Genetic analysis using the sommer package

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The sommer package has been developed to provide R users with a powerful mixed model solver for different genetic and non-genetic analysis in diploid and polyploid organisms. This package allows the user to estimate variance components for a mixed model with the advantage of specifying the variance-covariance structure of the random effects and obtain other parameters such as BLUPs, BLUEs, residuals, fitted values, variances for fixed and random effects, etc.

The package is focused on genomic prediction (or genomic selection) and GWAS analysis, although general mixed models can be fitted as well. The package provides kernels to estimate additive (A.mat), dominance (D.mat), and epistatic (E.mat) relationship matrices that have been shown to increase prediction accuracy under certain scenarios. The package provides flexibility to fit other genetic models such as full and half diallel models as well.

Vignettes aim to provide several examples in how to use the sommer package under different scenarios in breeding and genetics. We will spend the rest of the space providing examples for:

1) heritability ($h^2$) calculation
2) Half and full diallel designs
3) Genome wide association analysis (GWAS) in diploids and tetraploids
4) Genomic selection
5) Single cross prediction.

Background

The core of the package is the mmer function and solves the mixed model equations proposed by Henderson (1975). An user friendly version named mmer2 has been added as well, using the ASReml sintax. The functions are an interface to call one of the 4 ML/REML methods supported in the package; EMMA efficient mixed model association (Kang et al. 2008), AI average information (Gilmour et al. 1995; Lee et al. 2015), EM expectation maximization (Searle 1993; Bernardo 2010), and NR Newton-Raphson (Tunnicliffe 1989). The EMMA method can be implemented when only one variance component other than the error variance component ($\sigma^2_e$) is being estimated. On the other hand when more than one variance component needs to be estimated the AI, EM or NR methods should be used.

The mixed model solved by the algorithms has the form:

$$y = X\beta + Zu + \epsilon$$

or

$$y = X\beta + Zu_1 + ... + Zu_i + \epsilon$$

where:

- $X$ is an incidence matrix for fixed effects
- $Z$ is an incidence matrix for random effects
- $\beta$ is the vector for BLUEs of fixed effects
- $u$ is the vector for BLUPs of random effects
- $\epsilon$ are the residuals
The variance of the response is known to be the random part of the model:

\[ \text{Var}(y) = \text{Var}(Zu + \epsilon) = ZGZ + R \]

and with

\[ u \sim \text{MVN}(u, G\sigma_u^2) \]

\[ \epsilon \sim \text{MVN}(u, R\sigma_e^2) \]

When multiple random effects are present the Z matrix becomes the column binding of each of the \( Z_i \) matrices for the i random effects. And the G matrix becomes the diagonal binding of each of the variance covariance structures (K matrices) for the random effects:

\[
Z = \begin{bmatrix}
Z_1 & \ldots & Z_i
\end{bmatrix}
\]

\[
G = \begin{bmatrix}
K_1 & 0 & 0 \\
0 & \ldots & 0 \\
0 & 0 & K_i
\end{bmatrix}
\]

The program takes the Z and G for each random effect and construct the necessary structure inside and estimate the variance components by ML/REML using any of the 4 methods available in sommer; Average Information, Expectation-Maximization, Newton-Raphson, and Efficient Mixed Model Association. Please refer to the canonical paper list in the Literature section to check how the methods work. We have tested widely the methods to make sure they provide the same solution when the likelihood behaves well but for complex problems they might lead to different answers. If you have any concern please contact me at cova_ruber@live.com.mx or covarrubiasp@wisc.edu.

1) Marker and non-marker based heritability calculation

The heritability is one of the most famous parameters in breeding and genetics theory. The heritability is usually estimated as narrow sense (\( h^2; \) only additive variance in the numerator \( \sigma_A^2 \)), and broad sense (\( H^2; \) all genetic variance in the numerator \( \sigma_G^2 \)).

In a classical experiment with no molecular markers, special designs are performed to estimate and dissect the additive (\( \sigma_A^2 \)) and dominance (\( \sigma_D^2 \)) variance along with environmental variability. Designs such as generation analysis, North Carolina designs ae used to dissect \( \sigma_A^2 \) and \( \sigma_D^2 \) to estimate the narrow sense heritability (\( h^2 \)). When no special design is available we can still dissect the genetic variance (\( \sigma_G^2 \)) and estimate the broad sense. In this example we will show the broad sense estimation.

The dataset has 41 potato lines evaluated in 5 locations across 3 years in an RCBD design. We show how to fit the model and extract the variance components to calculate the \( h^2 \).

```r
library(sommer)
data(h2)
head(h2)
```

<table>
<thead>
<tr>
<th>#</th>
<th>Name</th>
<th>Env</th>
<th>Loc</th>
<th>Year</th>
<th>Block</th>
<th>y</th>
</tr>
</thead>
<tbody>
<tr>
<td>#1</td>
<td>W8822-3</td>
<td>FL</td>
<td>2012</td>
<td>FL.2012</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>#2</td>
<td>W8867-7</td>
<td>FL</td>
<td>2012</td>
<td>FL.2012</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>#3</td>
<td>MSL007-B</td>
<td>MO</td>
<td>2011</td>
<td>MO.2011</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>#4</td>
<td>CO00270-7W</td>
<td>FL</td>
<td>2012</td>
<td>FL.2012</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>#5</td>
<td>Manistee(MSL292-A)</td>
<td>FL</td>
<td>2013</td>
<td>FL.2013</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>#6</td>
<td>MSM246-B</td>
<td>FL</td>
<td>2012</td>
<td>FL.2012</td>
<td>2</td>
<td>3</td>
</tr>
</tbody>
</table>
ans1 <- `mmer2(y~1, random=~Name + Env + Name:Env + Block, data=h2, silent = TRUE)`

## Estimating variance components

vc <- ans1$var.comp
V_E <- vc[2,1]; V_GE <- vc[3,1]; V_G <- vc[1,1]; Ve <- vc[5,1]

n.env <- `length(levels(h2$Env))`

h2 <- V_G/(V_G + V_GE/n.env + Ve/(2*n.env)) #the 2 is a reference for block

h2

## [1] 0.9621128

Recently with markers becoming cheaper, thousand of markers can be run in the breeding materials. When markers are available, an special design is not neccessary to disect the additive variance. The estimation of the additive relationship matrix allow us to estimate the $\sigma_A^2$ and $\sigma_D^2$.

Assume you have a population and a similar model like the one displayed previously has been fitted. Now we have BLUPs for the genotypes but in addition we have genetic markers. NOTICE WE WILL USE THE `mmer` FUNCTION THIS TIME.

data(CPdata)
CPpheno <- CPdata$pheno
CPgeno <- CPdata$geno

```r
### look at the data
head(CPpheno)
## color Yield FruitAver Firmness
## 3 0.10075269 154.67 41.93 588.917
## 4 0.13891940 186.77 58.79 640.031
## 5 0.08681502 80.21 48.16 671.523
## 6 0.13408561 202.96 48.24 687.172
## 7 0.13519278 174.74 45.83 601.322
## 8 0.17406685 194.16 44.63 656.379
```

CPgeno[1:5,1:4]

```r
### scaffold_50439_2381 scaffold_39344_153 uneak_3436043 uneak_2632033
### P003 0 0 0 1
### P004 0 0 0 1
### P005 0 -1 0 1
### P006 -1 -1 -1 0
### P007 0 0 0 1
```

```
## fit a model including additive and dominance effects
y <- CPpheno$color
Za <- `diag(length(y))`; Zd <- `diag(length(y))`; Ze <- `diag(length(y))`
A <- A.mat(CPgeno) # additive relationship matrix
D <- D.mat(CPgeno) # dominance relationship matrix
E <- E.mat(CPgeno) # epistatic relationship matrix

ETA.ADE <- list(list(Z=Za,K=A),list(Z=Zd,K=D),list(Z=Ze,K=E))
ans.ADE <- `mmer(y=y, Z=ETA.ADE, silent = TRUE)`
```
## Estimating variance components

One or more variance components close to zero. Boundary constraint applied.

\[
H_2 \leftarrow \frac{\text{sum}(\text{ans.ADE$var.comp}[1:3,1])}{\text{sum}(\text{ans.ADE$var.comp}[1,1])}
\]

## 1] 0.7521203

\[
h_2 \leftarrow \frac{\text{sum}(\text{ans.ADE$var.comp}[1,1])}{\text{sum}(\text{ans.ADE$var.comp}[1,1])}
\]

## 1] 0.6222822

In the previous example we showed how to estimate the additive ($\sigma_A^2$), dominance ($\sigma_D^2$), and epistatic ($\sigma_I^2$) variance components based on markers and estimate broad ($H^2$) and narrow sense heritability ($h^2$).

### 2) Half and full diaelle designs

When breeders are looking for the best single cross combinations, diaelle designs have been by far the most used design in crops like maize. There are 4 types of diaelle designs depending if reciprocate and self cross are performed. In this example we will show a full diaelle design (reciprocate crosses are performed) and half diaelle designs (only one of the directions is performed).

In the first data set we show a full diaelle among 40 lines from 2 heterotic groups, 20 in each. Therefore 400 possible hybrids are possible. We have phenotypic data for 100 of them across 4 locations. We use the data available to fit a model of the form:

\[
y = X\beta + Zu_1 + Zu_2 + Zu_S + \epsilon
\]

We estimate variance components for $GCA_1$, $GCA_2$ and $SCA$ and use them to estimate heritability. Additionally BLUPs for GCA and SCA effects can be used to predict crosses.

data(cornHybrid)
hybrid2 <- cornHybrid$hybrid # extract cross data
head(hybrid2)

## Location GCA1 GCA2 SCA Yield PlantHeight
## 1 A258 AS5707 A258:AS5707 NA NA
## 2 A258 B2 A258:B2 NA NA
## 3 A258 B99 A258:B99 NA NA
## 4 A258 LH51 A258:LH51 NA NA
## 5 A258 Mo44 A258:Mo44 NA NA
## 6 A258 NC320 A258:NC320 NA NA

modFD <- mmer2(Yield~Location, random=~GCA1+GCA2+SCA, data=hybrid2,silent = TRUE)

## Estimating variance components

One or more variance components close to zero. Boundary constraint applied.
summary(modFD)

## Information contained in this fitted model:
## * Variance components
## * Residuals and conditional residuals
## * BLUEs and BLUPs
## * Inverse phenotypic variance (V)
## * Variance-covariance matrix for fixed effects
## * Variance-covariance matrix for random effects
## * Predicted error variance (PEV)
## * LogLikelihood
## * AIC and BIC
## * Fitted values
## Use the 'str' function to access such information
###
### Linear mixed model fit by restricted maximum likelihood
### ************** sommer 1.6 **************
### Method:[1] "NR"
###
### logLik  AIC  BIC
### -1342  2691  2707
###
### Random effects:
### VarianceComp
### 1  0.000
### 2  7.409
### 3  187.563
### 4  221.142
### Number of obs: 400  Groups: 20 20 400
###
### Fixed effects:
### Value  Std.Error t.value
### (Intercept) 1.3794e+02  2.1227e+00  64.9815
### Location2 -1.5987e-13  2.1031e+00  0.0000
### Location3  7.8353e+00  2.1031e+00  3.7257
### Location4 -9.0975e+00  2.1031e+00 -4.3258
###
### Var-Cov for Fixed effects:
### (diagonals are variances)
### (Intercept) Location2 Location3 Location4
### (Intercept)   4.5058   -2.2114   -2.2114   -2.2114
### Location2    -2.2114    4.4228    2.2114    2.2114
### Location3    -2.2114    2.2114    4.4228    2.2114
### Location4    -2.2114    2.2114    2.2114    4.4228
###
### Use the 'str' function to access all information

Vgca <- sum(modFD$var.comp[1:2,1])
Vsca <- modFD$var.comp[3,1]
Ve  <- modFD$var.comp[4,1]
\[ V_a = 4 \cdot V_{gca} \]
\[ V_d = 4 \cdot V_{sca} \]
\[ V_g \leftarrow V_a + V_d \]
\[ (H_2 \leftarrow \frac{V_g}{V_g + (V_e)} \) 

## [1] 0.7790852

\[ (h_2 \leftarrow \frac{V_a}{V_g + (V_e)} \) 

## [1] 0.02960619

In this second data set we show a small half diallel with 7 parents crossed in one direction. \( n(n-1)/2 \) crosses are possible \( 7(6)/2 = 21 \) unique crosses. Parents appear as males or females indistinctly. Each with two replications in a CRD. For a half diallel design a single GCA variance component can be estimated and an SCA as well \( (\sigma^2_{GCA} \text{ and } \sigma^2_{SCA} \text{ respectively}) \). And BLUPs for GCA and SCA of the parents can be extracted. We would create the design matrices in sommer using the `hdm` and `model.matrix` functions for the GCA and SCA matrices respectively.

\[ y = X\beta + Zu_g + Zu_s + \epsilon \]

data(HDdata)
head(HDdata)

```
## rep geno male female sugar
## 1  1  12  1  2  13.950509
## 2  2  12  1  2  9.756918
## 3  3  13  1  3  13.906355
## 4  4  13  1  3  9.119455
## 5  5  14  1  4  5.174483
## 6  6  14  1  4  8.452221
```

# GCA matrix for half diallel using male and female columns
Z1 <- hdm(HDdata[,c(3:4)])

# SCA matrix
Z2 <- model.matrix(~as.factor(geno)-1, data=HDdata)

# Fit the model
y <- HDdata$sugar
ETA <- list(GCA=list(Z=Z1), SCA=list(Z=Z2)) # Zu component
modHD <- mmer(y=y, Z=ETA, silent = TRUE)

## Estimating variance components
summary(modHD)

```
```
## Variance-covariance matrix for fixed effects

## Variance-covariance matrix for random effects

## Predicted error variance (PEV)

## LogLikelihood

## AIC and BIC

## Fitted values

Use the `str` function to access such information

---

Linear mixed model fit by restricted maximum likelihood

**sommer 1.6**

---

Method: "AI"

---

logLik   AIC   BIC
-7.543  17.086 18.824

---

Random effects:

```
VarianceComp
Var(GCA)   5.509
Var(SCA)   1.816
Var(Error) 3.117
```

---

Number of obs: 42  Groups: 7 21

---

Fixed effects:

```
Value  Std.Error  t.value
Intercept  10.3332   1.8189  5.6809
```

---

Var-Cov for Fixed effects:

```
(diagonals are variances)
1
```

---

Use the `str` function to access all information

```r
Vgca <- modHD$var.comp[1,1]
Vscas <- modHD$var.comp[2,1]
Ve <- modHD$var.comp[3,1]
Va = 4*Vgca
Vd = 4*Vscas
Vg <- Va + Vd
(H2 <- Vg / (Vg + (Ve/2)) ) # 2 technical reps
```

```r
# [1] 0.9494882
(h2 <- Va / (Vg + (Ve/2)) )
```

```r
# [1] 0.7140884
```

```r
plot(density(randef(modHD)$GCA[,1]), col="cadetblue", lwd=10, main="GCA BLUPs")
```
3) Genome wide association analysis (GWAS) in diploids and tetraploids

With the development of modern statistical machinery the detection of markers associated to phenotypic traits have become quite straight forward. The days of QTL mapping using biparental populations exclusively are in the past. In this section we will show how to perform QTL mapping for diploid and polyploid organisms with complex genetic relationships. In addition we will show QTL mapping in biparental populations to clarify that the fact that is not required anymore doesn’t limit the capabilities of modern mixed model machinery.

First we will start doing the GWAS in a biparental population with 363 individuals genotyped with 2889 SNP markers. This is easily done by creating the variance covariance among individuals and using it in the random effect for genotypes. The markers are added in the $W$ argument to fit the model of the form:

$$y = X\beta + Zu + Wg + \epsilon$$

In this case $X\beta$ is the fixed part only for the intercept, $Zu$ is the random effect for genotypes with the additive relationship matrix ($A$) as the variance-covariance of the random effect, $Wg$ is the marker matrix and the effects of each marker. This is done in this way:

```r
data(CPdata)
CPpheno <- CPdata$pheno
CPgeno <- CPdata$geno
### look at the data
head(CPpheno); CPgeno[1:5,1:4]
```

```r
## color Yield FruitAver Firmness
```

```r
```
```
# Estimating variance components
#
# Performing GWAS
#
# Running additive model
```
Now we will show how to do GWAS in a tetraploid using potato data. Is not very different from diploids. We only need to pay attention to the ploidy argument in the atcg1234 and A.mat functions. In addition, when running the \texttt{mmer} model there is more models that can be implemented according to Rosyara et al. (2016).

\begin{verbatim}
data(PolyData)
genotypes <- PolyData$PGeno
phenotypes <- PolyData$PPheno
## convert markers to numeric format
numo <- atcg1234(data=genotypes, ploidy=4, silent = TRUE); numo[1:5,1:5]; dim(numo)

## Obtaining reference alleles
## Checking for markers with more than 2 alleles. If found will be removed.
## Converting to numeric format
## Calculating minor allele frequency (MAF)
## Imputing missing data with mode

# get only plants with both genotypes and phenotypes
common <- intersect(phenotypes$Name,rownames(numo))
marks <- numo[common,]; marks[1:5,1:5]

phenotypes2 <- phenotypes[match(common,phenotypes$Name),]; phenotypes2[1:5,1:5]

# Additive relationship matrix, specify ploidy
yy <- phenotypes2$tuber_shape
K1 <- A.mat(marks, ploidy=4)
Z1 <- diag(length(yy))
ETA <- list( list(Z=Z1, K=K1)) # random effects for genotypes
\end{verbatim}
```r
# run the model
models <- c("additive","1-dom-alt","1-dom-ref","2-dom-alt","2-dom-ref")
ans2 <- mmer(y=yy, Z=ETA, W=marks, method="EMMA",
             ploidy=4, models=models[1], silent = TRUE)

## Estimating variance components
## Performing GWAS
## Running additive model

summary(ans2)
```

```
## Information contained in this fitted model:
## * Variance components
## * Residuals and conditional residuals
## * BLUEs and BLUPs
## * Inverse phenotypic variance(V)
## * Variance-covariance matrix for fixed effects
## * Variance-covariance matrix for random effects
## * Predicted error variance (PEV)
## * LogLikelihood
## * AIC and BIC
## * Fitted values
```
## Use the 'str' function to access such information
##
## Linear mixed model fit by restricted maximum likelihood
##                          sommer 1.6   ***************
##                          =======================================================
##                          Method:[1] "EMMA"
##                          # logLik  AIC   BIC
##                          # -192.5 387.0 390.3
##                          =======================================================
##                          # Random effects:
##                          # VarianceComp
##                          # V(u) 0.60778
##                          # V(e) 0.03807
##                          # Number of obs: 187 Groups: 187
##                          =======================================================
##                          # Fixed effects:
##                          # Value Std.Error  t.value
##                          # Intercept 3.307861 0.014268 231.83
##                          =======================================================
##                          # Var-Cov for Fixed effects:
##                          # (diagonals are variances)
##                          # 1
##                          # Intercept 2e-04
##                          =======================================================
## Use the 'str' function to access all information

### 4) Genomic selection

In this section we will use wheat data from CIMMYT to show how is genomic selection performed. This is the case of prediction of specific individuals within a population. It basically uses a similar model of the form:

\[ y = X\beta + Zu + \epsilon \]

and takes advantage of the variance covariance matrix for the genotype effect known as the additive relationship matrix (A) and calculated using the \( A.mat \) function to establish connections among all individuals and predict the BLUPs for individuals that were not measured. The prediction accuracy depends on several factors such as the heritability \( (h^2) \), training population used (TP), size of TP, etc.

```R
data(wheatLines)
X <- wheatLines$wheatGeno; X[1:5,1:5]; dim(X)
```

# wPt.0538 wPt.8463 wPt.6348 wPt.9992 wPt.2838
# [1,] -1 1 1 1 1
# [2,] 1 1 1 1 1
# [3,] 1 1 1 1 1
# [4,] -1 1 1 1 1
# [5,] -1 1 1 1 1

# [1] 599 1279
Y <- wheatLines$wheatPheno
rownames(X) <- rownames(Y)
# select environment 1
y <- Y[,1] # response grain yield
Z1 <- diag(length(y)) # incidence matrix
K <- A.mat(X) # additive relationship matrix
# GBLUP pedigree-based approach
set.seed(12345)
y.trn <- y
vv <- sample(1:length(y),round(length(y)/5))
y.trn[vv] <- NA
ETA <- list(g=list(Z=Z1, K=K))
ans <- mmer(y=y.trn, Z=ETA, method="EMMA", silent = TRUE) # kinship based

## Estimating variance components

cor(ans$u.hat$g[vv],y[vv])

## [1] 0.4886567

## maximum prediction value that can be achieved

sqrt(ans$var.comp[1,1]/sum(ans$var.comp[,1]))

## V(u)
## 0.5771923

### 5) Single cross prediction

When doing prediction of single cross performance the phenotype can be dissected in three main components, the general combining abilities (GCA) and specific combining abilities (SCA). This can be expressed with the same model analyzed in the diallel experiment mentioned before:

\[
y = X\beta + Zu_1 + Zu_2 + Zu_S + \epsilon
\]

with:

\[
u_1 \sim N(0, K_1\sigma_u^2)
\]

\[
u_2 \sim N(0, K_2\sigma_u^2)
\]

\[
u_s \sim N(0, K_3\sigma_u^2)
\]

And we can specify the K matrices. The main difference between this model and the full and half diallel designs is the fact that this model will include variance covariance structures in each of the three random effects (GCA1, GCA2 and GCA3) to be able to predict the crosses that have not occurred yet. We will use the data published by Technow et al. (2015) to show how to do prediction of single crosses.

data(technow_data)

A.flint <- Technow_data$AF # Additive relationship matrix Flint
A.dent <- Technow_data$AD # Additive relationship matrix Dent
M.flint <- Technow_data$MF # Marker matrix Flint
M.dent <- Technow_data$MD # Marker matrix Dent
pheno <- Technow_data$pheno # phentypes for 1254 single cross hybrids
pheno$hy <- paste(pheno$dent, pheno$flint, sep=";");head(pheno);dim(pheno)

## hybrid dent flint GY GM hy
## 1 518.298 518 298 -8.04 -0.85 518:298
## 2 518.305 518 305 -11.10 1.70 518:305
## 3 518.306 518 306 -16.85 2.24 518:306
## 4 518.316 518 316 2.08 -1.33 518:316
## 5 518.323 518 323 5.65 -2.71 518:323
## 6 518.327 518 327 -16.95 -0.52 518:327
## [1] 1254 6

# CREATE A DATA FRAME WITH ALL POSSIBLE HYBRIDS
DD <- kronecker(A.dent,A.flint,make.dimnames=TRUE)

hybs <- data.frame(sca=rownames(DD),yield=NA,matter=NA,gcad=NA, gcaf=NA)
hybs$yield[match(pheno$hy, hybs$sca)] <- pheno$GY
hybs$matter[match(pheno$hy, hybs$sca)] <- pheno$GM
hybs$gcad <- as.factor(gsub(":\.*","",hybs$sca))
hybs$gcaf <- as.factor(gsub("\.*","",hybs$sca))

head(hybs)

## sca yield matter gcad gcaf
## 1 513:316 10.02 -2.05 513 316
## 2 513:323 6.97 -3.78 513 323
## 3 513:330 NA NA 513 330
## 4 513:336 NA NA 513 336
## 5 513:340 NA NA 513 340
## 6 513:341 NA NA 513 341

# CREATE INCIDENCE MATRICES
Z1 <- model.matrix(~gcad-1, data=hybs)
Z2 <- model.matrix(~gcaf-1, data=hybs)

# SORT INCIDENCE MATRICES ACCORDING TO RELATIONSHIP MATRICES, REAL ORDERS
real1 <- match( colnames(A.dent), gsub("gcad","",colnames(Z1)))
real2 <- match( colnames(A.flint), gsub("gcaf","",colnames(Z2)))
Z1 <- Z1[,real1]
Z2 <- Z2[,real2]

# RUN THE PREDICTION MODEL
y.trn <- hybs$yield
vv1 <- which(!is.na(hybs$yield))
vv2 <- sample(vv1, 100)
y.trn[vv2] <- NA
ETA2 <- list(GCA1=list(Z=Z1, K=A.dent), GCA2=list(Z=Z2, K=A.flint))
anss2 <- mmer(y=y.trn, Z=ETA2, method="EM", silent=TRUE)

## Estimating variance components
In the previous model we only used the GCA effects (GCA1 and GCA2) for practicicy, although it’s been shown that the SCA effect doesn’t actually help that much in increasing prediction accuracy and increase a lot the computation intensity required since the variance covariance matrix for SCA is the kronecker product of the variance covariance matrices for the GCA effects, resulting in a 10578x10578 matrix that increases in a very intensive manner the computation required.
A model without covariance structures would show that the SCA variance component is insignificant compared to the GCA effects. This is why including the third random effect doesn’t increase the prediction accuracy.

**Literature**

Covarrubias-Pazaran G (2016) Genome assisted prediction of quantitative traits using the R package sommer. [https://cran.rstudio.com/web/packages/sommer/](https://cran.rstudio.com/web/packages/sommer/)


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