lasso DF3	Lasso DF5	Lasso DF10	Average Lasso	Horseshoe Default	Horseshoe .3 Par	Horseshoe .6 Par	Horseshoe .9 Par	Average Horse
RMSE	3.65	3.68	3.67	3.74	3.69	3.61	3.64	3.61	3.64	3.63
MEA	2.91	2.95	2.93	3.00	2.95	2.88	2.90	2.89	2.92	2.90
R2	0.35	0.34	0.37	0.35	0.35	0.39	0.38	0.41	0.38	0.39
Fitted R2	0.71	0.70	0.70	0.71	0.71	0.54	0.54	0.54	0.54	0.54
Height	Lasso DF1	Lasso DF3	Lasso DF5	Lasso DF10	Average Lasso	Horseshoe Default	Horseshoe .3 Par	Horseshoe .6 Par	Horseshoe .9 Par	Average Horse
RMSE	3.31	3.33	3.30	3.33	3.32	3.30	3.34	3.33	3.33	3.33
MEA	2.63	2.65	2.63	2.65	2.64	2.63	2.65	2.66	2.64	2.64
R2	0.25	0.25	0.26	0.25	0.25	0.27	0.25	0.24	0.24	0.25
Fitted R2	0.53	0.54	0.54	0.55	0.54	0.46	0.46	0.46	0.46	0.46

Test Weight	Lasso DF1	Lasso DF3	Lasso DF5	Lasso DF10	Average Lasso	Horseshoe Default	Horseshoe .3 Par	Horseshoe .6 Par	Horseshoe .9 Par	Average Horse
RMSE	2.90	2.88	2.93	2.89	2.90	2.94	2.92	2.92	2.92	2.93
MEA	2.24	2.24	2.26	2.24	2.25	2.29	2.28	2.27	2.27	2.28
R2	0.39	0.39	0.37	0.39	0.39	0.37	0.37	0.38	0.37	0.37
Fitted R2	0.69	0.69	0.69	0.70	0.69	0.55	0.55	0.55	0.55	0.55
Yield	Lasso DF1	Lasso DF3	Lasso DF5	Lasso DF10	Average Lasso	Horseshoe Default	Horseshoe .3 Par	Horseshoe .6 Par	Horseshoe .9 Par	Average Horse
RMSE	7.42	7.46	7.58	7.37	7.46	7.34	7.40	7.49	7.31	7.38
MEA	5.86	5.92	5.96	5.85	5.90	5.81	5.86	5.90	5.82	5.85
R2	0.31	0.30	0.29	0.32	0.30	0.32	0.32	0.30	0.33	0.32
Fitted R2	0.62	0.62	0.62	0.63	0.62	0.50	0.50	0.50	0.49	0.50
Protein	Lasso DF1	Lasso DF3	Lasso DF5	Lasso DF10	Average Lasso	Horseshoe Default	Horseshoe .3 Par	Horseshoe .6 Par	Horseshoe .9 Par	Average Horse
RMSE	1.03	1.02	1.04	1.02	1.03	1.05	1.05	1.05	1.04	1.05
MEA	0.80	0.80	0.81	0.80	0.81	0.83	0.82	0.82	0.81	0.82
R2	0.75	0.75	0.75	0.75	0.75	0.74	0.74	0.74	0.74	0.74
Fitted R2	0.76	0.76	0.76	0.77	0.76	0.73	0.73	0.73	0.73	0.73
RMSE, MEA, and R2 values are the result of five fold cross validation. Fitted R2 is a model with all data, no cross validation averaged posterior predictive checking.										

Although the prediction accuracies based on cross validation seem to be nearly identical for all traits comparing between the two different priors, there are meaningful differences in how the different priors assign marker effects. In the image below, a dot represents a single marker effect. The X axis represents that Markers effect with a Horseshoe prior and the Y axis represents the marker effect with a double exponential prior. The model intercept has been removed for these graphs; only genetic marker effects resultant from posterior median are shown.

Height Marker Effects
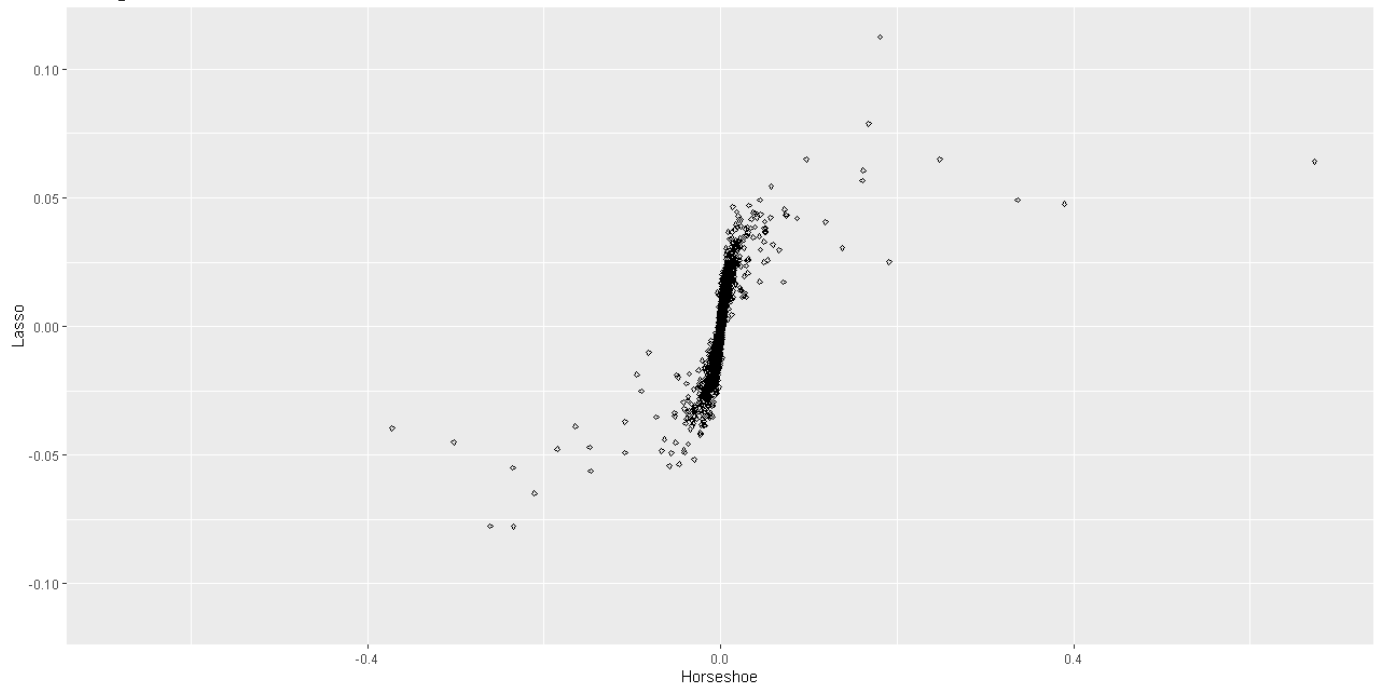
Protein Marker Effects
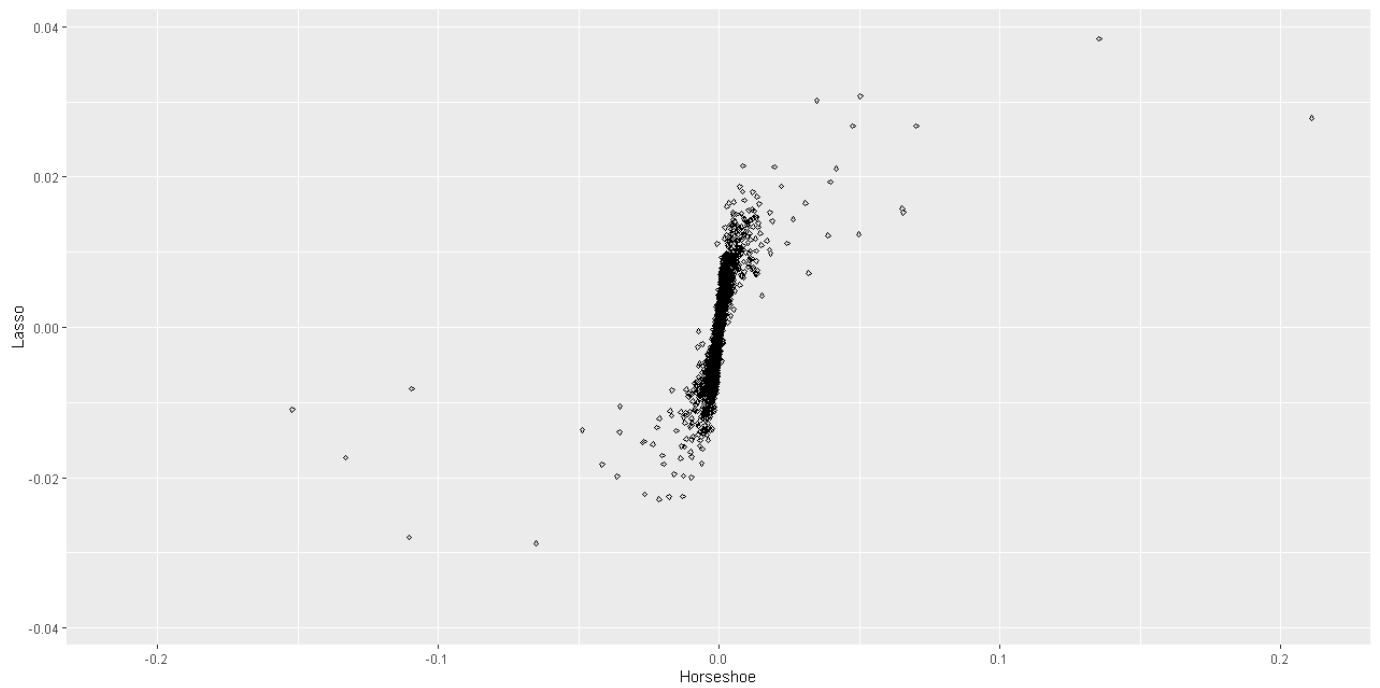
For the protein prediction comparison above, note the difference in maginute for marker effects. The largest positive effect for the Lasso model is just under .04% protein, the largest positive effect marker for the Horsesho prior model is over .2% protein.

The horseshoe prior had lower average error for marker coeffecients. However, this is due to the stronger variable removal that is present with the local shrinkage in the horeshoe prior. Markers that are assigned effects close to zero have relatively smaller posterior densities that leave posteriors draws very close to zero. However, even genetic markers that are assigned very large effects in models under a Horeshoe priors have 95% credible intervals that cross over having zero.

Average Marker Error	Lasso	Horseshoe
Height	0.054	0.042
Maturity	0.082	0.051
Protein	0.019	0.014
Test Weight	0.063	0.043
Yield	0.143	0.102

Different slab sizes were tested for the Horseshoe prior in predicting maturity, yield, and height. Greater slab sizes should reduce the regularization on large effect predictors. The table below shows that there is no clear advantage in predictive ability when regularization is reduced via greater slab sizes. Four slab sizes with the same par ratio of .3; default slab (in BRMS 2), 100 slab, 1000 slab, and 1000 slab were tested and cross validation was performed. Previous resulted for Average Horseshoe performance from the large table above are again shared for comparison. Although the effect is small, it does appear that there is a worse training data shown through the fitted R2 values being lower as slab sizes goes higher than default slab size of 2.

Maturity	Default Slab	100 Slab	1000 Slab	10000 Slab	Average Horse
RMSE	3.60	3.62	3.63	3.58	3.63
MEA	2.86	2.90	2.90	2.85	2.90
R2	0.39	0.38	0.38	0.40	0.39
Fitted R2	0.54	0.52	0.52	0.52	0.54
Yield	Default Slab	100 Slab	1000 Slab	10000 Slab	Average Horse
RMSE	7.40	7.49	7.32	7.35	7.38
MEA	5.86	5.91	5.83	5.82	5.85
R2	0.32	0.29	0.32	0.31	0.32
Fitted R2	0.50	0.44	0.44	0.44	0.50
Height	Default Slab	100 Slab	1000 Slab	10000 Slab	Average Horse

|					
RMSE	3.35	3.32	3.34	3.32	3.33
MEA	2.66	2.64	2.65	2.64	2.64
R2	0.24	0.24	0.23	0.25	0.25
Fitted R2	0.46	0.44	0.44	0.44	0.46

Increasing slab size does reduce shrinkage on the largest effect coefficients somewhat. The graph below shows several markers of large effect for yield with two different slab sizes. Given the very wide 95% interval covering the largest effect markers, these differences are subtle at best. There does not appear to be an advantage to trying to limit shrinkage on these largest effect predictors by increasing slab size.
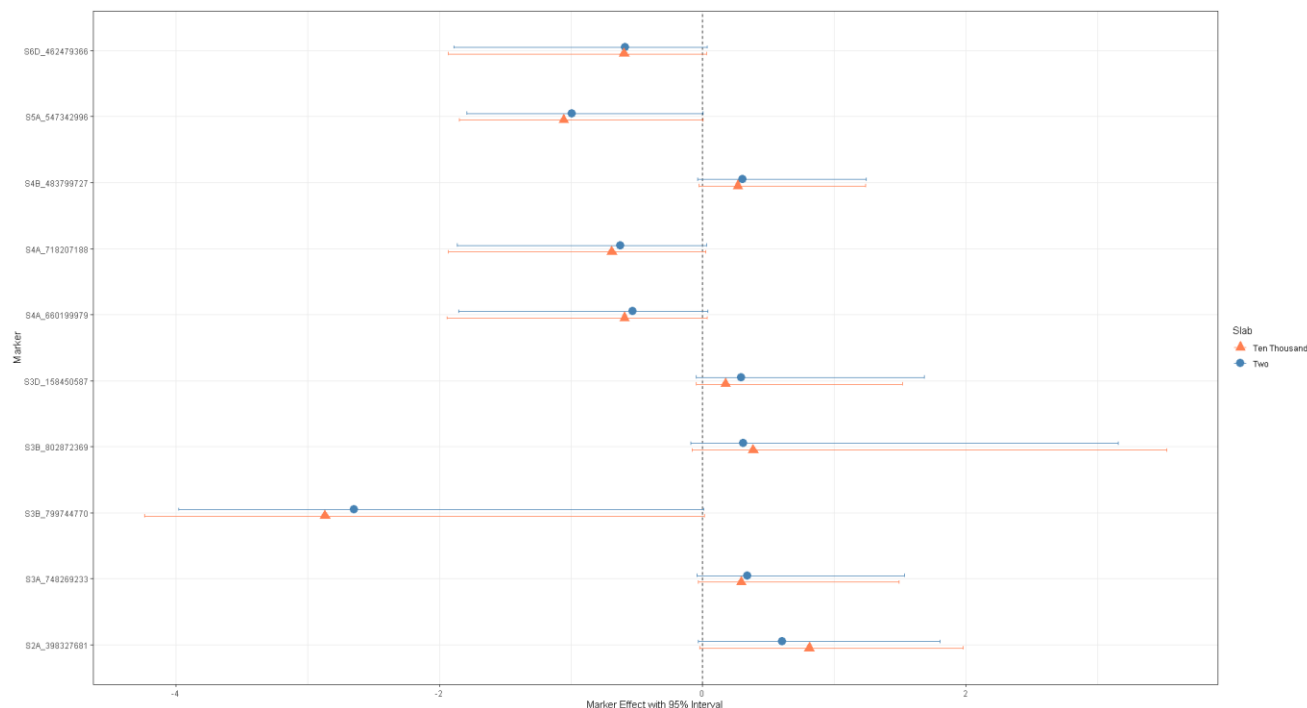

The table blow shows prediction accuracies for models with secondary traits as predictors when predicting yield. The average performance of models without secondary traits to predict yield is also shown. There are sizable improvements to prediction accuracies when secondary traits are included. There is a subtle advantage of NDRE1 as a secondary trait compared to NWI1. A model fitted with four secondary traits has slightly better loss values compared to the models fit with only one secondary trait. The models with a Horseshoe prior have a very slight advantage in prediction accuracy compared to Lasso in all three models that have secondary trait information included. Again, the Lasso models have a better to training data compared to Horseshoe prior models.

| All secondary traits	Lasso	Horseshoe		NWI1 included	Lasso	Horseshoe
RMSE	0.820	0.820		RMSE	0.826	0.829
MEA	0.643	0.642		MEA	0.650	0.656
R2	0.499	0.506		R2	0.489	0.491
Fitted R2	0.755	0.529		Fitted R2	0.754	0.527
NDRE1 included	Lasso	Horseshoe		no secondary trait	Average Lasso	Average Horse
RMSE	0.822	0.821		RMSE	1.155	1.100
MEA	0.642	0.642		MEA	0.754	0.731
R2	0.495	0.505		R2	0.304	0.319
Fitted R2	0.757	0.527		Fitted R2	0.621	0.496

The secondary traits have more well-defined posteriors in terms of distance from zero compared to marker effects. The graph below shows predictor effects with a 95% credible interval over the mean effect for a model fit with a Horseshoe prior. Only the top ten predictors in absolute terms are included in these graphs for ease of viewing. The gains in predictive accuracy with secondary traits and well-defined posteriors of these secondary traits show the merit in incorporating this type of information in predictive models for wheat.

Top Ten Predictors with Four Secondary Traits

Top Ten Predictors with NWI1 as a Secondary Trait

Top Ten Predictors with NDRE1 as a Secondary Trait
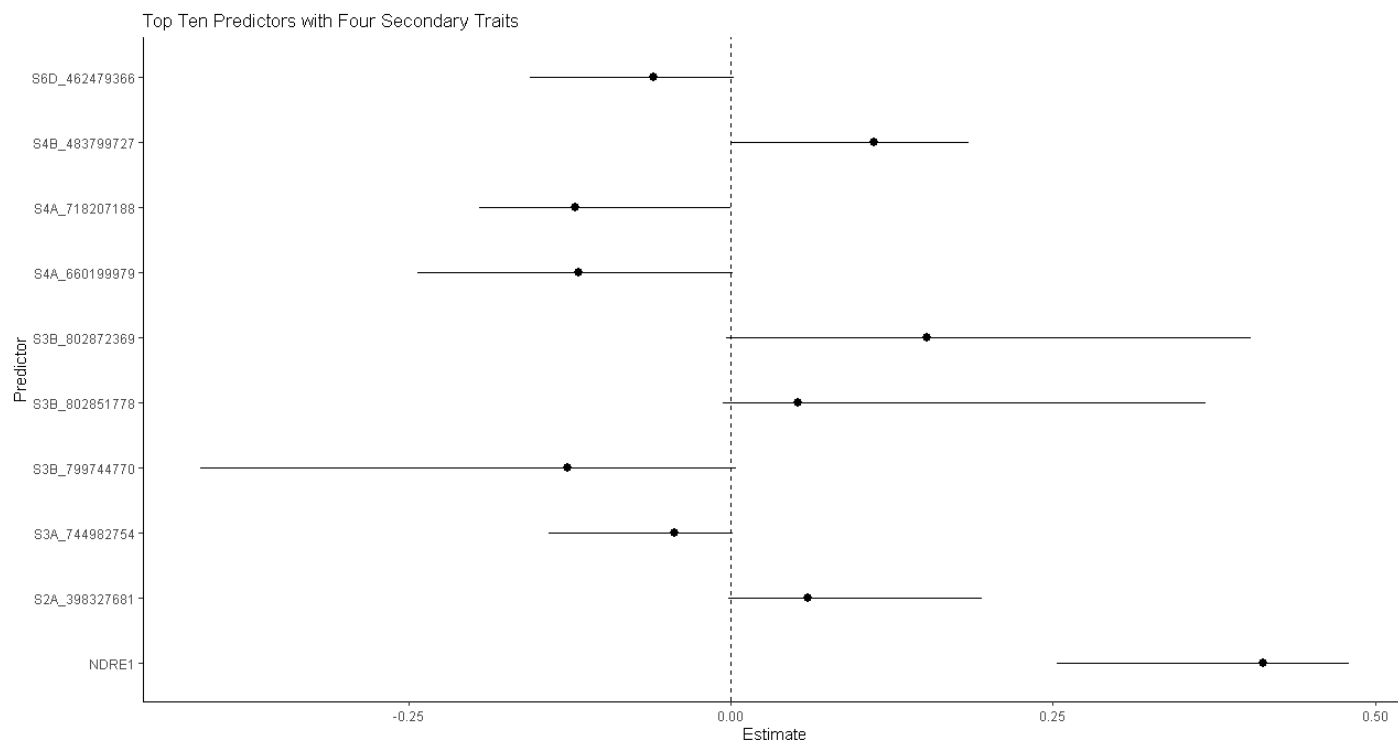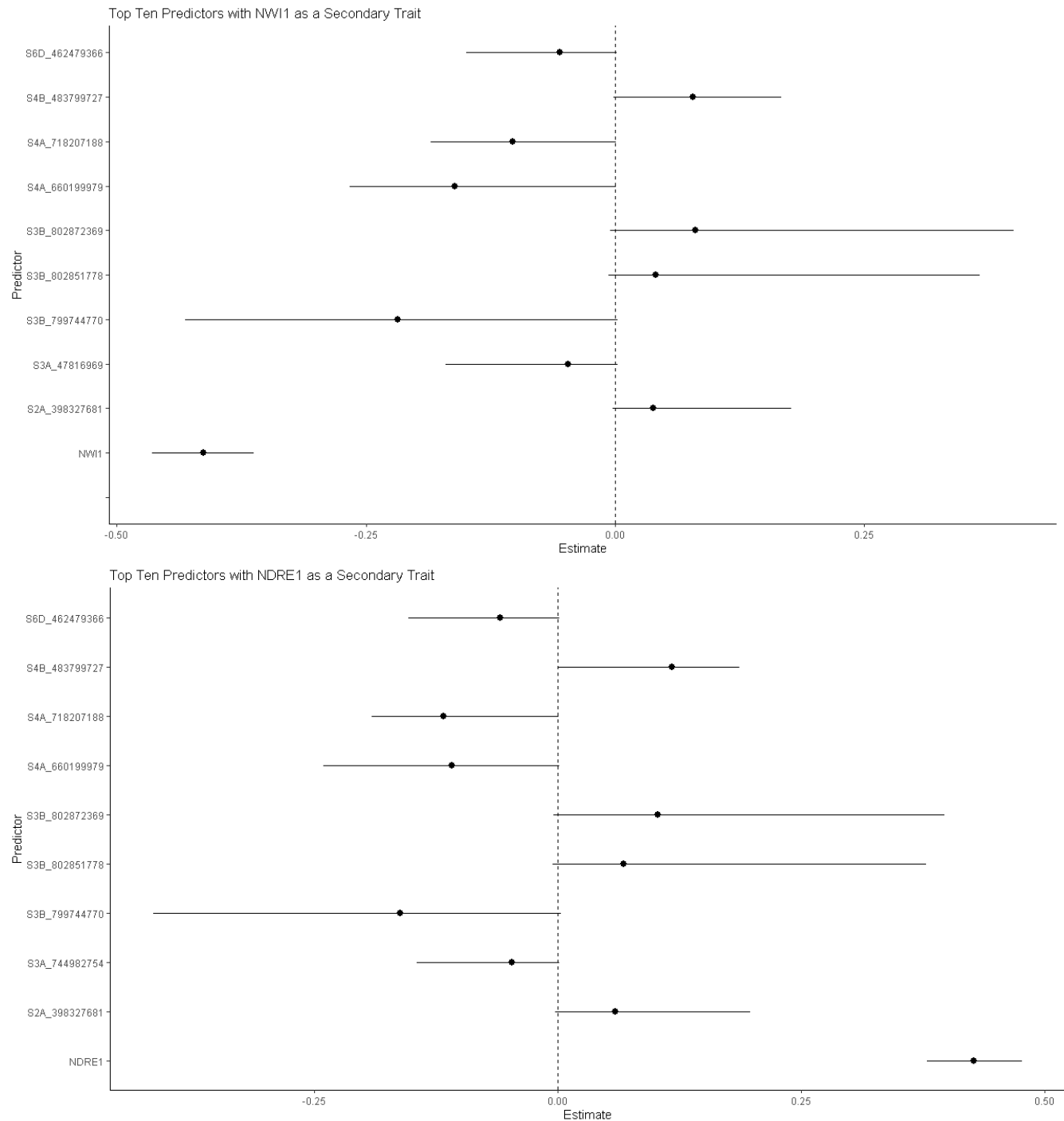
In looking for related trends in genetic marker effects between traits, there was only one trait pair that appeared to have possible genetic linkage. Test weight and yield shared several markers that had large effects on both traits. A graph below shows marker effects with a model fitted with a Horeshoe prior, there are several genetic markers that seem to strongly reduce yield and test weight. Conversely, there were several markers that increased both traits. This makes sense given the physgiology that explain both traits. Increased crop yields are mostly caused by increases in seed weight.

Higher test weights, which is what farmers look for in wheat varities, are caused by denser seeds due to tighter startch packing within the seed. Seed wheat and startch packing are strongly correlated traits. No other pairs of traits showed any meaningful relationships when comparing marker effects from models fit with either Lasso or Horseshoe priors. A table below shows four markers that have large effects on both yield and test weight.

Comparison of Marker Effects between Test Weight and Yield
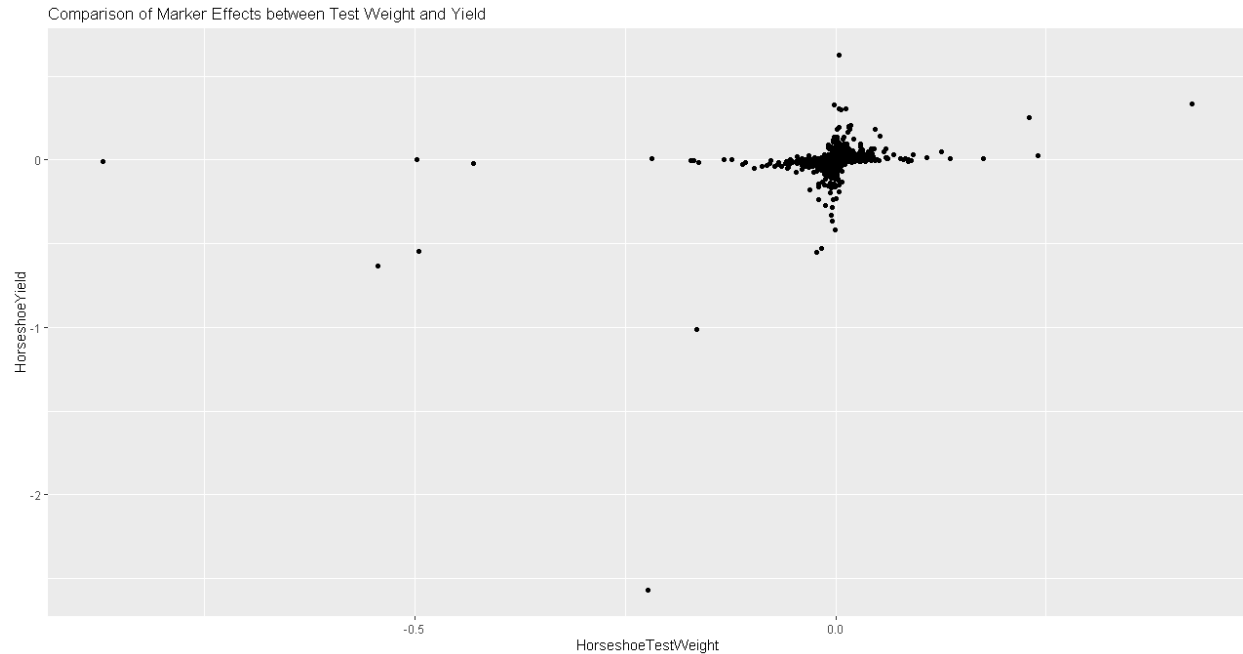
Marker	Test Weight Effect	Yield Effect
S4A_718207188	-0.543452742	-0.633779388
S4A_660199979	-0.495104301	-0.546434387
S3B_802872369	0.423618877	0.332804328
S3B_802851778	0.229561454	0.250470085

Conclusion

There is no significant advantage in choosing a Lasso or Horseshoe prior for out of fold testing prediction accuracy. However, the Lasso prior consistently explains more variance in the training data compared to the Horseshoe prior. Given that plants must be grown and phenotyped to be part of a training population and thus their merit is already known, picking a model that can explain more of the fitted data is not especially useful compared to more accurate predictions. The greater sparsity of the Horseshoe prior does not offer a significant advantage or disadvantage even when modifying prior specifications.

Changing prior specifications for Bayesian Lasso or the Horseshoe prior did not offer any clear benefits for prediction accuracy. In BRMS, increasing the degrees of freedom for the Lasso prior should reduce shrinkage. There was no benefit for moving from one to ten degrees of freedom for all studied traits. Specifying an expected number of impactful predictors to impact the global shrinkage power present in the Horseshoe prior also did not have a meaningful impact on prediction accuracy. Increasing

slab width will reduce the regularization of powerful predictors, but greater slab widths did not seem to impact prediction accuracy significantly. There was a small reduction in the regularization of the top few predictors in all traits that had wider slab widths tested.

Secondary traits greatly improve the prediction accuracy of yield. There are only subtle gains in accuracy by attempting to choose one secondary trait over another to include. Incorporating several secondary traits into yield prediction also only offers a slight improvement in predictive abilities. Variable selection priors like the Horseshoe prior seem to favor the strongest, individual predictors such as NDRE1 while weaker predictors like NWI2 are pulled to zero. Lasso prior leaves all secondary traits with non-zero coefficients although weaker predictors like NWI2 are assigned relatively small coefficients.

Test weight and yield predictive models with Horseshoe priors both assigned large coefficients to the same group of genetic markers. This offers some insight into the possibility for making rapid improvements in both traits through selection. The lack of negative linkages between other traits is surprising. Normally maturity and plant height have a negative genetic relationship. Plants that finish growing faster relative to the average also tend to be shorter than average, but there does not appear to be genetic markers present that highlight this relationship.

References

Bernardo, Rex. Essentials of Plant Breeding. Stemma Press. 2014. ISBN 978-0-9720724-2-7

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*(19), 2633–2635. https://doi.org/10.1093/bioinformatics/btm308

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software, 80(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Carvalho, C., Polson, N., & Scott, J. (2009). Handling Sparsity via the Horseshoe. *JMLR*.

Falconer, DS. Mackay, TFC. Introduction to Quantitative Genetics. Benjamin-Cummings Pub Co, 1996.

Gelman, A., Lee, D., & Guo, J. (2015). Stan. *Journal of Educational and Behavioral Statistics*, *40*(5), 530–543. https://doi.org/10.3102/1076998615606113

Meuwissen TH, Hayes BJ, Goddard ME. Prediction of total genetic value using genome-wide dense marker maps. Genetics. 2001 Apr;157(4):1819-29. doi: 10.1093/genetics/157.4.1819. PMID: 11290733; PMCID: PMC1461589.

Morgante, F., Huang, W., Maltecca, C., & Mackay, T. F. (2018). Effect of genetic architecture on the prediction accuracy of quantitative traits in samples of unrelated individuals. *Heredity*, *120*(6), 500–514. https://doi.org/10.1038/s41437-017-0043-0

Park, T., & Casella, G. (2008). The bayesian lasso. *Journal of the American Statistical Association*, *103*(482), 681–686. https://doi.org/10.1198/016214508000000337

Piironen, J., & Vehtari, A. (2017). On the Hyperprior Choice for the Global Shrinkage Parameter in the Horseshoe Prior. *AISTATS* . https://doi.org/ https://doi.org/10.48550/arXiv.1610.05559

Piironen, J., & Vehtari, A. (2017). Sparsity information and regularization in the Horseshoe and other shrinkage priors. *Electronic Journal of Statistics*, *11*(2). https://doi.org/10.1214/17-ejs1337si

Rutkoski J., Poland J., Mondal S,. Autrique E., Perez L., Crossa J., Reynolds M., Singh R., Canopy Temperature and Vegetation Indices from High-Throughput Phenotyping Improve Accuracy of Pedigree and Genomic Selection for Grain Yield in Wheat, G3 Genes|Genomes|Genetics, Volume 6, Issue 9, 1 September 2016, Pages 2799–2808, https://doi.org/10.1534/g3.116.032888

Stan Development Team. Stan User's Guide Version 2.31. https://mc-stan.org/docs/stan-users-guide/index.html#overview

Wang J., Zhang Z., GAPIT Version 3: Boosting Power and Accuracy for Genomic Association and Prediction, Genomics, Proteomics & Bioinformatics (2021), doi: https://doi.org/10.1016/j.gpb.2021.08.005.

Xu, S. (2003). Theoretical basis of the Beavis effect. *Genetics*, *165*(4), 2259–2268. https://doi.org/10.1093/genetics/165.4.2259

Zuk, O., Hechter, E., Sunyaev, S. R., & Lander, E. S. (2012). The mystery of missing heritability: Genetic interactions create phantom heritability. *Proceedings of the National Academy of Sciences*, *109*(4), 1193–1198. https://doi.org/10.1073/pnas.1119675109