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Estimation of Genetic Parameters of Selfing Population Derived from an Equilibrium One I. Theory

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ABSTRACT
Evaluation of inbred lines to develop hybrid is a key in a hybrid program. Inbred lines are extracted from the base population. During the process, extraction of inbred lines requires time and it is therefore interesting that during the extraction process, useful information appears for breeders, whether it is valuable or not. In response to the described useful information that appears for breeders, we formulate the concepts to estimate the value of the base population by genetic parameters. Using a single multi-allelic locus model, in addition to mean and variance, an inbreeding population derived by selfing an equilibrium one has other parameters similar to those of an F_2 from a line cross useful for a hybrid program. The theory and estimation procedure are discussed.

Key words: Genetic parameters, selfing population, mean, variance

INTRODUCTION

Commercial hybrid plant has potential to increase the world's agricultural productivity. The first step in hybrid program is the development of inbred lines for a hybrids parents. Inbred lines are a population of identical or nearly identical plants that are usually developed by self-pollination (Sleper and Poehlman, 2006) and breeders have been developing a large number of inbred lines and evaluating their performance in crosses (Guo *et al*., 2013). During the early inbred line development from base population, each plant possesses different combinations of genes, resulting in various combinations of traits that respond differently. At this point, the inbreds sort themselves into unique patterns as the offspring plants segregate from the parent lines. During the phases of inbred line development, researchers select the seeds from the best plants in the best rows and plant those seeds for the next generation of testing. For most hybrid breeding programs, only a small proportion of crosses can be evaluated in the field. An accurate prediction of hybrid performance prior to and after some field testing is of crucial importance in maize breeding (Guo *et al*., 2013). Extracting inbred lines from the base population takes time, so it will be interesting if, during the extraction, there is useful information that appears for breeders on whether it is valuable or not. In order to get valuable results for the development of elite inbred, we must know genetic parameter from the inbred lines.

An equilibrium population consists of inbred lines and hybrids. The hybrids do not know their superiority, so they need to be extracted. The process of extraction of an equilibrium population will form an inbreeding population. One consequence of inbreeding is changes in the distribution of genetic variance (Lopez-Fanjul *et al*., 1989; Fernandez *et al*., 1995; Fowler and Whitlock, 1999; Whitlock and Fowler, 1999). Under the assumption of segregation generation starting from selfing heterozygous individuals in the base population can form the structure of the F_2 genotypes (Falconer and Mackay, 1996; Kearsey and Pooni, 1996). If we look at the groups of heterozygous genotype in an equilibrium population, they are a form of group pairs of inbred lines which have the possibility of being good hybrids. One parameter that is often used to assess the inbreeding

population is variance component. Theory has shown that genetic parameters are present in an inbreeding population (Robertson, 1952; Mather and Jinks, 1982; Kearsey and Pooni, 1996; Hallauer *et al*., 2010).

With respect to a quantitative trait, a random mating population consists of a mixture of homozygous and non-homozygous individuals where the latter is at least heterozygous for one locus. When the population is in equilibrium, their frequency is the product of the frequency of the genes they possess. Information on dominance variance in the population and the average degree of dominance are the basis prior to starting a hybrid program: Inbred lines-homozygous individuals-are extracted, crossed in pairs and evaluated for heterosis in replicated experiments. Extraction is time consuming but there is no guarantee that elite in breds may be obtained in the evaluation phase. Using a single locus model with an arbitrary number of alleles, similar parameters relevant to a hybrid program are developed. The parameters: Heterosis, additive and dominance variance refer to the mixture of F_2S populations derived from all possible pairs of the in breds. Thus they are weighted averages.

Here we discuss the genetic parameters for selfing population through variance estimating of segregation generation in S_1 (F = 1/2) and S_2 (F = 3/4) families. In response to the described useful information that appears for breeders, we formulate the concepts to estimate the value of the base population by genetic parameters.

METHODOLOGY

Development of the theory: Consider a given locus in an equilibrium population π_0 where there exists allele A_i (i = 1, 2, ..., s) with frequency p_i. The genetic structure of π_0 is:

$$\pi_0 = \sum_{i,j} p_i p_j A_i A_j$$

The population mean is:

$$\mu_0 = \sum_{i,j} p_i p_j \mu_{ij}$$

where, μ_{ij} is genotypic value of A_iA_j. Modelling μ_{ij} statistically as $\mu_{ij} = \mu_0+\alpha_i+\alpha_j+\delta_{ij}$ with α_i and α_j is additive effect of allele A_i and A_j and δ_{ij} is the dominance deviation or the interaction effect of allele A_i and A_j, the genetic variance of the population is measured according to Kempthorne (1969), Steel and Torrie (1980) and Nyquist (1990):

$$\sigma_0^2 = \sigma_A^2 + \sigma_D^2$$

Where:

$$\sigma_A^2 = 2\sum_i p_i \alpha_i^2$$

Table 1: Composition of population, frequency, mean and variance when the coefficient of inbreeding is F

Population	Frequency	Mean	Variance
π_0	1-F	μ_0	σ^2_0
π_1	F	μ_1	σ^2_1

and:

$$\sigma_D^2 = \sum_{i,j} p_i p_j \delta_{ij}^2$$

Inbred population derived from π_0 is $\pi_1 = \sum_i p_i A_i A_i$ with mean $\mu_1 = \sum_i p_i \mu_{ii}$ and genetic variance $\sigma_1^2 = \sum_i p_i (\mu_{ii} - \mu_1)^2$. However, if inbreeding is up to an inbreeding coefficient of F, the resulting inbreeding population is $\pi_F = (1\text{-}F)\pi_0+F\pi_1$ and is depicted in Table 1. Note that π_F is a mixture of π_0 and π_1 with frequency of (1-F) and F, respectively. Therefore, the mean of π_F, denoted by μ_F, is the expected value of the mean:

$$\mu_F = (1\text{-}F)\ \mu_0+F\mu_1 \quad (1)$$

while the variance, denoted by is the sum of variance of the mean, $(1\text{-}F)\ (\mu_0\text{-}\mu_F)^2+F(\mu_1\text{-}\mu_F)^2 = F(1\text{-}\ F)\ (\mu_0\text{-}\mu_1)^2$ and the mean of the variance $(1-F)\sigma_0^2 + F\sigma_1^2$. Thus:

$$\sigma_F^2 = (1-F)\sigma_0^2 + F\sigma_1^2 + F(1-F)\ (\mu_1 - \mu_0)^2 \quad (2)$$

An equation that according to Crow and Kimura (1970), Jain (1982) and Nyquist (1990) it was formulated for the first time by Wright (1951).

With selfing (F = ½), the population structure, denoted by $\pi_{½}$ or π_{S_π} is:

$$\pi_{S_1} = \sum_i p_i^2 A_i A_i + \sum_{i\neq j} p_i p_j (¼A_iA_i + ½A_iA_j + ¼A_jA_j) \quad (3)$$

The population mean is:

$$\begin{aligned} \mu_{S_1} &= \sum_i p_i^2 \mu_{ii} + \sum_{i\neq j} p_i p_j (¼\mu_{ii} + ½\mu_{ij} + ¼\mu_{jj}) \\ &= \mu_0 - \sum_{i\neq j} p_i p_j (¼\mu_{ii} - ½\mu_{ij} + ¼\mu_{jj}) \\ &= \mu_0 - ½ \sum_{i\neq j} p_i p_j H_{ij} \end{aligned} \quad (4)$$

Where:

$$H_{ij} = \mu_{ij} - ½(\mu_{ii} + \mu_{jj})$$

$$\mu_{S_1} = \mu_0 - ½H^*$$

Where:

$$H^* = \sum_{i\neq j} p_i p_j H_{ij}$$

H* as weighted intra varietal heterosis or weighted average heterosis in Hardy-Weinberg population.

Note that the expression in parentheses in the second term in Eq. 3 is an F_2 genotypic array derived from $A_iA_i \times A_jA_j$ cross ($i \neq j$). Denote the variance of this F_2 by $\sigma^2_{ij} = \sigma^2_{A^*_{ij}} + \sigma^2_{D^*_{ij}}$. Then variance within the S_1 family is that with a common S_0 parent:

$$\sigma^2_{S_1|S_0} = \sum_{i \neq j} p_i p_j (\sigma^2_{A^*_{ij}} + \sigma^2_{D^*_{ij}}) = \sigma^2_{A^*} + \sigma^2_{D^*} \quad (5)$$

Further selfing gives an S_2 population (F = ¾), the structure of which is:

$$\pi_{S_2} = \sum_i p_i^2 A_iA_i + \sum_{i \neq j} p_i p_j [¼A_iA_i + ½(¼A_iA_i + ½A_iA_j + ¼A_jA_j) + ¼A_jA_j]$$

Note that in the second term, the expression in parentheses is an F_2 and those in brackets is an F_3 derived from $A_iA_i \times A_jA_j$ cross. The mean of S_2 population is:

$$\mu_{S_2} = \mu_0 - ¼H^* \quad (6)$$

Within the S_2 family variance is the variance within S_2 families having common S_1 parent is a half of F_2 variance. Denote this by $\sigma^2_{S_2|S_1}$, then:

$$\sigma^2_{S_2|S_1} = ½(\sigma^2_{A^*} + \sigma^2_{D^*}) \quad (7)$$

while within the S_2 family variance having a common S_0 parent is an F_3 variance. Denoting this by $\sigma^2_{S_2|S_0}$, then:

$$\sigma^2_{S_2|S_0} = ⅜\sigma^2_{A^*} + ¾\sigma^2_{D^*} \quad (8)$$

then using Eq. 7, 8 estimate of variance of F_3 mean can be obtained:

$$\sigma^2_{S_2|S_0} - \sigma^2_{S_2|S_1} = \sigma^2_{A^*} + ¼\sigma^2_{D^*} \quad (9)$$

Estimation procedure: From theory development, some parameters are of interest: $\mu_0, \mu_1, \mu_F, \sigma^2_0, \sigma^2_1, \sigma^2_F, \sigma^2_{A^*}, \sigma^2_{D^*}$ and H^*. For estimating these parameters, from an equilibrium population, self a random sample of n individuals to generate S_1 families. After saving some seeds from each ear for a replicated experiment, plant the remaining seeds in ear-to-rom. In the i-th (i = 1, 2, ..., n_i) row, self a random sample of n_i individuals to generate S_2 families. Evaluate these:

$$N = \sum_{i=1}^{n} n_i$$

S_2 families together with n S_1 families.

For simplicity of discussion, let the evaluation be conducted in a randomized complete block with r blocks as replicates. Analysis is done as shown in Table 2.

Table 2: Analysis of variance for S_1 and S_2 families

Source of variance	DF	MS	E(MS)
Replication	r-1		
Entry	N+n-1		
$S_1 \times S_2$	1		
Among S_1 families	n-1	M_5	$\sigma^2_{E2} + r\sigma^2_{\text{Among S1}}$
Among S_2 families	N-1	M_4	$\sigma^2_{E1} + r\sigma^2_{\text{Among S2}}$
Among $S_2\|S_0$	n-1		
Within $S_2\|S_0$	N-n	M_3	$\sigma^2_{E2} + r\sigma^2_{\text{Among S2\|S0}}$
Pooled error	(r-1) N+n-1		
($S_1 \times S_2$) *replication	r-1		
Plot-to-plot S_2 error	(r-1) (n-1)	M_2	σ^2_{E2}
Plot-to-plot S_1 error	(r-1) (N-1)	M_1	σ^2_{E1}

Let the mean of the S_1 family data be $\overline{Y}_{S1}$. It is an estimate of $\mu_{S1} = \mu_{1/2}$. Similarly for the S_2 family data: $\overline{Y}_{S2}$ is an estimate of $\mu_{S2} = \mu_{3/4}$ Using Eq. 1, estimate of μ_0 and μ_1 may be obtained. Using Eq. 4 and 6 give an estimate of H^*.

Plot-to-plot S_1 error variance consists of two components: Within plot environment and genetic within S_1 family. Thus:

$$\sigma^2_{E_1} = \sigma^2_{ew} + \sigma^2_{S_1|S_0}$$

and estimated by M_1. Similarly for plot-to-plot S_2 error variance:

$$\sigma^2_{E_2} = \sigma^2_{ew} + \sigma^2_{S_2|S_1}$$

and estimated by M_2. Recalling Eq. 5 and 7, these two equations can be solved to give $\sigma^2_{A^*} + \sigma^2_{D^*}$ and σ^2_{ew} incorporating Eq. 9 will yield $\sigma^2_{A^*}$ and $\sigma^2_{D^*}$. Finally, as $\sigma^2_{S_1} = \sigma^2_{½}$ and $\sigma^2_{S_2} = \sigma^2_{¾}$ using Eq. 2, they may be used to give σ^2_0 and σ^2_1.

RESULTS AND DISCUSSION

Inbreeding population may result from any inbreeding process. If this is so, only μ_0, μ_1, H^*, σ^2_0 and σ^2_1 can be estimated. Inbreeding through selfing will produce an F_2 population if the selfed individuals are heterozygous. This unique characteristic is exploited to get parameters similar to the ones in line cross. In line cross, the parameters refer to a single F_2 while ours refer to a mixture of F_2 populations, each weighted by its frequency; hence, the average weighted parameters.

H_{ij} in Eq. 4 is exactly d in Fisher notation with a subscript to remind that it refers to F_2 population derived from $A_iA_i \times A_jA_j$ cross. Being related to the difference of μ_0 and μ_F, H* measures inbreeding depression, considered the reverse of heterosis, disregarding the number of loci involved.

Estimation procedure discussed above is a general one in the sense that it applies also when S_2 families being evaluated may be generated from selfing S_1 ears not included in the replicated experiment as when the seed number is a constraint. However, when they are, additional information, i.e., $\text{Cov}(S_1, S_2) = \sigma^2_{A^*} + ½\sigma^2_{D^*}$ (Mather and Jinks, 1982) they can be

used together with Eq. 8 to get σ^2_{A*} and σ^2_{D*}. The latter is better in the sense that the estimation procedure is a direct one; no need to estimate σ^2_{ew}. Better still, all information is used and the estimate is obtained using the least square method.

Note that:

$$\sigma_I^2 = \tfrac{1}{2}\sum_{i,j} p_i p_j (\mu_{ii} - \mu_{jj})^2 = 2\sum_{i,j} p_i p_j a_{ij}^2 = 2\sigma_{A*}^2$$

using a notation of Fisher. It shows a better way to obtain σ_I^2. As:

$$\sigma_{D*}^2 = \sum_{i \neq j} p_i p_j d_{ij}^2$$

their similarity to those of F_2 in a line cross see standard textbooks on Quantitative Genetics such as Falconer and Mackay (1996) and Hallauer and Filho (1981) is apparent. Thus they may be extended to a multi-locus model if there is no epistasis. Model extension with epistasis being included has also been available (Nasrullah *et al*., 1995; Kempthorne, 1969). The only difference is that they are weighted by their frequencies as their coefficient, instead of 1 as in a line cross.

A final point is to be mentioned. Though homozygous individuals in π_0 are inbreds regardless of the number of loci, non-homozygous ones are a mixture F_1 hybrids in a single locus model but a mixture of F_1 hybrids for one locus or more in a multi-locus model.

CONCLUSION

Genetic parameters can be constructed by inbreeding. Inbreeding through selfing will produce an F_2 population if the selfed individuals are heterozygous. The selfing families as expression in parentheses derived from $A_iA_i \times A_jA_j$ cross ($i \neq j$), produce some parameters are of interest: $\mu_0, \mu_1, \mu_F, \sigma_0^2, \sigma_I^2, \sigma_F^2, \sigma_{A*}^2, \sigma_{D*}^2$ and H^*. The genetic parameters will then allow assessment for proper or improper assessment of hybrid programs before extraction of inbred lines are done too much.

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