

Genomic Selection:

Key Models, Methods, and Perspectives



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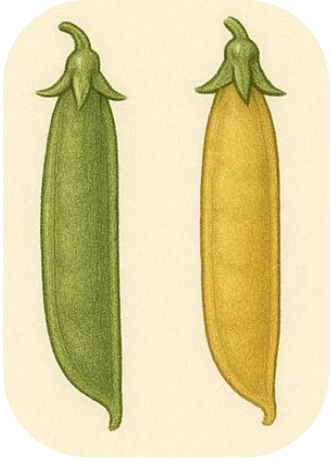
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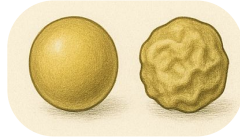
Genomic Selection: Key Models, Methods, and Perspectives

Pea Traits

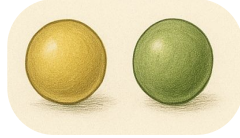
Pod Color



Seed Shape



Seed Color



Flower Color



Mendelian Traits Determined by a single or very few genes

Number of Pods



Yield



Plant Height



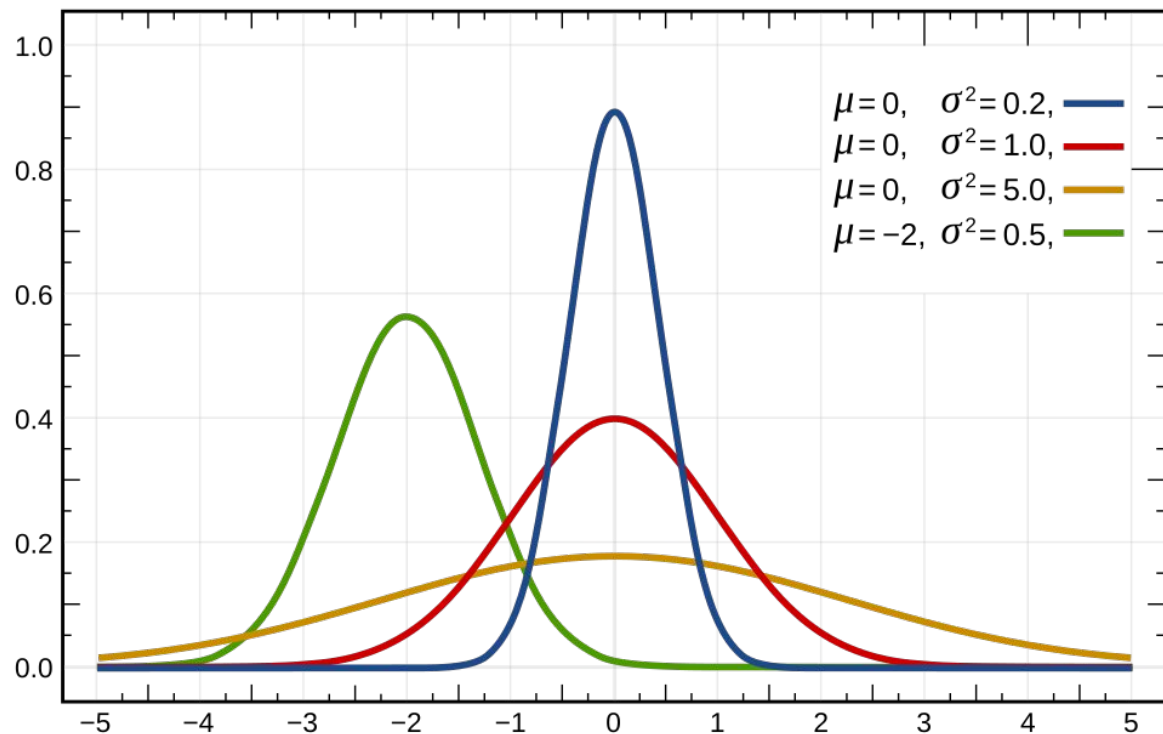
Determined by a large number of genes and non-genetic factors

Quantitative Traits

Normal Distribution

$$Y \sim N(\mu, \sigma^2)$$

$$f(x) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp \left[-\frac{(x-\mu)^2}{2\sigma^2} \right]$$



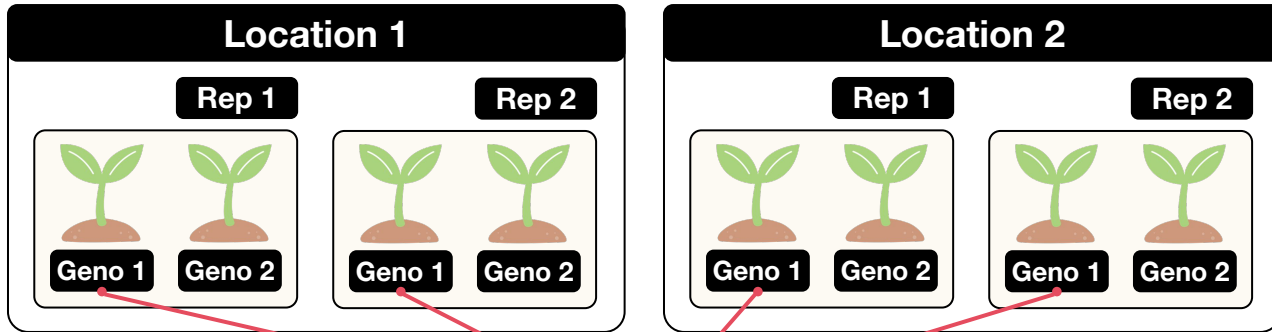
$$\mathbf{E}(Y) = \mu$$
$$\mathbf{Var}(Y) = \sigma^2$$

Quantitative Traits

Directly transmitted through generations

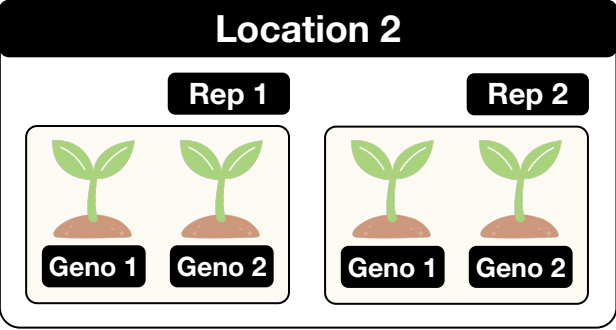
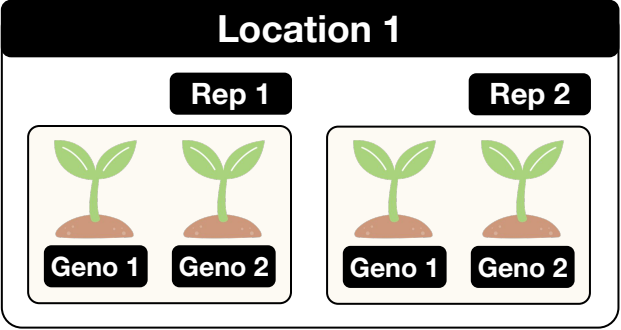
Additive Effects

Phenotype = Fixed Effects + **Genetics** + Environment + Residuals



Will these plants have the same phenotype?

Quantitative Traits

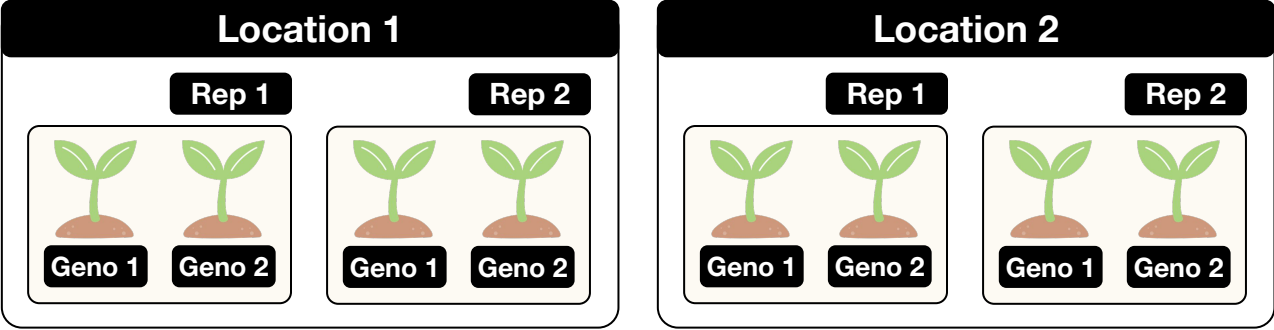


$$\begin{bmatrix} 65 \\ 64 \\ 46 \\ 45 \\ 94 \\ 94 \\ 76 \\ 74 \end{bmatrix} = \begin{bmatrix} 60 \\ 60 \\ 60 \\ 60 \\ 90 \\ 90 \\ 90 \\ 90 \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ -20 \\ -20 \\ 0 \\ 0 \\ -20 \\ -20 \end{bmatrix} + \begin{bmatrix} 2 \\ 3 \\ 4 \\ 1 \\ 2 \\ 3 \\ 4 \\ 1 \end{bmatrix} + \begin{bmatrix} 3 \\ 1 \\ 2 \\ 4 \\ 2 \\ 1 \\ 2 \\ 3 \end{bmatrix}$$

Labels for the matrices:

- Matrix 1 (left): **Geno 1** (rows 1-4), **Geno 2** (rows 5-8)
- Matrix 2 (middle): **Loc 1** (rows 1-2), **Loc 2** (rows 3-4), **Loc 1** (rows 5-6), **Loc 2** (rows 7-8)
- Matrix 3 (right): **Rep 1 | Loc 1** (rows 1-2), **Rep 2 | Loc 1** (rows 3-4), **Rep 1 | Loc 2** (rows 5-6), **Rep 2 | Loc 2** (rows 7-8)

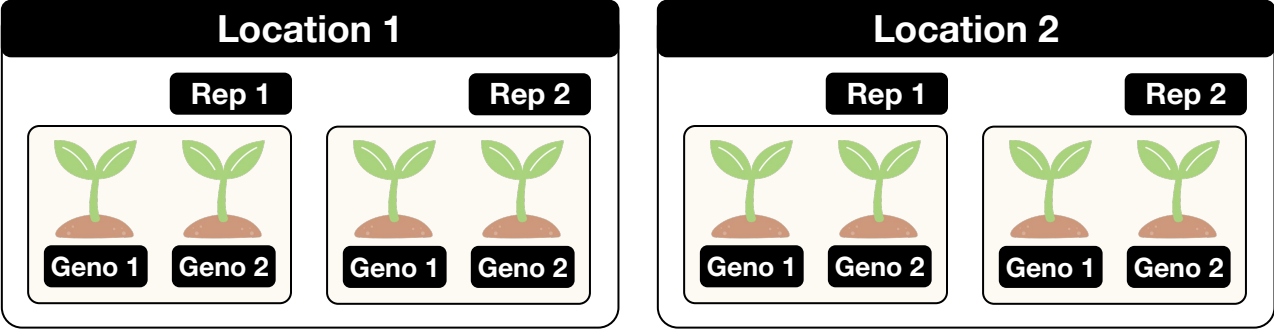
Quantitative Traits



$Y_{i,j,k}$
 Genotype i
 Location j
 Repetition k

$$\begin{bmatrix} Y_{1,1,1} \\ Y_{1,1,2} \\ Y_{1,2,1} \\ Y_{1,2,2} \\ Y_{2,1,1} \\ Y_{2,1,2} \\ Y_{2,2,1} \\ Y_{2,2,2} \end{bmatrix} = \begin{bmatrix} g_1 \\ g_1 \\ g_1 \\ g_1 \\ g_2 \\ g_2 \\ g_2 \\ g_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_1 \\ e_2 \\ e_2 \\ e_1 \\ e_1 \\ e_2 \\ e_2 \end{bmatrix} + \begin{bmatrix} e_1:r_1 \\ e_1:r_2 \\ e_2:r_1 \\ e_2:r_2 \\ e_1:r_1 \\ e_1:r_2 \\ e_2:r_1 \\ e_2:r_2 \end{bmatrix} + \begin{bmatrix} \square_{1,1,1} \\ \square_{1,1,2} \\ \square_{1,2,1} \\ \square_{1,2,2} \\ \square_{2,1,1} \\ \square_{2,1,2} \\ \square_{2,2,1} \\ \square_{2,2,2} \end{bmatrix}$$

Quantitative Traits



$$Y = X_1g + X_2e + X_3e:r + \square$$

Quantitative Traits

$$\begin{bmatrix} Y_{1,1,1} \\ Y_{1,1,2} \\ Y_{1,2,1} \\ Y_{1,2,2} \\ Y_{2,1,1} \\ Y_{2,1,2} \\ Y_{2,2,1} \\ Y_{2,2,2} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} g_1 \\ g_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} e_1:r_1 \\ e_1:r_2 \\ e_2:r_1 \\ e_2:r_2 \end{bmatrix} + \begin{bmatrix} \square_{1,1,1} \\ \square_{1,1,2} \\ \square_{1,2,1} \\ \square_{1,2,2} \\ \square_{2,1,1} \\ \square_{2,1,2} \\ \square_{2,2,1} \\ \square_{2,2,2} \end{bmatrix}$$

Linear Model

Coefficients

$$\begin{bmatrix} 65 \\ 64 \\ 46 \\ 45 \\ 94 \\ 94 \\ 76 \\ 74 \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} g_1 \\ g_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} e_1:r_1 \\ e_1:r_2 \\ e_2:r_1 \\ e_2:r_2 \end{bmatrix} + \begin{bmatrix} \square_{1,1,1} \\ \square_{1,1,2} \\ \square_{1,2,1} \\ \square_{1,2,2} \\ \square_{2,1,1} \\ \square_{2,1,2} \\ \square_{2,2,1} \\ \square_{2,2,2} \end{bmatrix}$$

Linear Model

$$\begin{bmatrix} 65 \\ 64 \\ 46 \\ 45 \\ 94 \\ 94 \\ 76 \\ 74 \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \hat{g}_1 \\ \hat{g}_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \hat{e}_1 \\ \hat{e}_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \hat{e}_1:r_1 \\ \hat{e}_1:r_2 \\ \hat{e}_2:r_1 \\ \hat{e}_2:r_2 \end{bmatrix} = \begin{bmatrix} \hat{\square}_{1,1,1} \\ \hat{\square}_{1,1,2} \\ \hat{\square}_{1,2,1} \\ \hat{\square}_{1,2,2} \\ \hat{\square}_{2,1,1} \\ \hat{\square}_{2,1,2} \\ \hat{\square}_{2,2,1} \\ \hat{\square}_{2,2,2} \end{bmatrix}$$

Linear Model - Assumption

$$\begin{bmatrix} \square_{1,1,1} \\ \square_{1,1,2} \\ \square_{1,2,1} \\ \square_{1,2,2} \\ \square_{2,1,1} \\ \square_{2,1,2} \\ \square_{2,2,1} \\ \square_{2,2,2} \end{bmatrix} \sim N \left[\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma^2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma^2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma^2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma^2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \sigma^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma^2 \end{bmatrix} \right]$$

Independent and Identically Distributed

Correlation, Variance, and Covariance

$$X = [1 \quad 2 \quad 1 \quad 3]$$

$$Y = [4 \quad 3 \quad 2 \quad 5]$$

$$\mu = \frac{1}{n} \sum_{i=1}^n x_i$$

$$\sigma^2 = \frac{1}{n} \sum_{i=1}^n (x_i - \mu)^2$$

Correlation, Variance, and Covariance

$$X = [1 \quad 2 \quad 1 \quad 3]$$

$$Y = [4 \quad 3 \quad 2 \quad 5]$$

$$\text{cov}(X, Y) = \frac{1}{n} \sum_{i=1}^n (x_i - \mu_x)(y_i - \mu_y)$$

$$\text{cor}(X, Y) = \frac{\text{cov}(X, Y)}{\sqrt{\sigma_X^2 \sigma_Y^2}}$$

Covariance Matrix

$$\begin{bmatrix} \sigma_X^2 & \sigma_{X,Y} \\ \sigma_{X,Y} & \sigma_Y^2 \end{bmatrix}$$

Linear Mixed Effects Models

Genomic Selection:
Key Models, Methods, and Perspectives

Linear Mixed Effects Model

$$\begin{bmatrix} Y_{1,1,1} \\ Y_{1,1,2} \\ Y_{1,2,1} \\ Y_{1,2,2} \\ Y_{2,1,1} \\ Y_{2,1,2} \\ Y_{2,2,1} \\ Y_{2,2,2} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} g_1 \\ g_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} e_1:r_1 \\ e_1:r_2 \\ e_2:r_1 \\ e_2:r_2 \end{bmatrix} + \begin{bmatrix} \square_{1,1,1} \\ \square_{1,1,2} \\ \square_{1,2,1} \\ \square_{1,2,2} \\ \square_{2,1,1} \\ \square_{2,1,2} \\ \square_{2,2,1} \\ \square_{2,2,2} \end{bmatrix}$$

Linear Mixed Effects Model

$$\begin{bmatrix} Y_{1,1,1} \\ Y_{1,1,2} \\ Y_{1,2,1} \\ Y_{1,2,2} \\ Y_{2,1,1} \\ Y_{2,1,2} \\ Y_{2,2,1} \\ Y_{2,2,2} \end{bmatrix} = \begin{bmatrix} 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} e_1 \\ e_2 \\ e_1:r_1 \\ e_1:r_2 \\ e_2:r_1 \\ e_2:r_2 \end{bmatrix} + \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} g_1 \\ g_2 \end{bmatrix} + \begin{bmatrix} \square_{1,1,1} \\ \square_{1,1,2} \\ \square_{1,2,1} \\ \square_{1,2,2} \\ \square_{2,1,1} \\ \square_{2,1,2} \\ \square_{2,2,1} \\ \square_{2,2,2} \end{bmatrix}$$

Linear Mixed Effects Model

$$\begin{bmatrix} Y_1 \\ Y_2 \\ Y_3 \\ Y_4 \\ Y_5 \\ Y_6 \\ Y_7 \\ Y_8 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \\ b_5 \\ b_6 \end{bmatrix} + \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} \square_1 \\ \square_2 \\ \square_3 \\ \square_4 \\ \square_5 \\ \square_6 \\ \square_7 \\ \square_8 \end{bmatrix}$$

Phenotype = Fixed Effects + Random Effects +
Residuals

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \square$$

Linear Mixed Effects Model

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \boldsymbol{\epsilon}$$

$$\begin{bmatrix} \square_1 \\ \square_2 \\ \square_3 \\ \square_4 \\ \square_5 \\ \square_6 \\ \square_7 \\ \square_8 \end{bmatrix} \sim N \left[\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \sigma_{\square}^2 \right]$$

R

$$\boldsymbol{\epsilon} \sim N(0, R\sigma_{\square}^2)$$

Linear Mixed Effects Model

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \square$$

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} \sim \mathcal{N} \left[\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \underbrace{\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}}_{\Sigma} \sigma_u^2 \right]$$

$$\mathbf{u} \sim \mathcal{N}(0, \Sigma \sigma_u^2)$$

Henderson Equations

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \boldsymbol{\epsilon}$$

$$\begin{bmatrix} \mathbf{X}^T \mathbf{y} \\ \mathbf{Z}^T \mathbf{y} \end{bmatrix} \equiv \begin{bmatrix} \mathbf{X}^T \mathbf{R}^{-1} \mathbf{X} & \mathbf{X}^T \mathbf{R}^{-1} \mathbf{Z} \\ \mathbf{Z}^T \mathbf{R}^{-1} \mathbf{X} & \mathbf{Z}^T \mathbf{R}^{-1} \mathbf{Z} + \boldsymbol{\Sigma}^{-1} \frac{\sigma_{\boldsymbol{\epsilon}}^2}{\sigma_u^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix}$$

$$\boldsymbol{\epsilon} \sim N(0, \mathbf{R}\sigma_{\boldsymbol{\epsilon}}^2)$$

$$\mathbf{u} \sim N(0, \boldsymbol{\Sigma}\sigma_u^2)$$

Henderson Equations

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \square$$

$$\begin{bmatrix} \mathbf{X}^T \mathbf{y} \\ \mathbf{Z}^T \mathbf{y} \end{bmatrix} \equiv \begin{bmatrix} \mathbf{X}^T \mathbf{R}^{-1} \mathbf{X} & \mathbf{X}^T \mathbf{R}^{-1} \mathbf{Z} \\ \mathbf{Z}^T \mathbf{R}^{-1} \mathbf{X} & \mathbf{Z}^T \mathbf{R}^{-1} \mathbf{Z} + \Sigma^{-1} \frac{\sigma_{\square}^2}{\sigma_u^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix}$$

$$\begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$$\square \sim N(0, \mathbf{R}\sigma_{\square}^2)$$

$$\mathbf{u} \sim N(0, \Sigma\sigma_u^2)$$

Henderson Equations

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \boldsymbol{\varepsilon}$$

$$\begin{bmatrix} \mathbf{X}^T \mathbf{y} \\ \mathbf{Z}^T \mathbf{y} \end{bmatrix} \equiv \begin{bmatrix} \mathbf{X}^T \mathbf{X} & \mathbf{X}^T \mathbf{Z} \\ \mathbf{Z}^T \mathbf{X} & \mathbf{Z}^T \mathbf{Z} + \Sigma^{-1} \frac{\sigma_{\boldsymbol{\varepsilon}}^2}{\sigma_u^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix}$$

$$\boldsymbol{\varepsilon} \sim N(0, R\sigma_{\boldsymbol{\varepsilon}}^2)$$

$$\mathbf{u} \sim N(0, \Sigma\sigma_u^2)$$

Example



Variance Components

Genomic Selection:
Key Models, Methods, and Perspectives

Henderson Equations

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \boldsymbol{\epsilon}$$

What about the distribution of \mathbf{y} ?

$$\begin{bmatrix} \mathbf{X}^T \mathbf{y} \\ \mathbf{Z}^T \mathbf{y} \end{bmatrix} \equiv \begin{bmatrix} \mathbf{X}^T \mathbf{X} & \mathbf{X}^T \mathbf{Z} \\ \mathbf{Z}^T \mathbf{X} & \mathbf{Z}^T \mathbf{Z} + \Sigma^{-1} \frac{\sigma_{\boldsymbol{\epsilon}}^2}{\sigma_u^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix}$$

$$\boldsymbol{\epsilon} \sim N(0, R\sigma_{\boldsymbol{\epsilon}}^2)$$

$$\mathbf{u} \sim N(0, \Sigma\sigma_u^2)$$

$$\mathbf{y} \sim N(\mathbf{Xb}, \mathbf{Z} \Sigma \sigma_u^2 \mathbf{Z}^T + R \sigma_{\boldsymbol{\epsilon}}^2)$$

Phenotypic Variance

$$\underline{y} \sim N(\underline{X}\underline{b}, \underline{Z} \Sigma \underline{Z}^T + \underline{R} \sigma_{\square}^2)$$

**Genetic
Variance**

**Residual
Variance**

**Broad Sense
Heritability**

$$\frac{\sigma_g^2}{\sigma_g^2 + \sigma_{\square}^2}$$

How well the trait will
respond to selection

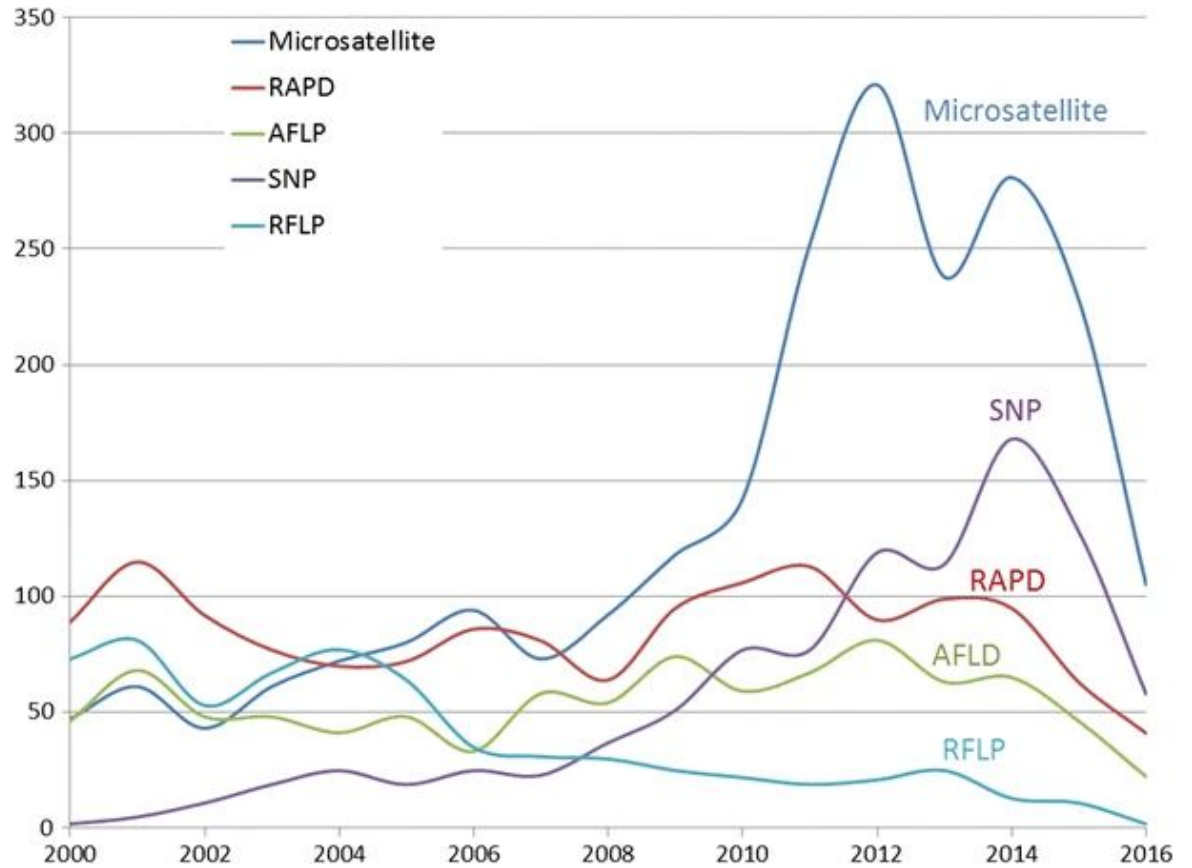
The Infinitesimal Model

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Key Models, Methods, and Perspectives

Infinitesimal Model (Fisher, 1918)

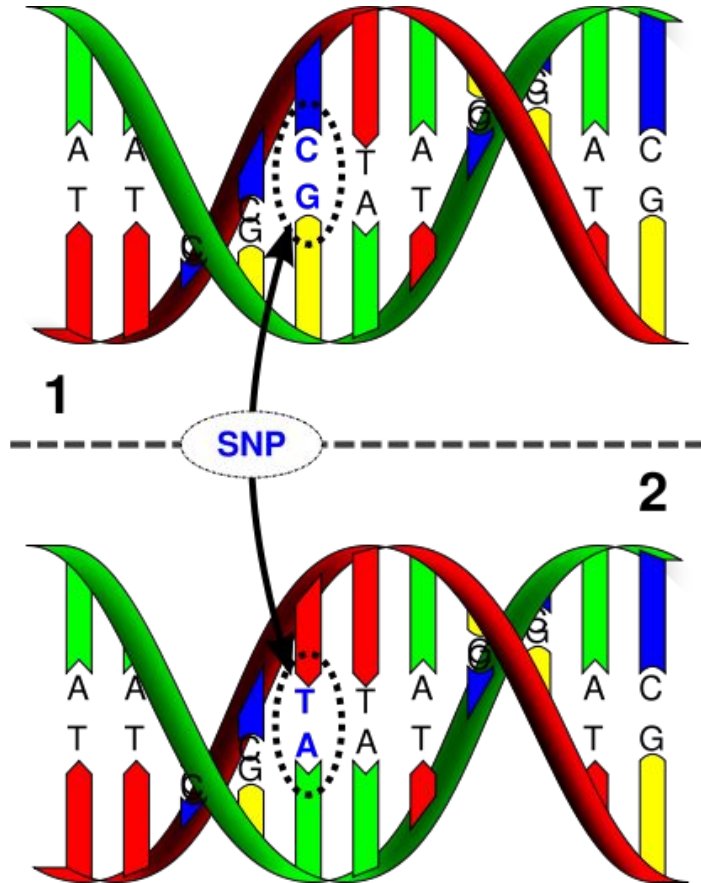
- Quantitative traits are polygenic: **very small genetic effects** over a **very large number of genes**
- Random sampling of alleles at each locus results in **continuous and normally distributed phenotypes** in the population
- Assumes that **phenotypic variation** due to genetics is **constant**

Molecular Markers



Garrido-Cardenas, Jose Antonio, Concepción Mesa-Valle, and Francisco Manzano-Agugliaro. "Trends in plant research using molecular markers." *Planta* 247 (2018): 543-557.

Single Nucleotide Polymorphisms



Geno	Allele 1	Allele 2	Code
G1	C	C	0
G2	C	G	1
G3	G	G	2

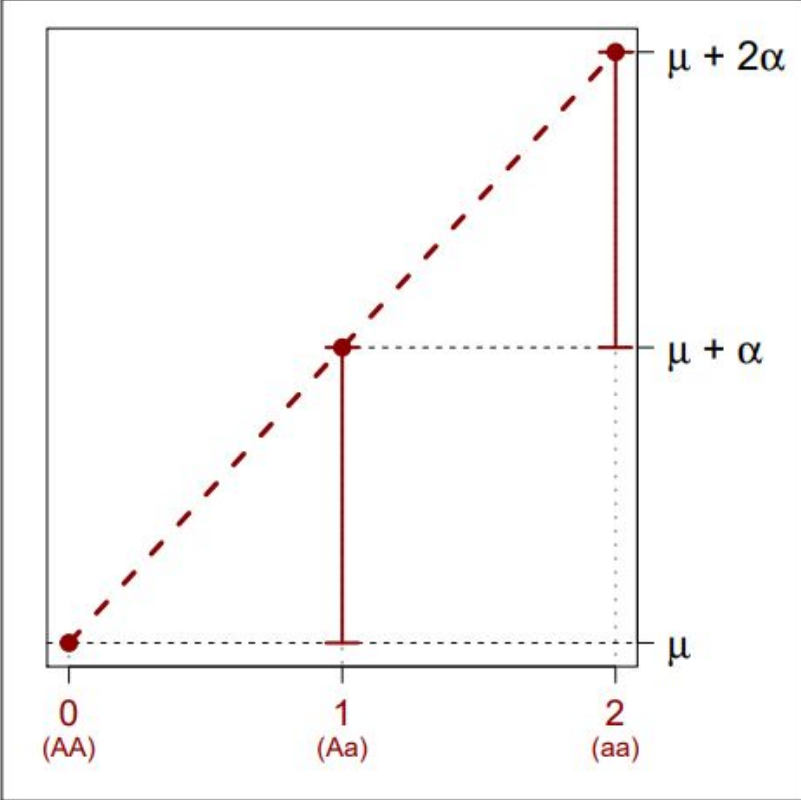
One Locus Model

$$y = \mu + M\alpha + \epsilon$$

Effect

Marker Genotype

0 1 2



Infinitesimal Model

$$y_i = \mu + \sum_{j=1}^m M_{ij} \alpha_j + \epsilon_i$$

Infinitesimal Model

M_1 M_2 M_3 M_4

Ind 1 **A**CTG**C**TATGC**G**CGATAT**T**CGCGATCG Allele 1
 ACTG**C**TATGC**A**CGATAT**T**CGCGATCG Allele 2

$$Y_1 = \mu + M_{1,1}\alpha_1 + M_{1,2}\alpha_2 + M_{1,3}\alpha_3 + M_{1,4}\alpha_4 + E_1$$

$$Y_1 = G_1 + E_1$$

Ind 2 **A**CTG**T**TATGC**A**CGATAT**T**CGCGATCG Allele 1
 CCTG**T**TATGC**A**CGATA**A**CGCGATCG Allele 2

$$Y_2 = \mu + M_{2,1}\alpha_1 + M_{2,2}\alpha_2 + M_{2,3}\alpha_3 + M_{2,4}\alpha_4 + E_2$$

$$Y_2 = G_2 + E_2$$

Ind 3 **C**CTG**C**TATGC**G**CGATA**A**CGCGATCG Allele 1
 CCTG**T**TATGC**G**CGATA**A**CGCGATCG Allele 2

$$Y_3 = \mu + M_{3,1}\alpha_1 + M_{3,2}\alpha_2 + M_{3,3}\alpha_3 + M_{3,4}\alpha_4 + E_3$$

$$Y_3 = G_3 + E_3$$

Infinitesimal Model

$$y_i = \mu + \sum_{j=1}^m M_{ij} \alpha_j + \epsilon_i$$

Only Additive Effects

The individual additive effect of each locus is very small
Epistasis and dominance effects are disregarded

Infinitesimal Model

$$y_i = \mu + \sum_{j=1}^m M_{ij} \alpha_j + \epsilon_i$$

$m \rightarrow \infty$

The number of loci affecting the trait is so large that approximates infinity, assuming that many additive effects can absorb epistasis and dominance

Infinitesimal Model

$$y_i = \mu + \sum_{j=1}^m M_{ij} \alpha_j + \epsilon_i$$

Genetic (Breeding) Values

Infinitesimal Model

$$y_i = \mu + \sum_{j=1}^m M_{ij} \alpha_j + \epsilon_i$$

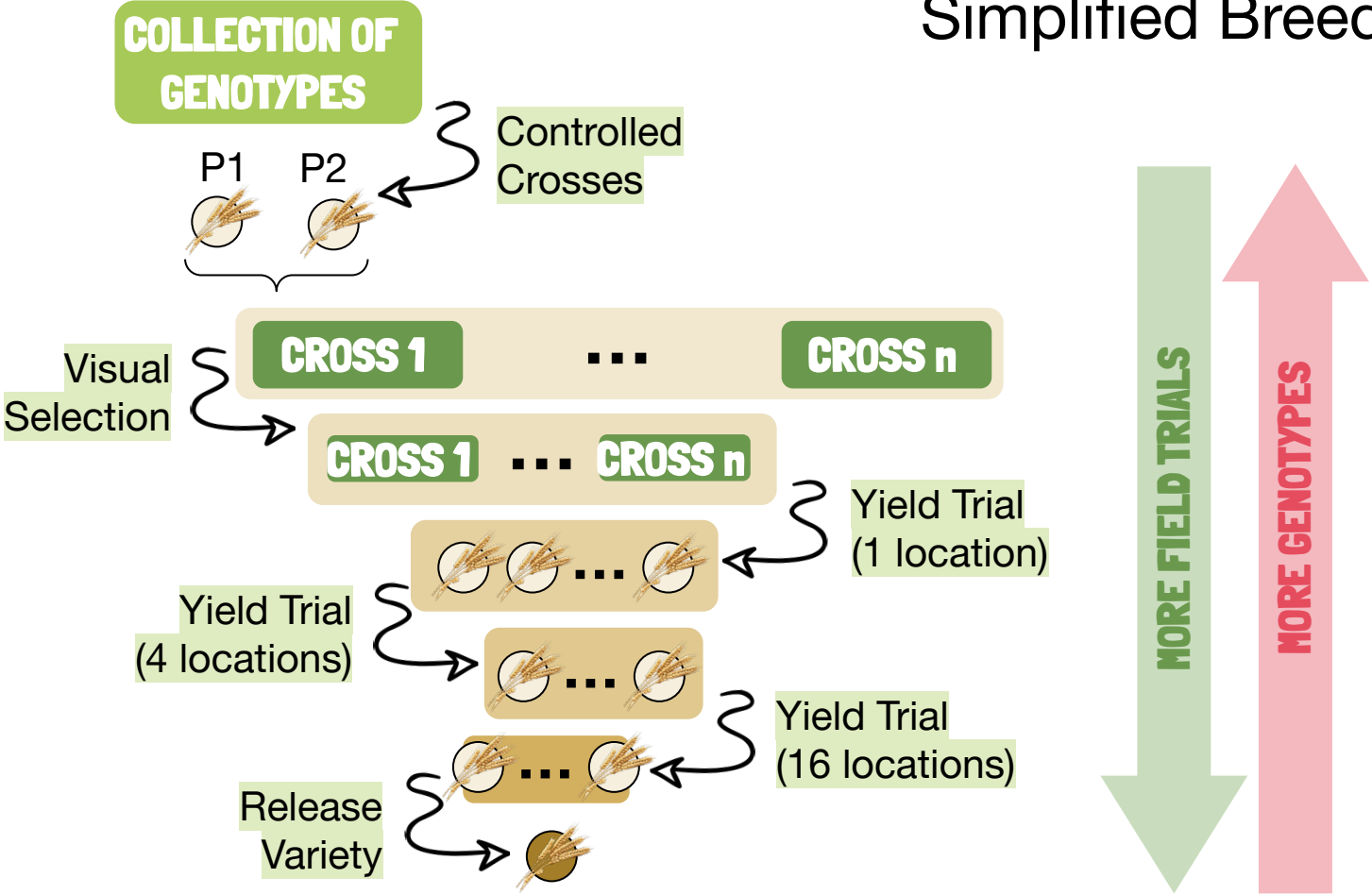
Genetic (Breeding) Values

$$y_i = \mu + g_i + \epsilon_i$$

Marker-Assisted and Genomic Selection

Genomic Selection:
Key Models, Methods, and Perspectives

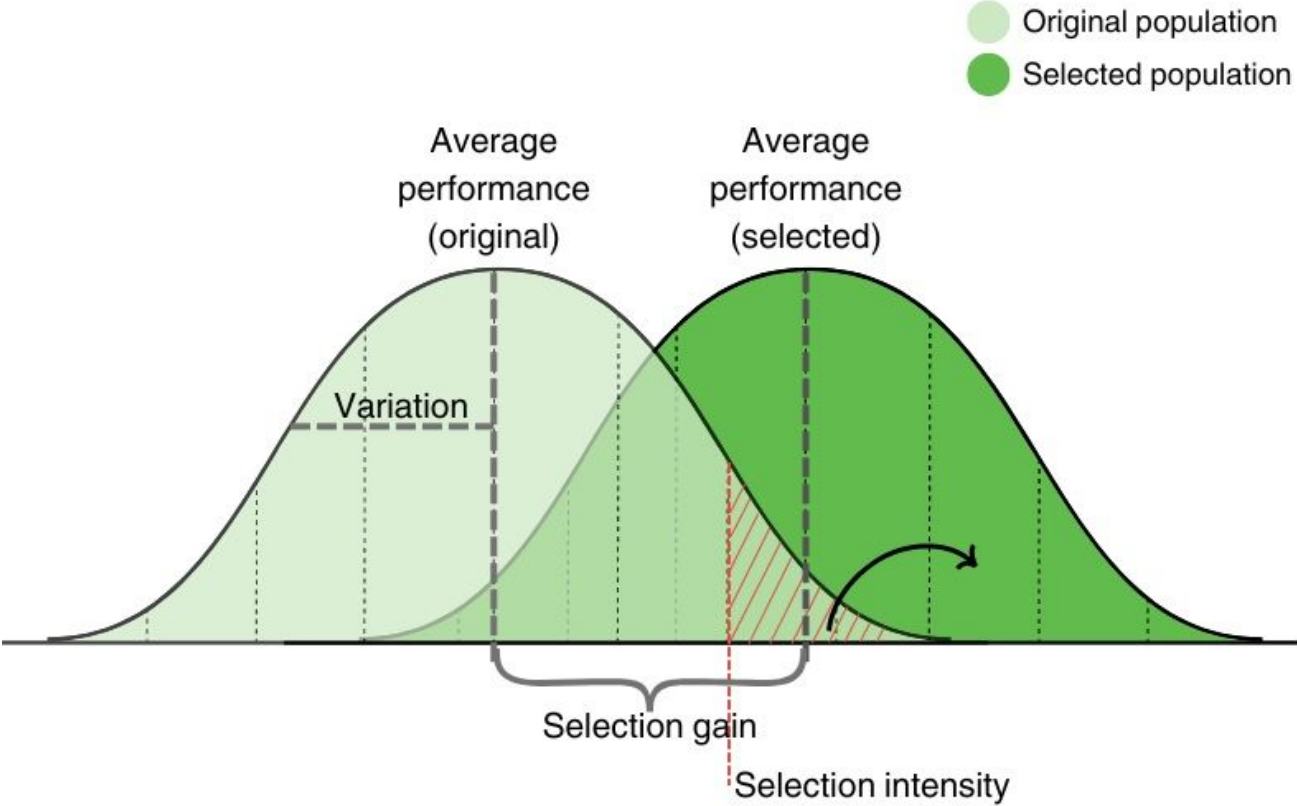
Simplified Breeding Program



How to Maximize the Genetic Gains?

- Increasing the **intensity of selection**
- Minimizing the **environmental effect** (replicate and randomize)
- Increasing the **genetic variability**
- Using **more accurate or less time-consuming** breeding schemes

Genetic Gain Obtained



Estimated Genetic Gain

$$\Delta G = \frac{i \times r \times \sigma_A}{L}$$

Genetic Gain

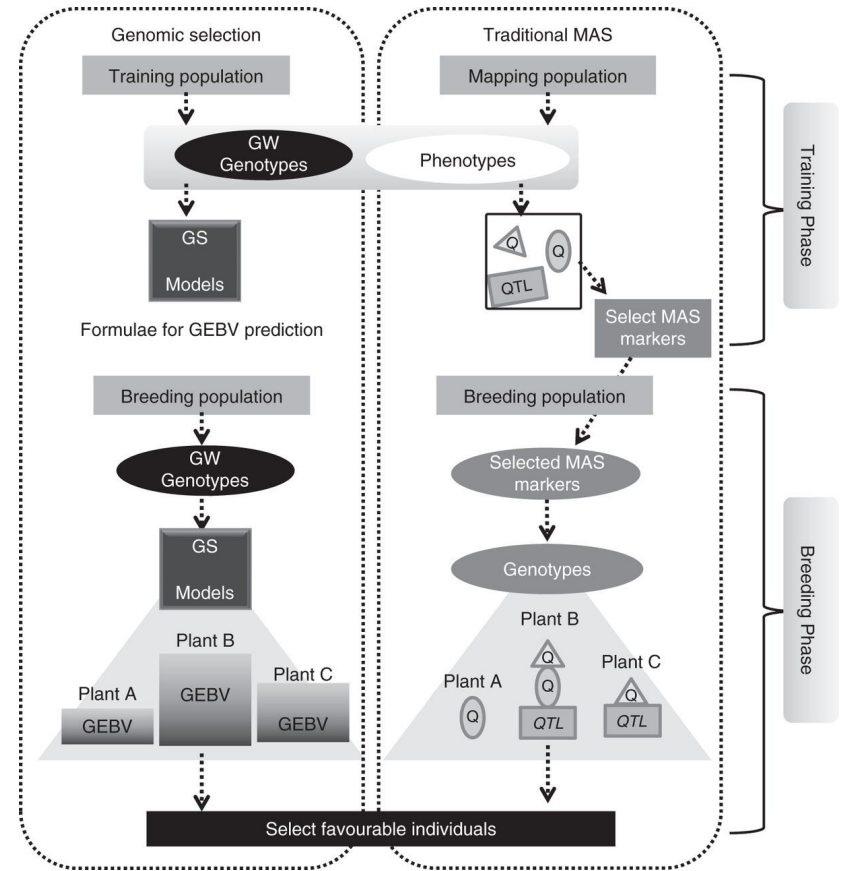
Selection Intensity

Accuracy of Selection

Genetic Variance

Generation Interval

Molecular Markers



Nakaya, Akihiro, and Sachiko N. Isobe. "Will genomic selection be a practical method for plant breeding?." *Annals of Botany* 110.6 (2012): 1303-1316.

Marker Assisted Selection

QTL Mapping

Low allelic diversity
Biparental population
needs to be created
Lower resolution (few
recombination events)
Low resolution, **large QTLs**

GWAS

Sometimes results are **not replicated** across
populations
Results need to be
validated
Size of population and
markers

Meuwissen et al. (2001)

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Prediction of Total Genetic Value Using Genome-Wide Dense Marker Maps

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Past Perspectives

Annals of Botany **110**: 1303–1316, 2012

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ANNALS OF
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REVIEW: PART OF A HIGHLIGHT ON BREEDING STRATEGIES
FOR FORAGE AND GRASS IMPROVEMENT

Will genomic selection be a practical method for plant breeding?

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Past Perspectives



OPINION · Volume 31, Issue 9, P497-504, September 2013

Opinion

Cell
P R E S S

Does genomic selection have a future in plant breeding?

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Swedish University of Agricultural Sciences, Department of Animal Breeding and Genetics, Box 7023, 75007 Uppsala, Sweden

Feature Review

Genomic Selection in Plant Breeding: Methods, Models, and Perspectives

José Crossa,^{1,*} Paulino Pérez-Rodríguez,² Jaime Cuevas,³
Osvaal Montesinos-López,⁴ Diego Jarquín,⁵
Gustavo de los Campos,⁶ Juan Burgueño,¹
Juan M. Camacho-González,² Sergio Pérez-Elizalde,²
Yoseph Beyene,¹ Susanne Dreisigacker,¹ Ravi Singh,¹
Xuecai Zhang,¹ Manje Gowda,¹ Manish Roorkiwal,⁷
Jessica Rutkoski,⁸ and Rajeev K. Varshney^{7,*}

Strategy Evaluations

Plant Science 242 (2016) 23–36



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journal homepage: www.elsevier.com/locate/plantsci



Breeding schemes for the implementation of genomic selection in wheat (*Triticum* spp.)

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Strategy Evaluations

Theoretical and Applied Genetics (2019) 132:669–686
<https://doi.org/10.1007/s00122-018-3270-8>

REVIEW ARTICLE

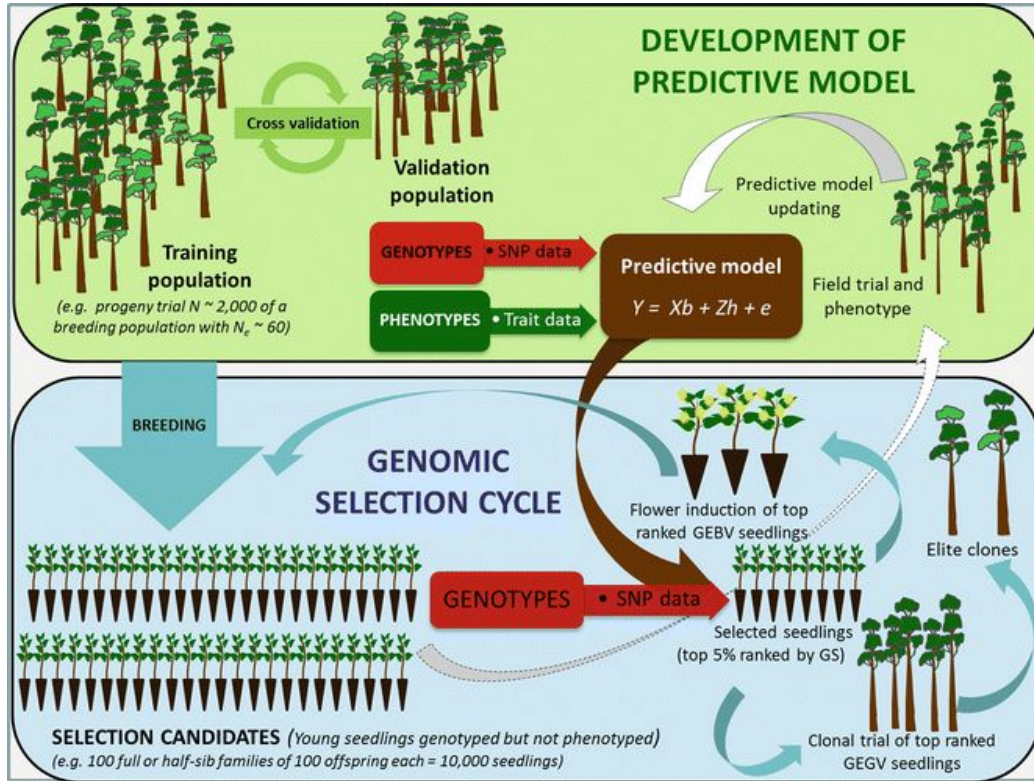


Accelerating crop genetic gains with genomic selection

Kai Peter Voss-Fels¹  · Mark Cooper¹  · Ben John Hayes¹ 

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Genomic Selection



Grattapaglia, Dario. "Status and perspectives of genomic selection in forest tree breeding." *Genomic selection for crop improvement: New molecular breeding strategies for crop improvement* (2017): 199-249.

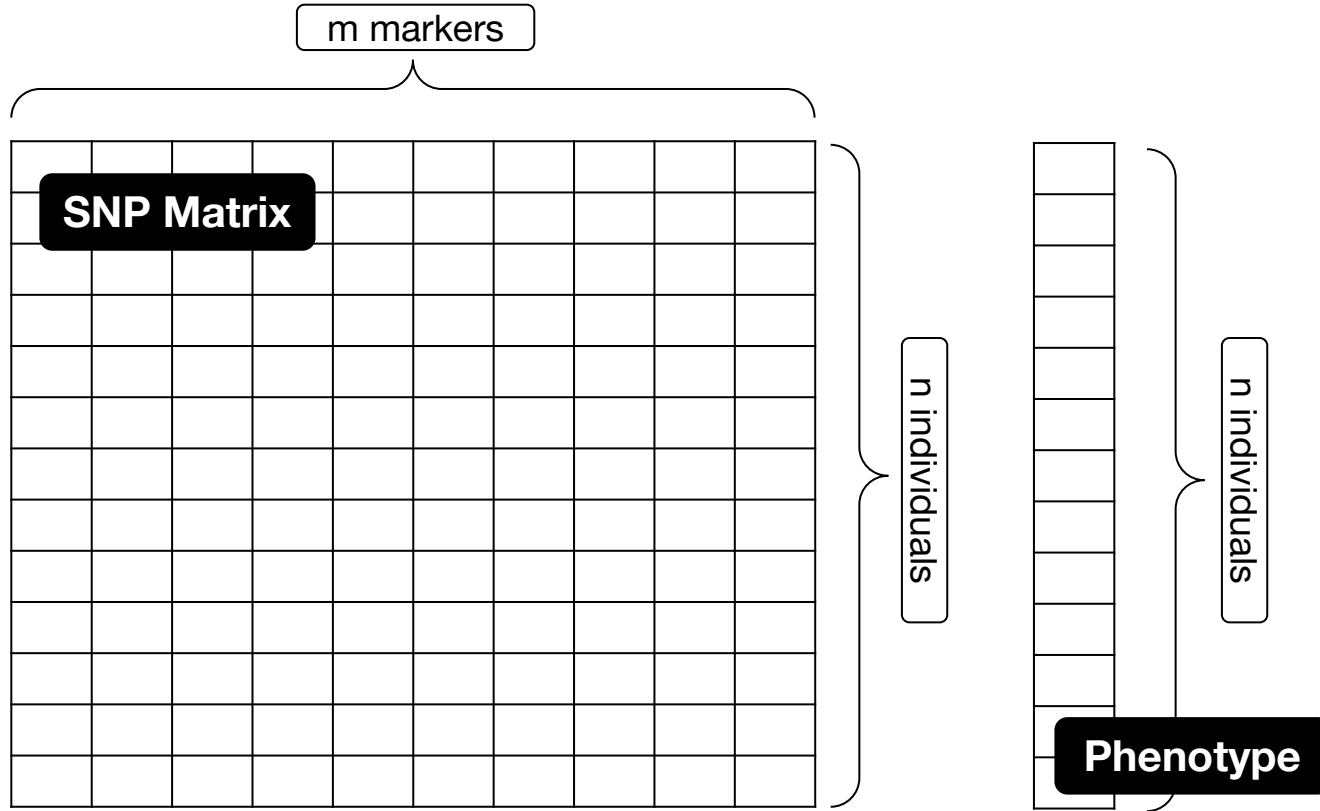
Genomic Selection Applied to Breeding Programs

- Reducing the time to develop cultivars
- Increasing the effective size and selection intensity
- Increasing the genetic gain per unit time

Genomic Prediction Models

Genomic Selection:
Key Models, Methods, and Perspectives

Genomic Prediction



Daetwyler, Hans D., et al. "Genomic prediction in animals and plants: simulation of data, validation, reporting, and benchmarking." *Genetics* 193.2 (2013): 347-365.

Henderson Equations

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \boldsymbol{\varepsilon}$$

$$\begin{bmatrix} \mathbf{X}^T \mathbf{y} \\ \mathbf{Z}^T \mathbf{y} \end{bmatrix} \equiv \begin{bmatrix} \mathbf{X}^T \mathbf{X} & \mathbf{X}^T \mathbf{Z} \\ \mathbf{Z}^T \mathbf{X} & \mathbf{Z}^T \mathbf{Z} + \Sigma^{-1} \frac{\sigma_{\boldsymbol{\varepsilon}}^2}{\sigma_u^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix}$$

$$\boldsymbol{\varepsilon} \sim N(0, R\sigma_{\boldsymbol{\varepsilon}}^2)$$

$$\mathbf{u} \sim N(0, \Sigma\sigma_u^2)$$

SNP-BLUP

SNP Matrix

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \boldsymbol{\epsilon}$$

$$\begin{bmatrix} \mathbf{X}^T \mathbf{y} \\ \mathbf{Z}^T \mathbf{y} \end{bmatrix} \equiv \begin{bmatrix} \mathbf{X}^T \mathbf{X} & \mathbf{X}^T \mathbf{Z} \\ \mathbf{Z}^T \mathbf{X} & \mathbf{Z}^T \mathbf{Z} + \mathbf{I} \frac{\sigma_{\boldsymbol{\epsilon}}^2}{\sigma_{\mathbf{u}}^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix}$$

All SNPs explain the same proportion of variance on each trait

$$\boldsymbol{\epsilon} \sim N(0, R\sigma_{\boldsymbol{\epsilon}}^2)$$

$$\mathbf{u} \sim N(0, \mathbf{I}\sigma_{\mathbf{u}}^2)$$

G-BLUP

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \boldsymbol{\epsilon}$$

$$\begin{bmatrix} \mathbf{X}^T \mathbf{y} \\ \mathbf{Z}^T \mathbf{y} \end{bmatrix} \equiv \begin{bmatrix} \mathbf{X}^T \mathbf{X} & \mathbf{X}^T \mathbf{Z} \\ \mathbf{Z}^T \mathbf{X} & \mathbf{Z}^T \mathbf{Z} + \mathbf{G}^{-1} \frac{\sigma_{\boldsymbol{\epsilon}}^2}{\sigma_{\mathbf{u}}^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix}$$

**Genomic
Relationship Matrix**

$$\boldsymbol{\epsilon} \sim N(0, R\sigma_{\boldsymbol{\epsilon}}^2)$$

$$\mathbf{u} \sim N(0, \mathbf{G}\sigma_{\mathbf{u}}^2)$$

G-BLUP

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} \sim N \left[\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \sigma_u^2 \right]$$

$$G_{jk} = \sum_{i=1}^m \frac{(x_{ij} - 2p_i)(x_{ik} - 2p_i)}{2p_i(1-p_i)}$$

G-BLUP

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} \sim N \left[\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \sigma_u^2 \right]$$

Going SNP
by SNP

$$G_{jk} = \sum_{i=1}^m \frac{(x_{ij} - 2p_i)(x_{ik} - 2p_i)}{2p_i(1 - p_i)}$$

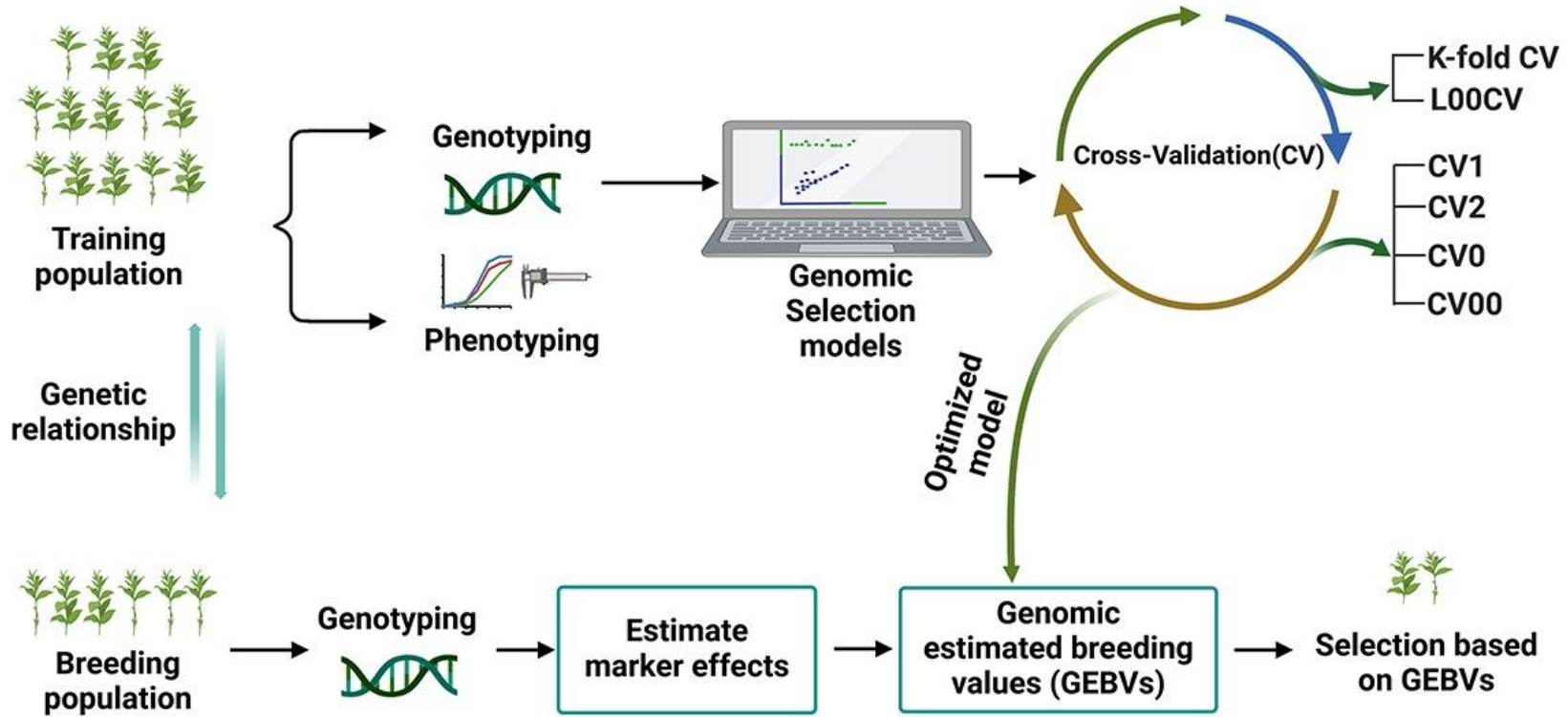
Genomic relationship
between individual j
and individual k

Minor allele
frequency of
SNP i

Cross Validation Strategies

Genomic Selection:
Key Models, Methods, and Perspectives

Cross Validation Strategies



Mbebi, Alain J., et al. "Advances in multi-trait genomic prediction approaches: classification, comparative analysis, and perspectives." *Briefings in Bioinformatics* 26.3 (2025): bbaf211.

Cross Validation Strategies

Five-fold	Folds				
Iteration 1	F1	F2	F3	F4	F5
Iteration 2	F1	F2	F3	F4	F5
Iteration 3	F1	F2	F3	F4	F5
Iteration 4	F1	F2	F3	F4	F5
Iteration 5	F1	F2	F3	F4	F5

LOOCV	Genotypes											
Iteration 1	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	---	n
Iteration 2	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	---	n
Iteration 3	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	---	n
Iteration 4	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	---	n
Iteration 5	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	---	n
...												
Iteration n	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	---	n

	Tested environments			Untested environments		
	E1	E2	E3	E4	E5	E6
Tested genotypes	G1	G1	G1	G1	G1	G1
	G2	G2	G2	G2	G2	G2
	G3	G3	G3	G3	G3	G3
	G4	G4	G4	G4	G4	G4
	G5	G5	G5	G5	G5	G5
Untested genotypes	G6	G6	G6	G6	G6	G6
	G7	G7	G7	G7	G7	G7
	G8	G8	G8	G8	G8	G8
	G9	G9	G9	G9	G9	G9
	G10	G10	G10	G10	G10	G10

	Tested environments			Untested environments		
	E1	E2	E3	E4	E5	E6
Tested genotypes	G1	G1	G1	G1	G1	G1
	G2	G2	G2	G2	G2	G2
	G3	G3	G3	G3	G3	G3
	G4	G4	G4	G4	G4	G4
	G5	G5	G5	G5	G5	G5
Untested genotypes	G6	G6	G6	G6	G6	G6
	G7	G7	G7	G7	G7	G7
	G8	G8	G8	G8	G8	G8
	G9	G9	G9	G9	G9	G9
	G10	G10	G10	G10	G10	G10

	Tested environments			Untested environments		
	E1	E2	E3	E4	E5	E6
Tested genotypes	G1	G1	G1	G1	G1	G1
	G2	G2	G2	G2	G2	G2
	G3	G3	G3	G3	G3	G3
	G4	G4	G4	G4	G4	G4
	G5	G5	G5	G5	G5	G5
Untested genotypes	G6	G6	G6	G6	G6	G6
	G7	G7	G7	G7	G7	G7
	G8	G8	G8	G8	G8	G8
	G9	G9	G9	G9	G9	G9
	G10	G10	G10	G10	G10	G10

	Tested environments			Untested environments		
	E1	E2	E3	E4	E5	E6
Tested genotypes	G1	G1	G1	G1	G1	G1
	G2	G2	G2	G2	G2	G2
	G3	G3	G3	G3	G3	G3
	G4	G4	G4	G4	G4	G4
	G5	G5	G5	G5	G5	G5
Untested genotypes	G6	G6	G6	G6	G6	G6
	G7	G7	G7	G7	G7	G7
	G8	G8	G8	G8	G8	G8
	G9	G9	G9	G9	G9	G9
	G10	G10	G10	G10	G10	G10

Training set
 Test set

Alemu, Admas, et al. "Genomic selection in plant breeding: Key factors shaping two decades of progress." *Molecular Plant* 17.4 (2024): 552-578.

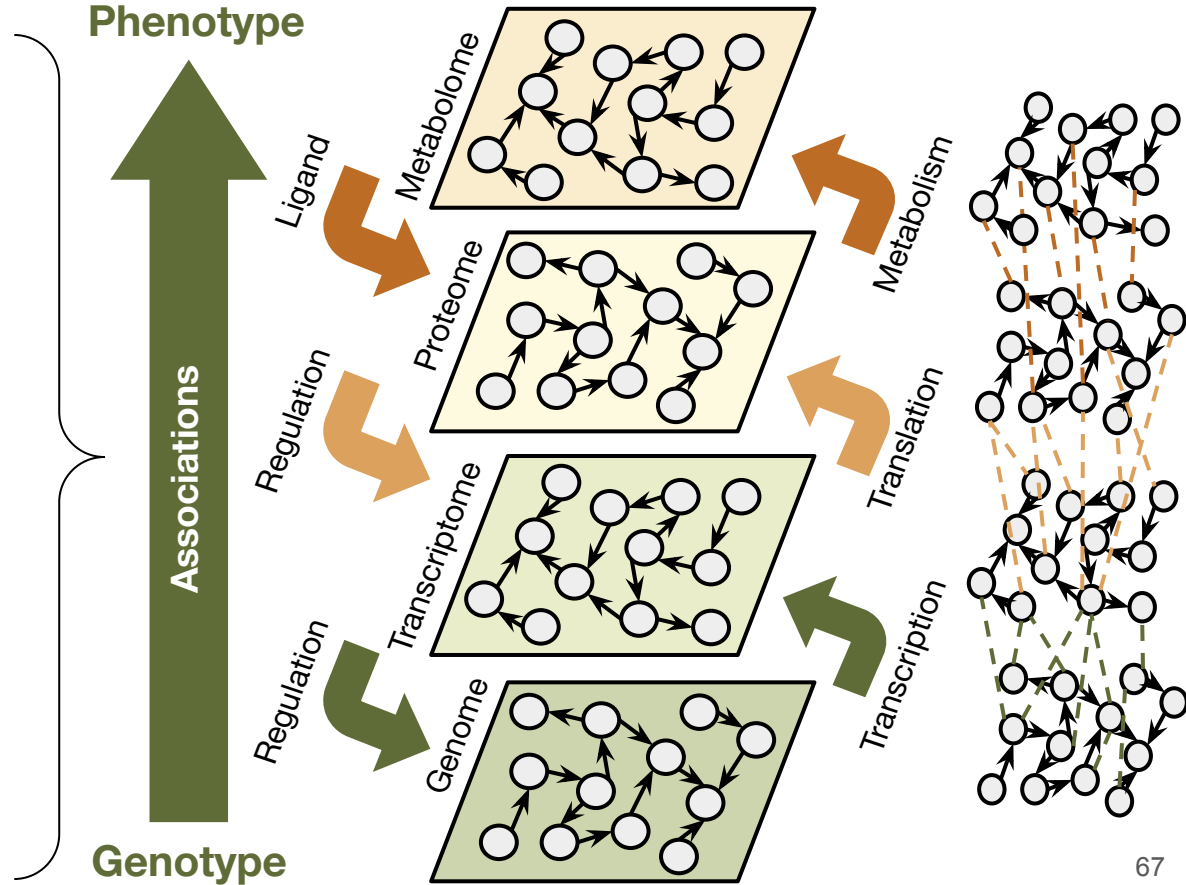
Factor Affecting Prediction Accuracy

- Marker density
- Population diversity and effective population size
- Training set
- Genetic relationship between training population and selection candidates
- Rare alleles
- Missing data and imputation
- Ploidy
- GxE

Multi-Omics Approaches

Genomic Selection:
Key Models, Methods, and Perspectives

Unraveling Complex Phenotypes



Breeding Stages

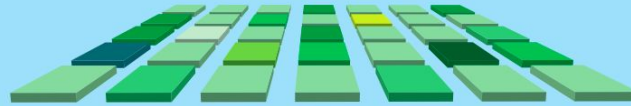
BREEDING 1.0

Incidental selection by farmers



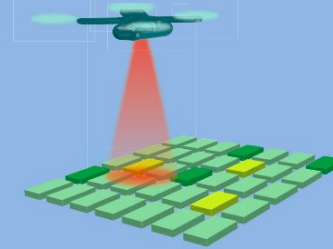
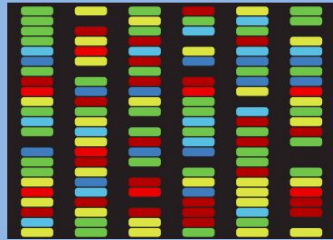
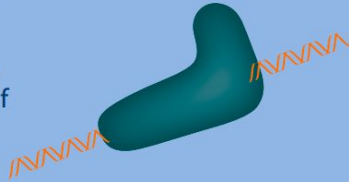
BREEDING 2.0

Statistical and experimental design to improve selection effort



BREEDING 3.0

Integration of genetic and genomic data; current state of the art

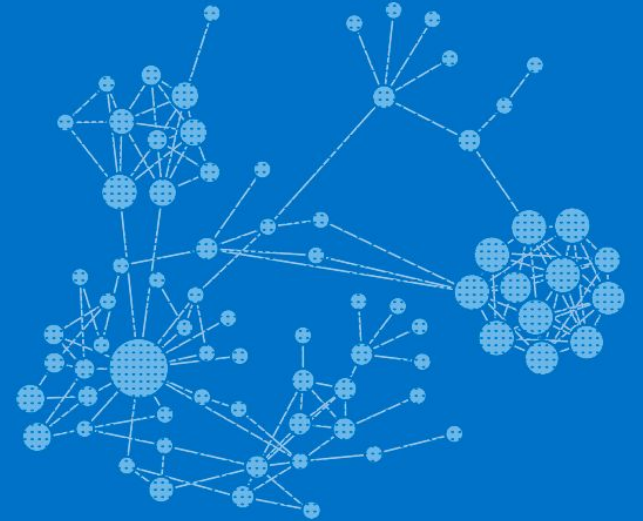


Wallace, Jason G., Eli Rodgers-Melnick, and Edward S. Buckler. "On the road to breeding 4.0: unraveling the good, the bad, and the boring of crop quantitative genomics." *Annual review of genetics* 52 (2018): 421-444.

Breeding Stages

BREEDING 4.0

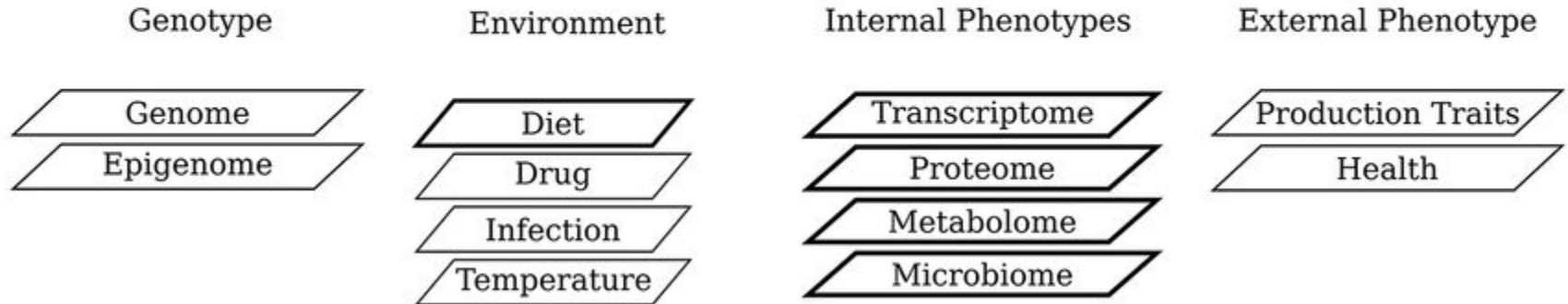
Ability to combine any known alleles into optimal combinations; will be reached soon for some crops



Wallace, Jason G., Eli Rodgers-Melnick, and Edward S. Buckler. "On the road to breeding 4.0: unraveling the good, the bad, and the boring of crop quantitative genomics." *Annual review of genetics* 52 (2018): 421-444.

Unraveling Complex Phenotypes

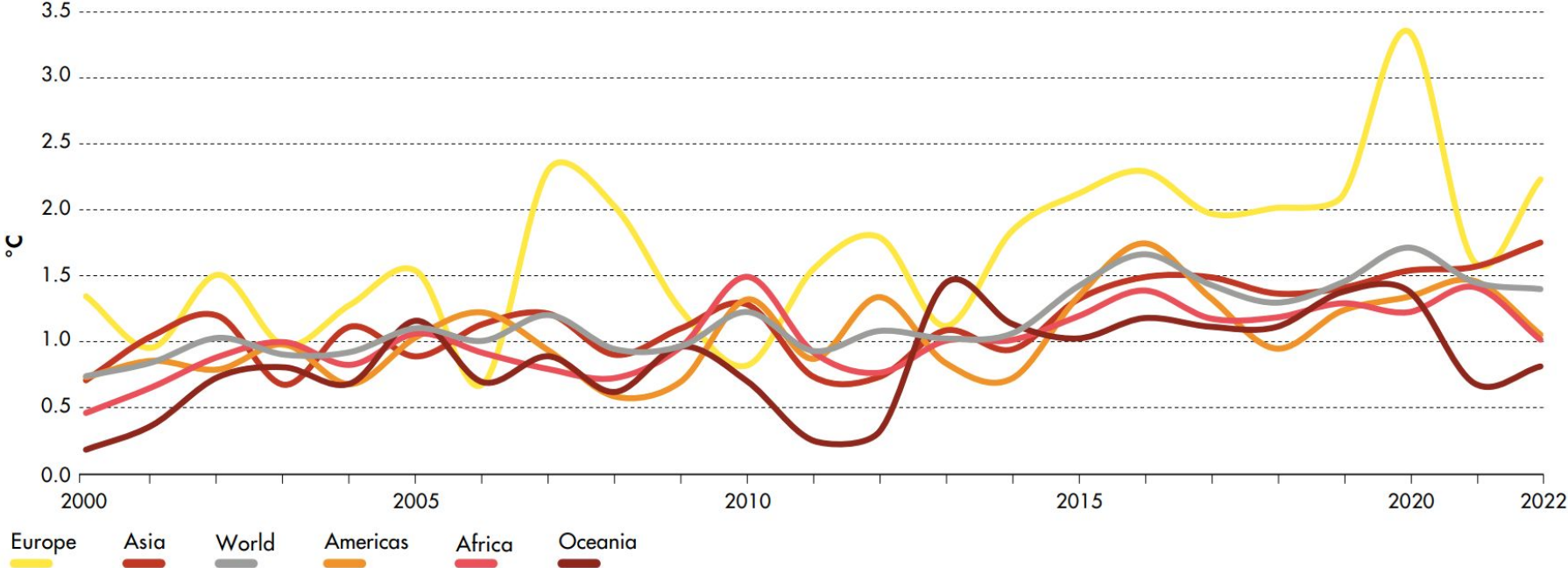
G + E + GE → P



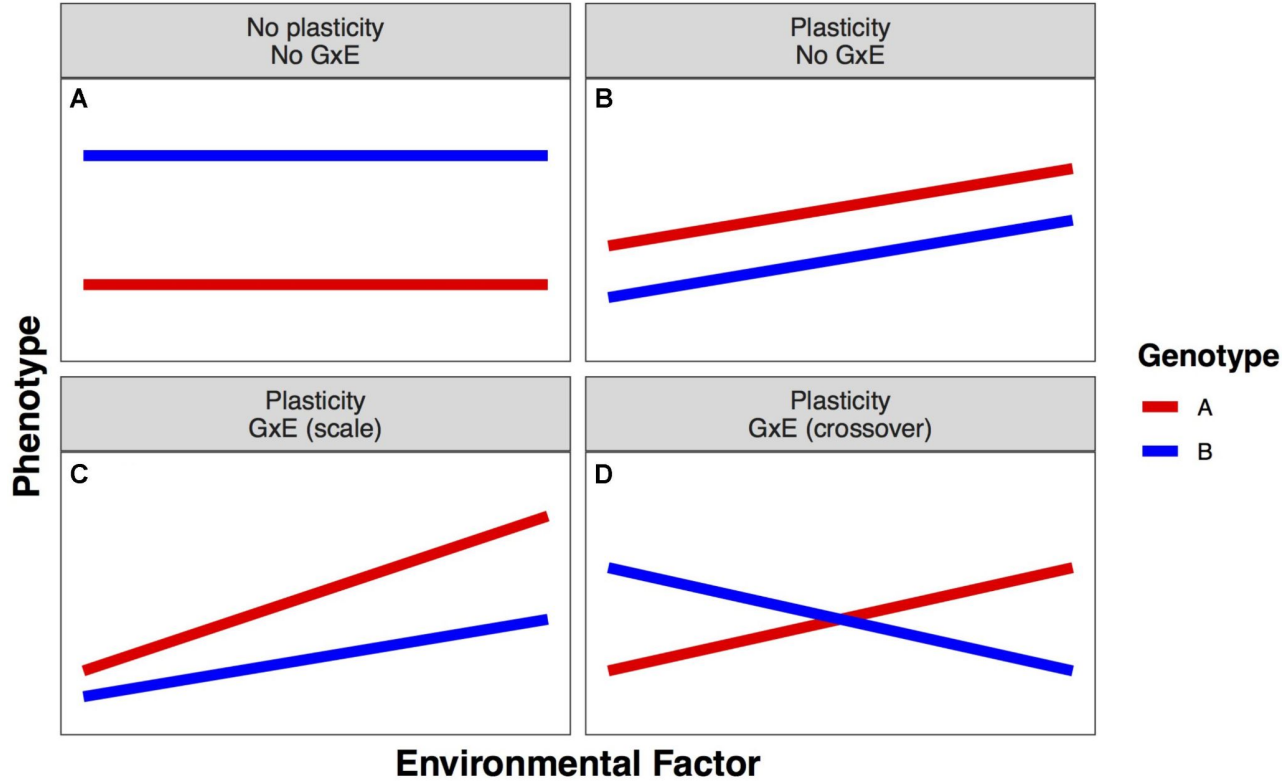
Benis, Nirupama, et al. "Multi-level integration of environmentally perturbed internal phenotypes reveals key points of connectivity between them." *Frontiers in Physiology* 8 (2017): 388.

Genomic Selection: Key Models, Methods, and Perspectives

Environmental Changes



GxE



Kusmec, Aaron, Natalia de Leon, and Patrick S. Schnable. "Harnessing phenotypic plasticity to improve maize yields." *Frontiers in Plant Science* 9 (2018): 1377.

