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MULTI-PARENTAL MATING DESIGN ANALYSIS: MODEL EVALUATION AND APPLICATION IN SPRING WHEAT

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Abstract

Conventional quantitative genetics studies have mainly focused on bi-parental mating systems. However, genetic potential of selected individuals within a segregating population may be limited due to only two parents being used for each cross. Multiple-parental mating systems have been proposed that involve three or four diverse parents. This provides a higher potential of combining desirable genes. Due to complexity of the data structure of multi-parental mating systems, analysis of variance (ANOVA) methods are not applicable in analysis. The objective of this study is to validate and apply a mixed linear model approach, minimum norm quadratic unbiased estimation (MINQUE), to analyze a widely used additive-dominance (AD) genetic model. Various simulations were conducted to validate the use of this approach. Twelve different spring wheat genotypes were used to develop populations in the study. Phenotypic data containing parents and their F_2 (second filial generation) on preharvest sprouting (PHS) resistance in spring wheat (*Triticum aestivum* L.) developed by multi-parental crosses were used as a demonstration. The simulation study showed that a modified AD model can be used to estimate variance components in an unbiased manner within this complex data structure. Actual data analysis revealed that both additive and dominance effects were responsible for PHS resistance. Several parents associated with desirable additive effects for PHS were identified. In addition, some crosses with desirable heterozygous dominance effects were also identified, which can be used for hybrid development. Results should help breeders to obtain useful genetic information by using the methods suggested in this study.

Key words: Preharvest sprouting, minimum norm quadratic unbiased estimation, additive dominance-model.

1. Introduction

Wheat (*Triticum aestivum* L.) is a major food source for millions of people in the world. There are many factors limiting wheat production, and out of these pre-harvest sprouting (PHS) of grain has been a severe problem in many parts of the world including the US. Pre-harvest sprouting is defined as the condition of in-spike germination of physiologically mature seeds during unfavorable harvest conditions. In other words, PHS occurs when harvest time coincides with relatively high humidity in the field due to untimely rainfall (King, 1984; Derera et al., 1976).

Pre-harvest sprouting has resulted in yield loss, as well as degradation of nutritional and processing quality of grain. This will eventually lead to economic losses to farmers and the processing industry. Exposure of grain to wet conditions during the ripening stage triggers a sequence of physiological processes such as release of alpha-amylase enzyme. With increased alpha-amylase activity, the grain carbohydrate reserve is hydrolyzed affecting bread wheat quality causing yield loss, reduced test weight, sticky crumb, collapsed loaves, and dark-colored crusts (Derera et al., 1976; Mares et al., 2005). Hagberg falling number test (AACC, 2000) is used to quantify sprout damage, which measure starch degradation due to alpha amylase activity before appearance of any visible sprouting symptoms (Stoy, 1982). Sound, non-sprouted grain contains less alpha-amylase activity, which prolongs the time to degrade gelatinized starch, and results in a higher falling number. In durum wheat (*Triticum turgidum* L.), PHS can decrease test weight, increase semolina bran specks, cooking losses, poor color, decreased firmness, and reduced spaghetti stickiness values. Thus, PHS limits the production of high quality wheat for export and also for domestic use.

Since PHS can cause significant damage to wheat growers and processors by reducing yield and baking quality, improving PHS resistance is a prioritized breeding objective that breeders have sought for years. Development of PHS-resistant cultivars is likely the most effective way to address the problem. Pre-harvest sprouting resistant cultivars are highly desirable in wheat growing areas where periods of wet weather frequently occur during harvest. Breeding for PHS resistance is challenging however, as it is quantitatively inherited and influenced by many factors including genetic constitution of the line, gene interaction, environmental conditions, and genotype × environment interactions. Screening and selection on the basis of phenotype is difficult, and DNA markers linked to genes involved in PHS represent a more reliable tool for selecting resistant genotypes (Tan et al., 2006).

Developing desirable PHS resistance lines with competitive yield potential rely on identification of genetic information among various crosses being made. Data analyses on these crosses play an important role. Many quantitative genetic studies are based on bi-parental mating schemes, which include North Carolina I (NCI), North Carolina II (NC II), and diallel mating designs (Comstock and Robinson, 1948, 1952; Griffing, 1956). By using analysis of variance (ANOVA) methods, valuable genetic information, such as genetic variance components and genetic effects, can be obtained and used for crop improvement. Since selection from bi-parental crosses may be limited, three- or four-parental crosses (i.e., multi-parental crosses) have been used to develop populations for selection (Nandarajan & Gunasekaran, 2005). Unlike bi-parental mating designs, a multi-parental cross can contain more diverse alleles for selection. However, theoretical investigations on multi-parental mating designs are limited due to complex genetic structures and pedigrees. Further theoretical investigation of multi-parental mating designs will be an important addition to current knowledge associated with genetic mating designs.

Mixed linear model approaches have been proposed and can be used for complex model and unbalanced data structure from long time (Hartley and Rao, 1967; Rao 1971, Zhu, 1998). These are matrix and vector based approaches, which offer flexibility in analyzing complex data structures. There are three types of mixed linear model approaches: maximum likelihood (ML), restricted maximum likelihood (REML), and minimum norm quadratic unbiased estimation (MINQUE) (Hartley and Rao, 1967; Rao, 1971; Searle et al., 1992). The MINQUE approach was proposed by Rao (1971) for estimating variance components and to predict effects of interest. Both ML and REML process requires iteration procedure and assumption of normally distributed data. MINQUE approach can be applied to different data distribution and does not require iteration process (Rao, 1971).

Among various genetic models proposed (Zhu, 1993; Wu et al., 2010a), the additive-dominance (AD) model is one of the most commonly used genetic models. Our first objective of this study was to develop and validate an AD model for the complex data structure developed from three- and four-parental crosses. Using mixed linear model approaches, we numerically evaluated empirical Type I errors and testing powers for variance components with simulated genetic data. Our second objective was to apply this AD model and approach to an actual data set composed of 12 spring wheat parents and 109 three- or four-parental crosses. Variance components, heritability, and genetic effects for PHS were calculated.

2. Materials and Methods

2.1. Population development and structure

In order to increase genetic diversity and combine more favorable alleles in line development, the population in our study was developed from three- or four-way crosses of different spring wheat genotypes. Figure 1, provides an example of development of a single family from a three-way cross giving rise to four individual progeny. In total, 12 spring wheat genotypes were used as parents to create 109 multi-parent families which gave rise to 729 F_2 individuals. Complete list of families developed in this along with respective parents used in crosses is presented in Appendix 1. These spring wheat genotypes were selected from spring wheat breeding program and had varying level of PHS resistance.

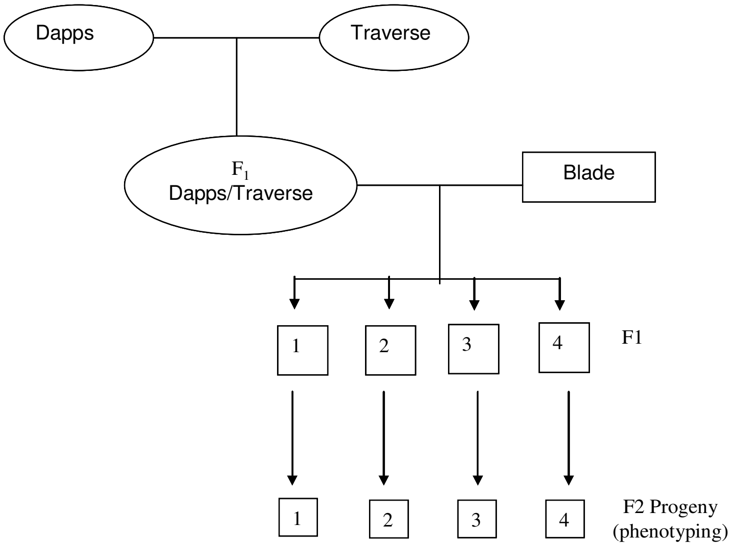

Figure 1. Example of a family

2.2. Phenotypic evaluation

Pre-harvest sprouting resistance test were conducted with F_2 progeny from each individual within F_1 families. Phenotyping based on a progeny test was performed as a measure of PHS. Intact spikes were hand harvested at physiological maturity (loss of green color from the peduncle and glumes). Harvested spikes were air dried for 3-5 days under ambient temperature and stored in -20^0 C to preserve dormancy prior to evaluation. Sprouting experiments were carried out in a greenhouse mist chamber developed for this purpose. About 10 spikes from each line were tested visually for sprouting resistance. All spikes were tested by being placed in a rack made of wire mesh. To maximize uniformity of the mist treatment, racks were repositioned daily within chamber (Rasul et al., 2009). Humidity conditions inside the chamber were maintained by applying mist for 60 sec at 60 min intervals throughout the entire experiment. Spikes were kept inside the chamber for 3-5 days. Spikes of each line were rated based on 0 to 9 scale, where 0 indicated no visible sprouting and 9 indicated extensive visible sprouting over entire spike (McMaster and Derera, 1976). All parents used in developing populations were also tested for PHS resistance and considered checks.

2.3. Genetic Model and Data analysis

The AD genetic model and its extensions have been widely used in different studies (Zhu, 1998; Tang et al., 1996; Wu et al., 2010a; Saha et al., 2006; Jenkins, 2006, 2007). Assume that there are no genotype-by-environment interaction effects and there are normal segregations in each cross. Given an AD model, genetic components for parents and crosses (bi-, tri-, and tetra-parental crosses) at different generations are different. For generalization and simplicity, we assume that the female is a F_1 cross of parents *i* and *j* and the male is a F_1 cross of parents *k* and *l*. If these genotypes are evaluated in a field with a randomized complete block (RCB) design, a generalized AD model for the cross of $F_{1(ij)}$ and $F_{1(kl)}$ in the r block can be developed based on Cockerham's genetic model (1980):

For F_1:

$$Y_{ijklr(F_1)} = \mu + \frac{1}{2}A_i + \frac{1}{2}A_j + \frac{1}{2}A_k + \frac{1}{2}A_l + \frac{1}{4}D_{ik} + \frac{1}{4}D_{jk} + \frac{1}{4}D_{il} + \frac{1}{4}D_{jl} + B_r + e_{ijklr(F_1)} \quad (1)$$

For F_2:

$$Y_{ijklr(F_2)} = \mu + \frac{1}{2}A_i + \frac{1}{2}A_j + \frac{1}{2}A_k + \frac{1}{2}A_l + \frac{1}{8}D_{ii} + \frac{1}{8}D_{jj} + \frac{1}{8}D_{kk} + \frac{1}{8}D_{ll} + \frac{1}{8}D_{ik} + \frac{1}{8}D_{jk} + \frac{1}{8}D_{il} + \frac{1}{8}D_{jl} + B_r + e_{ijklr(F_2)} \quad (2)$$

Where μ is the population mean; A_i, A_j, A_k or A_l is the additive effect; $(D_{ii}, D_{jj}, D_{kk}, D_{ll}, D_{ik}, D_{jk}, D_{il}$ or $D_{jl})$ is the dominance effect; B_r is the block effect. The last term is the random error. It is reasonable to treat additive and dominance effects as random because parents were chosen from a large population.

It must be pointed out that these two equations can be converted to different mating designs. For example, if i=j=k=l, the AD model in equations (1) and (2) becomes an AD model for parent. If i=j and k=l, the above equations are for a bi-parental cross. If i=j and k≠l or i≠j and k=l, these two equation are for a tri-parental cross. If i≠j and k≠l, then these equations are for a tetra-parental cross. These two equations are more generalized than those for bi-parental crosses reported previously. In addition, if no block effect is included in the model, then this effect B_r can be deleted from these two equations.

Analysis of variance methods are unable to estimate variance components and genetic effects for the above two equations which include complex genetic structures. Thus, we applied a mixed linear model approach, minimum norm quadratic unbiased estimation (MINQUE), which has been extensively used in various studies (Zhu, 1989, 1994; Zhu and Weir, 1994; Wu et al., 2006a, b, 2010a,b), to estimate variance components. In order to apply MINQUE approach, the above two equations can be expressed in terms of vectors and matrices as follows:

$$y = 1\mu \ + U_A e_A + U_D e_D + U_E e_B + e_e \tag{3}$$

Where, **y** is an observation vector with dimension $n \times 1$, known; μ is the population mean as defined as above;
1 is the vector with all elements 1;
e_A is the vector for additive effects, $e_A \sim MVN\ (0, \sigma_A^2 \mathrm{I})$;
$\boldsymbol{U_A}$ is the incidence matrix for additive effects;
e_D is the vector for dominance effects, $e_D \sim MVN\ (0, \sigma_D^2 \mathrm{I})$;
$\boldsymbol{U_D}$ is the incidence matrix for dominance effects;
e_B is the vector for block effects, $e_B \sim MVN\ (0, \sigma_B^2 \mathrm{I})$;
$\boldsymbol{U_B}$ is the incidence matrix for block effects;
e_e is the vector for random errors, $e_e \sim MVN\ (0, \sigma_e^2 \mathrm{I})$.

Variance components in the above AD model can be estimated by solving the following MINQUE normal equations for u, v = 1, 2, …, 4 if block effects are included:

$$[tr(U_u^T Q_\alpha U_v^T U_v Q_\alpha U_u)][\sigma_u^2] = [y^T Q_\alpha U_u U_u^T Q_\alpha y] \tag{4}$$

where the trace *tr* is the sum of diagonals of a matrix and

$$Q_\alpha = V_\alpha^{-1} - V_\alpha^{-1} X (X^T V_\alpha^{-1} X)^{-1} X^T V_\alpha^{-1} \tag{5}$$

Where $V_\alpha = \sum_{u=1}^{4} \alpha_u U_u U_u^T$ and V_α^{-1} is the inverse matrix of V_α with prior values α_u in place of σ_u^2 in V_α. Since different prior values yield similar variance component estimation (Zhu, 1989), we set $\alpha_u = 1$.

In this study, we primarily focused on spring wheat data sets which simply follow complete randomized design (CRD), so there were no block effects and block effects were deleted from the model accordingly. Thus, only three components were included. The first section of this study was that of genetic model evaluation, as data set was complicated with either 3 or 4 parents. Simulation study was conducted to evaluate appropriateness of using mentioned genetic model for data analysis. Bias, Type I error, testing power and mean square error (MSE) (Wu et al., 2006a, 2010b) were calculated from simulation procedure based on 200 simulations. In the first case, all variance components were set to zero except random error. This case evaluated Type I error for all variance components except random error. In the second case, all variance components, including random error, were set to 20. This was done to determine testing powers for different variance components at different probability levels. The jackknife procedure was applied for statistical tests by randomly removing 10% of observations each time and repeated 20 times (Wu et al., 2010b).

The second section of this study was the application of this genetic model to an actual spring wheat data set. Phenotypic data from F_2 progeny from families and parents were analyzed for genetic model evaluation. In addition to variance component estimation, genetic effects for additive effects and dominance effects were predicted by the adjusted unbiased prediction approach (Zhu, 1993). All genetic model evaluation and actual data analysis were conducted by a computer program GenMod (Wu et al., 2010a). Details about this computer program and its use have been described in the paper from previous proceedings of this conference (Wu et al., 2010a).

3. Results and Discussion

3.1 Simulation study

The simulation study was important to evaluate appropriateness of using this model with the data structure discussed. Simulation results from two different specific cases are presented in Tables 1 and 2. Results showed that each variance component was estimated in an unbiased manner (Table 1). Type I error for both additive and dominance variance were 0.05 and 0.04 respectively.

Table 1. Estimated Type I error for estimating Variance Component for AD model

	Pre-set value	**Bias**	**Type I error**	**MSE**
V_A	0	0.00	0.050	0.816
V_D	0	0.114	0.040	0.675
V_e	20	0.037	-	0.013

The testing power of both additive and dominance effects were desirable (Table 2). Thus simulated results indicated that using the modified AD genetic model gives an unbiased estimation of variance components with desirable biases, type I error, and testing power.

Table 2. Estimated Testing Power for estimating Variance Component for AD Model

	Pre-set value	Bias	Power	MSE
V_A	20	-0.617	1.000	0.816
V_D	20	0.614	0.98	0.675
V_e	20	0.081	1.000	0.013

3.2. Actual data analysis

3.2.1. Phenotypic means for parents and F_2 progeny

In this study, only the PHS trait is discussed among parents and F_2 populations. Preharvest sprouting resistance scores of individual plant of parent ranged from 2 to 9 explaining the range of resistance. Mean PHS score of all parents is about 6.798. Mean PHS scores of F_2 progeny within F_1 families range from 4.96 to 7.38 slightly lower than overall parent's score (Table 3). However, each F_2 individual's PHS score within F_1 families range from 1 to 9, explaining range of resistance level present in populations.

Table 3. Mean, minimum, and maximum PHS score for parents and F_1 families

		PHS score
Parent	Mean	6.798
	Min	2.000
	Max	9.000
F_1 families	Mean	6.286
	Min	4.960
	Max	7.380

Lists of parents used in the developing populations along with their average PHS scores are listed in Table 4. Among the 12 parents used in this study, 'Dapps' had the lowest PHS score and was most resistant whereas 'Ingot', with highest score was the most susceptible parent. Most of the parents used in the study are susceptible to PHS, whereas some genotypes such as 'AC-Snowbird', 'Argent', 'Blade', and 'Grandin' appear moderately susceptible.

Table 4. Parental means for PHS score

Parents	Average PHS score
AC-SNOWBIRD	6.008
ARGENT	6.566
BLADE	6.425
DAPPS	5.150
GRANDIN	6.126
GRANGER	7.13
HAT-TRICK	7.35
INGOT	7.96
LOLO	7.103
LOSCHA	7.031
TRAVERSE	7.042
ULEN	7.304

3.2.2. Variance Components

Explained AD model was used in actual data analysis of this study. Different variance components that make up genetic effects were calculated and summarized as Table 5. Both additive and dominance variance were significant for PHS. This revealed that both variance components were responsible for PHS resistance. Estimated variance components expressed as proportions of total phenotypic variance are summarized in Table 6.

Table 5. Estimation of Variance Components

Parameter	Estimate	SE
Additive variance (V_A)	0.549^{****}	0.036
Dominance variance (V_D)	0.442^{**}	0.095
Residuals (V_E)	0.746^{****}	0.018
Phenotypic variance (V_P)	1.738^{****}	0.084

=0.01, **=0.0001 significance level

Heritability estimates are useful in formulating breeding plans to achieve the most progress from selection. Heritability can be defined in several ways, but stated simply it describes how much a character is transferred to offspring from parents. Both broad- and narrow-sense heritabilities were calculated. Broad-sense heritability (ratio of both additive and dominance to phenotypic variance) was 0.57 and narrow-sense heritability (ratio of additive to phenotypic variance) was 0.315 (Table 4). Higher narrow-sense heritability allows for greater progress to be made through early-generation trait selection and few tests are generally required. However in this case, where narrow-sense heritability was not high, selection in later generations using tests carried out in space and time is suggested to most effectively improve PHS resistance.

Table 6. Estimated Proportion of Variance Component for AD Model using F_2 and Parent's PHS Trait

Parameter	Estimate	SE
V_A/V_P	0.315****	0.022
V_D/V_P	0.254***	0.041

=0.001, *=0.0001 significance level

3.2.3. Additive effects

Additive effects which are equivalent to general combining ability in an AD model, is important in line development. Table 7 summarizes additive effects for each spring wheat parent used in this study. Genotypes such as 'Dapps', 'AC-Snowbird' and 'Loscha' had significant negative additive effects, whereas 'Ingot', 'Hat-Trick', 'Granger' and 'Lolo' had significant positive effects for PHS resistance. In order to increase PHS resistance, lower phenotypic values are required. Negative additive effects will increase resistance and positive additive effects will decrease resistance. Parents with significant negative additive effects are good general combiners for increasing resistance. These genotypes can be considered while making crosses to improve resistance against PHS. Parents with significant positive effects will more likely increase susceptibility and should be avoided as much as possible.

Table 7. Predicted Additive Effects for PHS Resistance

Parents	Estimate	SE
DAPPS	-0.718***	0.051
AC-SNOWBIRD	-0.796***	0.044
LOSCHA	-0.639***	0.052
GRANDIN	-0.065	0.036
ULEN	0.0003	0.033
ARGENT	-0.090	0.031
INGOT	0.775***	0.038
HAT-TRICK	0.646***	0.000
GRANGER	0.583***	0.000
LOLO	0.256***	0.001

***=0.001 significance level

3.2.4. Dominance effects

Two types of dominance effects, homozygous (Table 8) and heterozygous dominance effects (Table 9) were predicted. Homozygous dominant effects measure the degree of inbreeding depression following hybrid selfing. Negative homozygous dominance for parents results in greater amount of inbreeding depression in progeny, if the parents are used in cross, following selfing. Both effects are useful in the case where breeders are interested in hybrid development and utilization.

Table 8. Predicted homozygous dominant effect for PHS resistance

Parent	Estimate	SE
DAPPS	0.567^{*}	0.138
AC-SNOWBIRD	0.866^{****}	0.125
LOSCHA	1.496^{****}	0.216
GRANDIN	-0.779^{**}	0.152
ULEN	2.004^{****}	0.270
ARGENT	-0.176	0.119
INGOT	-0.116	0.127
HAT-TRICK	-0.526^{**}	0.112
BLADE	-0.249	0.104
GRANGER	-0.522	0.188
TRAVERSE	0.435^{*}	0.121
LOLO	0.052	0.111

*=0.05, **=0.01, ****=0.0001 significance level

Heterozygous dominant effects are related to specific combining ability for the pair of parents in a cross. Significant heterozygous dominant effect is useful for hybrid development. In this study, crosses that lead to negative estimates of dominance effects can increase resistance against PHS in early generations; where as positive estimates in the crosses might further increase susceptibility. Such information can be used by breeders for capturing heterosis. For example, crosses with negative heterozygous dominance effects such as ‘Dapps × AC-Snowbird’, Loscha × Dapps’, ‘Dapps × Ulen’ etc from following can be used to capture heterosis for PHS resistance.

Table 9. Predicted Heterozygous Dominance Effects for PHS Resistance

Parents in cross	Estimate	SE
DAPPS × AC-SNOWBIRD	-0.694****	0.107
LOSCHA × DAPPS	-0.855*	0.255
DAPPS × GRANDIN	-0.037	0.181
DAPPS × ULEN	-0.972**	0.232
DAPPS × ARGENT	-0.009	0.131
DAPPS × INGOT	-0.545	0.179
DAPPS × HAT-TRICK	0.007	0.150
BLADE × DAPPS	-0.767*	0.200
GRANGER × DAPPS	0.197	0.174
DAPPS × TRAVERSE	-0.311*	0.077
LOLO × DAPPS	0.136	0.167
LOSCHA × AC-SNOWBIRD	-0.684	0.266
AC-SNOWBIRD × GRANDIN	-0.557*	0.159
ULEN × AC-SNOWBIRD	-0.479	0.194
AC-SNOWBIRD × ARGENT	-0.027	0.095
INGOT × AC-SNOWBIRD	-0.810**	0.159
GRANGER × AC-SNOWBIRD	0.403	0.160
LOSCHA × GRANDIN	0.439	0.217
ULEN × LOSCHA	-1.423****	0.223
LOSCHA × ARGENT	-0.436	0.247
LOSCHA × INGOT	-0.228	0.142
LOSCHA × BLADE	-0.285	0.202
BLADE × LOSCHA	-0.256	0.166
LOSCHA × GRANGER	-0.056	0.310
TRAVERSE × LOSCHA	0.394*	0.100
LOLO × LOSCHA	0.525	0.244
ULEN × GRANDIN	0.188	0.076
ARGENT × GRANDIN	1.220****	0.182
INGOT × GRANDIN	-0.168	0.069
GRANDIN × HAT-TRICK	0.114	0.102
BLADE × GRANDIN	-0.369*	0.110
GRANGER × GRANDIN	0.109	0.170
TRAVERSE × GRANDIN	-0.968****	0.106
ARGENT × ULEN	0.079	0.148
ULEN × INGOT	-0.218	0.206
ULEN × HAT-TRICK	1.182***	0.216
ULEN × BLADE	1.027*	0.272
GRANGER × ULEN	-0.851****	0.114
ULEN × TRAVERSE	-0.995****	0.156
LOLO × ULEN	0.094	0.079

Parents in cross	Estimate	SE
INGOT × ARGENT	-0.035	0.195
ARGENT × HAT-TRICK	0.219	0.115
BLADE × ARGENT	-0.018	0.134
GRANGER × ARGENT	-0.030	0.085
TRAVERSE × ARGENT	1.233^{***}	0.200
LOLO × ARGENT	0.861^{*}	0.229
INGOT × HAT-TRICK	-0.199	0.103
BLADE × INGOT	-0.156	0.182
INGOT × GRANGER	0.114	0.122
TRAVERSE × INGOT	0.024	0.173
LOLO × INGOT	0.067	0.114
HAT-TRICK × BLADE	0.272	0.160
HAT-TRICK × GRANGER	0.486^{*}	0.142
TRAVERSE × HAT-TRICK	1.155^{****}	0.162
LOLO × HAT-TRICK	0.443	0.138
GRANGER × BLADE	0.371^{*}	0.100
TRAVERSE × BLADE	-0.274	0.211
LOLO × BLADE	0.355	0.210
TRAVERSE × GRANGER	-0.016	0.132
LOLO × GRANGER	-1.034^{**}	0.238

*=0.05, **=0.01, ***=0.001, ****=0.0001 significance level

4. Summary

The simulation study showed that a modified AD model can be used to estimate variance components in an unbiased manner within this complex data structure. Application of this model to actual data analysis revealed that both additive and dominance effects were responsible for PHS resistance. Several parents were associated with desirable additive effects for PHS and can be used as good general combiners for improving the trait. In addition, some crosses had desirable heterozygous dominance effects, which can be used for hybrid development. Finally, additional studies can be done using multiple environment case in this study. Modified AD model can be further used in analyzing complex data structure with multiple traits and environments.

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Appendix 1. List of families along with respective spring wheat gentotypes used in crossing.

Family	Parent 1	Parent 2	Parent 3	Parent 4	Progeny
1	Dapps	Ac-snowbird	Loscha		4
2	Dapps	Ac-snowbird	Grandin		14
3	Dapps	Ac-snowbird	Ulen		5
4	Dapps	Ac-snowbird	Dapps	Argent	3
5	Dapps	Ac-snowbird	Ingot		3
6	Dapps	Argent	Hat-trick		6
7	Dapps	Argent	Blade		1
8	Dapps	Argent	Ulen		5
9	Dapps	Argent	Grandin		5
10	Dapps	Argent	Argent		5
11	Dapps	Argent	Dapps	Ulen	2
12	Dapps	Argent	Dapps	Ingot	2
13	Dapps	Blade	Blade		12
14	Dapps	Blade	Ingot		12
15	Dapps	Blade	Grandin		2
16	Dapps	Blade	Granger		4
17	Dapps	Blade	Loscha	Dapps	4
18	Dapps	Blade	Ulen		4
19	Dapps	Blade	Dapps	Granger	10
20	Dapps	Blade	Dapps	Hat-Trick	3
21	Dapps	Grandin	Grandin		7
22	Dapps	Grandin	Ulen		4
23	Dapps	Grandin	Loscha		2
24	Dapps	Grandin	Hat-Trick		3
25	Dapps	Granger	Granger		4
26	Dapps	Granger	Hat-Trick		7
27	Dapps	Granger	Ulen		7
28	Dapps	Granger	Ingot		14
29	Dapps	Granger	Ac-snowbird		8
30	Dapps	Granger	Loscha		5
31	Dapps	Granger	Traverse		10
32	Dapps	Granger	Blade		8
33	Dapps	Granger	Grandin		8
34	Dapps	Granger	Dapps	Hat-Trick	5
35	Dapps	Granger	Argent		5
36	Dapps	Hat-Trick	Blade		7
37	Dapps	Hat-Trick	Dapps	Loscha	9
38	Dapps	Hat-Trick	Granger		6
39	Dapps	Hat-Trick	Ulen		4

Family	Parent 1	Parent 2	Parent 3	Parent 4	Progeny
40	Dapps	Hat-Trick	Traverse		11
41	Dapps	Hat-Trick	Ingot		9
42	Dapps	Hat-Trick	Dapps	LoLo	6
43	Dapps	Hat-Trick	Dapps	Ulen	6
44	Dapps	Ingot	Ulen		5
45	Dapps	Ingot	Ac-snowbird		11
46	Dapps	Ingot	Loscha		3
47	Dapps	Ingot	Ingot		13
48	Dapps	Ingot	Granger		5
49	Dapps	Ingot	Argent		6
50	Dapps	Ingot	Traverse		12
51	Dapps	Ingot	Dapps	Ulen	3
52	Dapps	Ingot	Grandin		9
53	Dapps	Ingot	Dapps	Hat-Trick	11
54	Dapps	Ingot	Dapps	Loscha	7
55	Dapps	Ingot	Dapps	Traverse	4
56	Dapps	Ingot	Blade		3
57	Dapps	LoLo	Ulen		8
58	Dapps	LoLo	Dapps	Hat-Trick	8
59	Dapps	LoLo	Granger		8
60	Dapps	LoLo	Loscha	Dapps	2
61	Dapps	LoLo	Ingot		3
62	Dapps	LoLo	Blade		6
63	Dapps	LoLo	Traverse		7
64	Dapps	LoLo	Argent		4
65	Dapps	LoLo	Traverse	Dapps	5
66	Dapps	LoLo	Dapps	Ingot	12
67	Dapps	LoLo	Loscha		3
68	Dapps	Loscha	Ingot		6
69	Dapps	Loscha	Argent		10
70	Dapps	Loscha	Granger		10
71	Dapps	Loscha	Grandin		19
72	Dapps	Loscha	Traverse		11
73	Dapps	Loscha	Hat-Trick		7
74	Dapps	Loscha	Ac-snowbird		7
75	Dapps	Loscha	Dapps	Ulen	7
76	Dapps	Loscha	Dapps	Ingot	15
77	Dapps	Loscha	Loscha		6
78	Dapps	Loscha	Dapps	Granger	7
79	Dapps	Loscha	Ulen		3
80	Dapps	Traverse	Ulen		10

Family	Parent 1	Parent 2	Parent 3	Parent 4	Progeny
81	Dapps	Traverse	Grandin		8
82	Dapps	Traverse	Ingot		12
83	Dapps	Traverse	Granger		9
84	Dapps	Traverse	Hat-Trick		12
85	Dapps	Traverse	Blade		4
86	Dapps	Traverse	Traverse		5
87	Dapps	Traverse	Loscha	Dapps	5
88	Dapps	Traverse	Argent		6
89	Dapps	Traverse	Dapps	Ulen	6
90	Dapps	Traverse	Dapps	Loscha	2
91	Dapps	Traverse	Dapps	Hat-Trick	4
92	Dapps	Traverse	Dapps	Blade	2
93	Dapps	Ulen	Ingot		6
94	Dapps	Ulen	Traverse		10
95	Dapps	Ulen	Ulen		6
96	Dapps	Ulen	Hat-Trick		6
97	Dapps	Ulen	Ac-snowbird		8
98	Dapps	Ulen	Blade		10
99	Dapps	Ulen	Grandin		4
100	Dapps	Ulen	Dapps	Blade	7
101	Dapps	Ulen	Dapps	Hat-Trick	10
102	Dapps	Ulen	Dapps	Granger	2
103	Dapps	Ulen	Loscha		7
104	Dapps	Ulen	Dapps	Loscha	5
105	Dapps	Ulen	Dapps	Ingot	7
106	Dapps	Blade	Argent		5
107	Dapps	Granger	Dapps	Ingot	4
108	Dapps	Granger	Dapps	Ulen	8
109	Dapps	Loscha	Dapps	Hat-Trick	3