

11 Genetic Statistical Model to Estimate Epistasis, Additive and Dominance Genetic Effects Using Advanced Populations

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ESTIMATING gene effects contributing to metric traits has been investigated in several studies. Most estimation methods focused on means of earlier filial (\bar{F}_1 and \bar{F}_2) and backcross populations (\bar{BC}_{11} and \bar{BC}_{12}). In this paper, a novel approach is proposed to estimate gene effect using the data generated from advanced filial ($\bar{F}_3, \bar{F}_4, \dots, \bar{F}_n$) and backcross populations (\bar{BC}_{n1} and \bar{BC}_{n2}). Where the following set of equations is derived by algebraic solution of $\bar{P}_1, \bar{P}_2, \bar{F}_3, \bar{F}_4, \bar{BC}_{31}$ and \bar{BC}_{32} means:

$$\text{Mean (M)} = \frac{1}{98} (49 \bar{P}_1 + 49 \bar{P}_2 - 64 \bar{BC}_{31} - 64 \bar{BC}_{32} + 128 \bar{F}_4),$$

$$\text{Additive effect (D)} = \frac{1}{7} (\bar{P}_1 - \bar{P}_2),$$

Dominance effect (H)

$$= \frac{1}{49} (384 \bar{BC}_{31} + 384 \bar{BC}_{32} - 196 \bar{F}_3 - 294 \bar{P}_1 - 294 \bar{P}_2 + 16 \bar{F}_4),$$

Three types of epistasis:

$$\text{Additive x additive effect (I)} = \frac{32}{49} (\bar{BC}_{31} + \bar{BC}_{32} - 2 \bar{F}_4),$$

Additive x dominance effect (J) =

$$\frac{1}{7} (32 \bar{BC}_{31} - 32 \bar{BC}_{32} - 28 \bar{P}_1 + 28 \bar{P}_2) \text{ and}$$

Dominance x dominance effect (L) =

$$\frac{16}{49} (98 \bar{F}_3 - 68 \bar{F}_4 + 49 \bar{P}_1 + 49 \bar{P}_2 - 64 \bar{BC}_{31} - 64 \bar{BC}_{32})$$

The proposed equations have been proved by means of algebra, in addition to mathematical proof using real data. The results suggest that, the model can serve as a viable particularly to estimate epistasis, additive and dominance genetic effects using the data generated from advanced filial and backcross populations $\bar{P}_1, \bar{P}_2, \bar{F}_3, \bar{F}_4, \bar{BC}_{31}$ and \bar{BC}_{32} .

Keywords: Advanced filial and backcross populations, Algebraic and Mathematical proof, Gene effects.

INTRODUCTION

Several designs have been developed for genetic analysis of metric traits using the earlier six population means (i. e., $\bar{P}_1, \bar{P}_2, \bar{F}_1, \bar{F}_2, \bar{BC}_{11}$ and \bar{BC}_{12}). Mather,

(1949) defined the scaling test for adequacy of the additive dominance model based on generation means of these six populations. Afterward, an improved model of this test have been formulated in different studies, where the by joint scaling

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test based on weighted least squares estimates of the same populations was proposed (Cavalli, 1952; Anderson & Kempthorne, 1954; Jinks, 1956 and Hayman, 1957). Designs have been extended to estimate the different types of gene effects by analyzing means of some or all the six earlier populations. Accordingly six population's designs for estimating all types of gene effects have been proposed by Anderson & Kempthorne (1954), Cockerham (1954) and Hayman (1958). However, model based on only varieties and their crosses have been suggested by Gardner & Eberhart (1966) to estimate these gene effects.

In comparison, models based only on inbred lines have been adopted but are merely satisfactory for estimating epistatic effects. Kearsey & Jinks (1968) suggested the triple test-cross of inbred lines to estimate the epistatic variation while Jinks *et al.* (1969) derived a simplified test for this purpose. Similarly, only backcrosses have been utilized in designs for testing epistasis. Mather & Jinks (1971) and Chahal & Jinks (1978) proposed standard backcross scale for testing epistasis in case of absence of inbred testers. The only design based on an advanced population was that proposed by Jinks & Jones (1958). They postulated a five population design including ($\bar{P}_1, \bar{P}_2, \bar{F}_1, \bar{F}_2$ and \bar{F}_3) in case backcross progenies are not available. The defect of this design is that it is limited for estimating only single gene effects. Such classical designs are impractical for full analysis of metric traits if any of the earlier six populations is not available or its size is not quite enough for satisfactory analysis. On the other hand, in practice, breeders may have different advanced filial and backcross populations which are sufficient for perfect investigation. Generation mean analysis (Mather & Jinks, 1982) consists of six populations, *i.e.* parent 1 (\bar{P}_1), parent 2 (\bar{P}_2), first filial (\bar{F}_1), second generation (\bar{F}_2), first filial of the backcross with recurrent parent 1 (\bar{BC}_{11}) and first filial of the backcross with recurrent parent 2 (\bar{BC}_{12}). Generation mean analysis is a useful technique that provides the estimation of the average effects of the genes (additive, dominance and epistasis) involved in the expression of quantitative traits such as yield and yield components which benefits breeders in designing the most appropriate breeding approaches for developing a new varieties (Pooni & Treharne, 1994; Iqbal & Nadeem, 2003; Checa *et al.*, 2006 and Sharmila *et al.*, 2007). Genome scans for quantitative trait loci (QTL) have proved

to be a successful strategy for identifying genetic effects and interactions (Carlborg *et al.*, 2004).

The present study proposed a design for estimating all types of gene effects based on means of advanced filial and backcross generation's means ($\bar{P}_1, \bar{P}_2, \bar{F}_1, \bar{F}_2, \bar{BC}_{31}$ and \bar{BC}_{32}).

PROTOCOL OF DEDUCTION

The protocol employed for finding out the six formulas involves the following three methods:

1. Algebraic solution: The key point in this analysis is solution of means of the two filial generations to find values of each of the unknowns H and L in terms of population means. Meanwhile, D is considered as half of the difference between the two parents. These three derived parameters were used in compensation in specific appropriate group of populations to each of the gene effects.

2. Algebraic proof: Components of the population means that are involved in each formula are compensated in terms of gene effects.

3. Mathematical proof via working example: For this purpose, real data was utilized to obtain the six gene effects, which were used for calculating the expected genetic values according to their genetic components. Thereafter, these numerical means were used for re-estimating gene effects according to the deduced formulas.

\bar{P}_1 = mean of the superior parent or homozygous dominant, selfed.

\bar{P}_2 = mean of the inferior parent or homozygous recessive, selfed.

\bar{F}_3 = mean of the 3rd selfing filial generation.

\bar{F}_4 = mean of the 4th selfing filial generation.

\bar{BC}_{31} = mean of the 3rd backcross to the larger parent generation (where $\bar{BC}_{31} = \bar{BC}_{21} * \bar{P}_1$ and $\bar{BC}_{21} = \bar{BC}_{11} * \bar{P}_1$ and $\bar{BC}_{11} = \bar{F}_1 * \bar{P}_1$)

\bar{BC}_{32} = mean of the 3rd backcross to the smaller parent generation

where $\bar{BC}_{32} = \bar{BC}_{22} * \bar{P}_2$ and $\bar{BC}_{22} = \bar{BC}_{12} * \bar{P}_2$ and $\bar{BC}_{12} = \bar{F}_1 * \bar{P}_2$

As shown in Fig. 1.

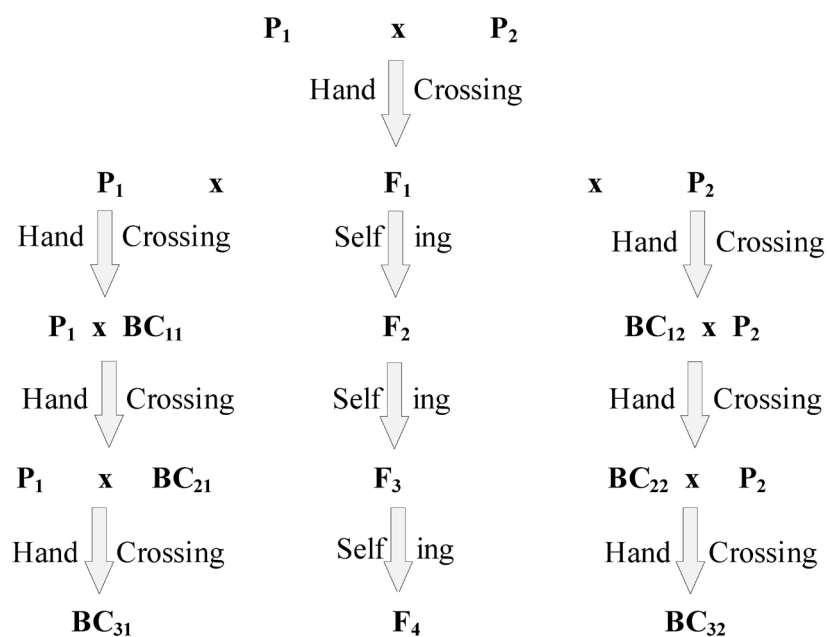


Fig. 1. Crossing chart indicating how the plant material was obtained.

Algebraic proof

Components of population genetic means in case of adequacy of the additive-dominance model (Table 1):

$$\bar{P}_1 = m + d$$

$$\bar{P}_2 = m - d$$

$$\bar{F}_2 = m + \frac{1}{4} h$$

$$\bar{F}_4 = m + \frac{1}{8} h$$

$$\bar{BC}_{31} = m + \frac{7}{8} d + \frac{1}{8} h$$

$$\bar{BC}_{32} = m - \frac{7}{8} d + \frac{1}{8} h$$

Components of population genetic means if non-allelic gene actions are involved (Table 1):

$$\bar{P}_1 = m + d$$

$$\bar{P}_2 = m - d + i$$

$$\bar{F}_2 = m + \frac{1}{4} h + \frac{1}{16} l$$

$$\bar{F}_4 = m + \frac{1}{8} h + \frac{1}{64} l$$

$$\bar{BC}_{31} = m + \frac{7}{8} d + \frac{1}{8} h + \frac{49}{64} i + \frac{7}{64} j + \frac{1}{64} l$$

$$\bar{BC}_{32} = m - \frac{7}{8} d + \frac{1}{8} h + \frac{49}{64} i - \frac{7}{64} j + \frac{1}{64} l$$

where (m) is mean, (d) is additive effect, (h) is dominance effect, (i) is additive x additive effect, (j) is additive x dominance effect and (l) is dominance x dominance effect.

Scaling test formula

The scaling test A, B, C, D and E for additive-dominance model were applied to test the appropriate genetic model formulae (A, B, C, D and E) and their variances to test the presence of non-allelic gene interaction. If the value of A, B, C, D and E equal about "zero" or insignificant, this means that epistasis (non-allelic interaction) is absent, so the simple genetic model (m), (d) and (h) is adequate. If any one of A, B, C, D and E was significantly different from "zero" this means the presence of non-allelic interaction and the scaling test analysis is inadequate and needs other scales or data transformation. The analysis should be proceeded to estimate the interaction types of gene effect involved, using the six-parameters genetic model.

TABLE1. Coefficients of the parameters used in the genetic model for generation means analysis.

Generations	Generation Parameters					
	Simple Effect			Epistasis		
	m	d	h	i	j	l
P ₁	1	+1	0	+1	0	0
P ₂	1	-1	0	+1	0	0
F ₃	1	0	+1/4	0	0	+1/16
F ₄	1	0	+1/8	0	0	+1/64
BC ₃₁	1	+7/8	+1/8	+49/64	+7/64	+1/64
BC ₃₂	1	-7/8	+1/8	+49/64	-7/64	+1/64

Where: (m = mean effects; [d] = additive; [h] = dominance; [i] = additive x additive; [j] = additive x dominance; [l] = dominance x dominance)

$$A = 4\bar{F}_4 - 2\bar{F}_3 - \bar{P}_1 - \bar{P}_2$$

$$B = 2\bar{F}_4 - \bar{BC}_{31} - \bar{BC}_{32}$$

$$C = 32\bar{BC}_{31} - 32\bar{BC}_{32} - 28\bar{P}_1 + 28\bar{P}_2$$

$$D = 98\bar{F}_3 - 68\bar{F}_4 + 49\bar{P}_1 + 49\bar{P}_2 - 64\bar{BC}_{31} - 64\bar{BC}_{32}$$

$$E = \bar{BC}_{31} + \bar{BC}_{32} - 2\bar{F}_4$$

Algebraic solution to deduce six parameters M, D, H, I, J and L:

The key point in this analysis is the solution of means of the \bar{F}_3 and \bar{F}_4 filial generations to find values of each of the unknown H and L in terms of population means as follow:

$$\bar{F}_3 = m + \frac{1}{4}h + \frac{1}{16}l$$

Multiplying to sides of formula by 1/4, which can be rewritten as

$$\frac{1}{4}\bar{F}_3 = \frac{1}{4}m + (\frac{1}{4} \times \frac{1}{4})h + (\frac{1}{4} \times \frac{1}{16})l$$

$$\frac{1}{4}\bar{F}_3 = \frac{1}{4}m + \frac{1}{16}h + \frac{1}{64}l$$

Then subtract above formula from below one to get value of h

$$\bar{F}_4 = m + \frac{1}{8}h + \frac{1}{64}l$$

$$\bar{F}_4 - \frac{1}{4}\bar{F}_3 = m - \frac{1}{4}m + \frac{1}{8}h - \frac{1}{16}h + \frac{1}{64}l - \frac{1}{64}l$$

$$h = 16\bar{F}_4 - 4\bar{F}_3 - 12m$$

... Equation (1)

When h is compensated in next formula

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$$\bar{F}_3 = m + \frac{1}{4}h + \frac{1}{16}l$$

We can estimate L

$$\bar{F}_3 = m + \frac{1}{4}(16\bar{F}_4 - 4\bar{F}_3 - 12m) + \frac{1}{16}l$$

$$L = 32\bar{F}_3 - 64\bar{F}_4 + 32m$$

.....Equation (2)

For estimating M by summing \bar{P}_1 and \bar{P}_2 means and substitution from sum of \bar{BC}_{31} and \bar{BC}_{32} as follow:

$$= (\bar{P}_1 + \bar{P}_2) - (\bar{BC}_{31} + \bar{BC}_{32})$$

$$= 49(2m + 2i) - 64\left(2m + \frac{1}{4}h + \frac{98}{64}i + \frac{1}{32}l\right)$$

$$= 98m + 98i - 128m - 16h - 98i - 2l$$

$$= -30m - 16h - 2l$$

When compensated h and L from above Equations 1 and 2.

$$L = 32\bar{F}_3 - 64\bar{F}_4 + 32m$$

$$h = 16\bar{F}_4 - 4\bar{F}_3 - 12m$$

$$49(\bar{P}_1 + \bar{P}_2) - 64(\bar{BC}_{31} + \bar{BC}_{32}) = -30m - 16h - 2l$$

$$= -30m - 16(16\bar{F}_4 - 4\bar{F}_3 - 12m) - 2(32\bar{F}_3 - 64\bar{F}_4 + 32m)$$

$$49(\bar{P}_1 + \bar{P}_2) - 64(\bar{BC}_{31} + \bar{BC}_{32}) = 98m - 128\bar{F}_4$$

Equation for estimating mean effect (M)

$$m = \frac{1}{98} (49 \bar{P}_1 + 49 \bar{P}_2 - 64 \overline{BC}_{31} - 64 \overline{BC}_{32} + 128 \bar{F}_4)$$

When m is compensated in formula of L in Equation 2 we can estimate L as follow

$$L = 32 \bar{F}_3 - 64 \bar{F}_4 + \frac{32}{98} (49 \bar{P}_1 + 49 \bar{P}_2 - 64 \overline{BC}_{31} - 64 \overline{BC}_{32} + 128 \bar{F}_4)$$

Formula for estimating Dominance x dominance effect (L):

$$L = \frac{16}{49} (98 \bar{F}_3 - 68 \bar{F}_4 + 49 \bar{P}_1 + 49 \bar{P}_2 - 64 \overline{BC}_{31} - 64 \overline{BC}_{32})$$

When m is compensated in formula of H in Equation 1 we can estimate H as follow

$$H = 16 \bar{F}_4 - 4 \bar{P}_1 - \frac{16}{98} (49 \bar{P}_1 + 49 \bar{P}_2 - 64 \overline{BC}_{31} - 64 \overline{BC}_{32} + 128 \bar{F}_4)$$

Formula for estimating Dominance effect (H)

$$h = \frac{1}{49} (384 \overline{BC}_{31} + 384 \overline{BC}_{32} - 196 \bar{F}_3 - 294 \bar{P}_1 - 294 \bar{P}_2 + 16 \bar{F}_4)$$

D is coered as half of the difference between the two parents.

Equation for estimating the additive effect:

$$d = \frac{1}{2} (\bar{P}_1 - \bar{P}_2)$$

For estimating Additive x Additive (i) \overline{BC}_{31} and \overline{BC}_{32} means are summed together and compensated h and L from above formula 1 and 2:

$$\overline{BC}_{31} + \overline{BC}_{32} = m + \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i + \frac{1}{64}j + \frac{1}{64}l + m - \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i - \frac{1}{64}j + \frac{1}{64}l$$

$$\overline{BC}_{31} + \overline{BC}_{32} = 2m + \frac{1}{4}h + \frac{98}{64}i + \frac{1}{32}j$$

$$\overline{BC}_{31} + \overline{BC}_{32} = 2m + \frac{1}{4}(16 \bar{F}_4 - 4 \bar{F}_3 - 12m) + \frac{98}{64}i + \frac{1}{32}(32 \bar{F}_3 - 64 \bar{F}_4 + 32m)$$

Equation for estimating the Additive x Additive effect (i).

$$i = \frac{32}{49} (\overline{BC}_{31} + \overline{BC}_{32} - 2 \bar{F}_4)$$

For estimating j by subtract \overline{BC}_{31} and \overline{BC}_{32} means and compensated D from above formula

$$\overline{BC}_{31} - \overline{BC}_{32} = m + \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i + \frac{1}{64}j + \frac{1}{64}l - m + \frac{7}{8}d - \frac{1}{8}h - \frac{49}{64}i + \frac{1}{64}j - \frac{1}{64}l$$

$$\overline{BC}_{31} - \overline{BC}_{32} = \frac{7}{4}d + \frac{7}{32}j$$

$$\overline{BC}_{31} - \overline{BC}_{32} = \frac{7}{4} * \frac{1}{2} (\bar{P}_1 - \bar{P}_2) + \frac{7}{32}j$$

$$j = \frac{32}{56} (8 \overline{BC}_{31} - 8 \overline{BC}_{32} - 7 \bar{P}_1 + 7 \bar{P}_2)$$

Equation for estimating the Additive x dominance effect (J)

$$j = \frac{1}{7} (32 \overline{BC}_{31} - 32 \overline{BC}_{32} - 28 \bar{P}_1 + 28 \bar{P}_2)$$

Algebraic proof

Algebraic proof of scaling tests formulae

Note that, the following proof depends only on additive-dominance model which means no non-allelic interaction.

$$A = 4\bar{F}_4 - 2\bar{F}_3 - \bar{P}_1 - \bar{P}_2$$

$$= 4(m + \frac{1}{8}h) - 2(m + \frac{1}{4}h) - (m + d) - (m - d)$$

$$= m(4-2-1-1) + h(\frac{1}{2} - \frac{1}{2}) + d(1-1) = \text{zero}$$

$$B = 2\bar{F}_4 - \overline{BC}_{31} - \overline{BC}_{32}$$

$$= 2(m + \frac{1}{8}h) - (m + \frac{7}{8}d + \frac{1}{8}h) - (m - \frac{7}{8}d + \frac{1}{8}h)$$

$$= m(2-1-1) + h(\frac{1}{4} - \frac{1}{8} - \frac{1}{8}) + d(\frac{7}{8} - \frac{7}{8}) = \text{zero}$$

$$C = 32 \overline{BC}_{31} - 32 \overline{BC}_{32} - 28 \bar{P}_1 + 28 \bar{P}_2$$

$$= 32(m + \frac{7}{8}d + \frac{1}{8}h) - 32(m - \frac{7}{8}d + \frac{1}{8}h) - 28(m + d) + 28(m - d)$$

$$= m(32-32-28+28) + d(28+28-28-28) + h(4-4) = \text{zero}$$

$$D = (98 \bar{F}_3 - 68 \bar{F}_4 + 49 \bar{P}_1 + 49 \bar{P}_2 - 64 \overline{BC}_{31} - 64 \overline{BC}_{32})$$

$$= 98(m + \frac{1}{4}h) - 68(m + \frac{1}{8}h) + 49(m + d) + 49(m - d) - 64(m + \frac{7}{8}d + \frac{1}{8}h) - 64(m - \frac{7}{8}d + \frac{1}{8}h)$$

$$= m(98-68+49+49-64-64) + h(\frac{98}{4} - \frac{68}{8} - \frac{64}{8} - \frac{64}{8}) + d(49-49-448/8+448/8) = \text{zero}$$

$$E = \overline{BC}_{31} + \overline{BC}_{32} - 2 \overline{F}_4$$

$$= (m + \frac{7}{8}d + \frac{1}{8}h) + (m - \frac{7}{8}d + \frac{1}{8}h) - 2(m + \frac{1}{8}h)$$

$$= m(1+1-2) + d(\frac{7}{8} - \frac{7}{8}) + h(\frac{1}{8} + \frac{1}{8} - \frac{1}{4}) = \text{zero}$$

Algebraic proof of six parameters M, D, H, I, J and L.

$$m = \frac{1}{98}(49 \overline{P}_1 + 49 \overline{P}_2 - 64 \overline{BC}_{31} - 64 \overline{BC}_{32} + 128 \overline{F}_4)$$

$$= \frac{1}{98} [49(m + d + i) + 49(m - d + i) + 128(m + \frac{1}{8}h + \frac{1}{64}l) - 64(m + \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i + \frac{1}{64}j + \frac{1}{64}l) - 64(m - \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i - \frac{1}{64}j + \frac{1}{64}l)]$$

$$= [\frac{1}{98} (98)] m = m$$

$$d = \frac{1}{7}(\overline{P}_1 - \overline{P}_2)$$

$$+ \frac{1}{2}(m + d + i)$$

$$- \frac{1}{2}(m - d + i)$$

$$= \frac{1}{2}d + \frac{1}{2}d = d$$

$$h = \frac{1}{49}(384 \overline{BC}_{31} + 384 \overline{BC}_{32} - 196 \overline{F}_3 - 294 \overline{P}_1 - 294 \overline{P}_2 + 16 \overline{F}_4)$$

$$= \frac{1}{49} [384(m + \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i + \frac{1}{64}j + \frac{1}{64}l)$$

$$+ 384(m - \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i - \frac{1}{64}j + \frac{1}{64}l)$$

$$- 294(m - d + i)$$

$$- 294(m + d + i)$$

$$+ 16(m + \frac{1}{8}h + \frac{1}{64}l)$$

$$- 196(m + \frac{1}{4}h + \frac{1}{16}l)]$$

$$49) \frac{1}{49} = H) = h$$

$$i = \frac{32}{49}(\overline{BC}_{31} + \overline{BC}_{32} - 2 \overline{F}_4)$$

$$= \frac{32}{49} [(m + \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i + \frac{7}{64}j + \frac{1}{64}l)$$

$$+ (m - \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i - \frac{7}{64}j + \frac{1}{64}l)]$$

$$- 2(m + \frac{1}{8}h + \frac{1}{64}l)]$$

$$= (\frac{32}{49} \times \frac{49}{32}) i = i$$

$$j = \frac{1}{7}(32 \overline{BC}_{31} - 32 \overline{BC}_{32} - 28 \overline{P}_1 + 28 \overline{P}_2)$$

$$= 32] \frac{1}{7} (m + \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i + \frac{7}{64}j + \frac{1}{64}l)$$

$$- 32(m - \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i - \frac{7}{64}j + \frac{1}{64}l)$$

$$- 28(m + d + i)$$

$$+ 28(m - d + i)]$$

$$= (\frac{1}{7}) (7 j) = j$$

$$L = \frac{16}{49}(98 \overline{F}_3 - 68 \overline{F}_4 + 49 \overline{P}_1 + 49 \overline{P}_2 - 64 \overline{BC}_{31} - 64 \overline{BC}_{32})$$

$$49) \frac{16}{49} = (m + d + i)$$

$$+ 49(m - d + i)$$

$$- 68(m + \frac{1}{8}h + \frac{1}{64}l)$$

$$+ 98(m + \frac{1}{4}h + \frac{1}{16}l)$$

$$- 64(m + \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i + \frac{1}{64}j + \frac{1}{64}l)$$

$$- 64(m - \frac{7}{8}d + \frac{1}{8}h + \frac{49}{64}i - \frac{1}{64}j + \frac{1}{64}l)]$$

$$\frac{16}{49} = L) = L$$

Mathematical proof via working example

To validate the new model, real data of mean(m), additive (d), dominance (h), additive x additive (i), additive x dominance (j) and dominance x dominance (l) gene effects in the six-parameter model for phosphorus-use efficiency in cross number one of soybean were used (Veronica *et al.*, 2017) as shown in the following table.

Genotype	m	d	h	i	j	l
Value	0.02	0.01	-0.02	0.003	-0.01	0.01

Thus, the expected genetic means of the different population deduced according to their genotypic segregation distribution would be as follows:

$$\bar{P}_1 = m + d + i = 0.02 + 0.01 + 0.003 = \mathbf{0.033}$$

$$\bar{P}_2 = m - d + i = 0.02 - 0.01 + 0.003 = \mathbf{0.013}$$

$$\bar{F}_3 = m + \frac{1}{4}h + \frac{1}{16}l = 0.02 + \frac{1}{4}(-0.02) + \frac{1}{16}(0.01) = \mathbf{0.015625}$$

$$\bar{F}_4 = m + \frac{1}{8}h + \frac{1}{64}l = 0.02 + \frac{1}{8}(-0.02) + \frac{1}{64}(0.01) = \mathbf{0.017656}$$

$$\begin{aligned} \overline{BC}_{31} &= m + \frac{7}{8}d + \frac{1}{2}h + \frac{49}{64}i + \frac{7}{64}j + \frac{1}{64}l \\ &= 0.02 + \frac{7}{8}(0.01) + \frac{1}{2}(-0.02) + \frac{49}{64}(0.003) + \frac{7}{64}(-0.01) + \frac{1}{64}(0.01) = \mathbf{0.027609} \end{aligned}$$

$$\begin{aligned} \overline{BC}_{32} &= m - \frac{7}{8}d + \frac{1}{2}h + \frac{49}{64}i - \frac{7}{64}j + \frac{1}{64}l \\ &= 0.02 - \frac{7}{8}(0.01) + \frac{1}{2}(-0.02) + \frac{49}{64}(-0.01) - \frac{7}{64}(-0.01) + \frac{1}{64}(0.01) = \mathbf{0.012297} \end{aligned}$$

Populations	\bar{P}_1	\bar{P}_2	\bar{F}_3	\bar{F}_4	\overline{BC}_{31}	\overline{BC}_{32}
Genetic Mean	0.033	0.013	0.015625	0.017656	0.027609	0.012297

Re-estimation of population genetic means based on the proposed formulae

$$m = \frac{1}{98}(49\bar{P}_1 + 49\bar{P}_2 - 64\overline{BC}_{31} - 64\overline{BC}_{32} + 128\bar{F}_4) = \mathbf{0.02}$$

$$m = \frac{1}{98}(49 \times 0.033 + 49 \times 0.013 - 64 \times 0.027609 - 64 \times 0.012297 + 128 \times 0.017656) = \mathbf{0.02}$$

$$d = \frac{1}{2}(\bar{P}_1 - \bar{P}_2)$$

$$d = \frac{1}{2}(0.033 - 0.013) = \mathbf{0.01}$$

$$h = \frac{1}{49}(384\overline{BC}_{31} + 384\overline{BC}_{32} - 196\bar{F}_3 - 294\bar{P}_1 - 294\bar{P}_2 + 16\bar{F}_4) = \mathbf{-0.02}$$

$$\begin{aligned} h &= \frac{1}{49}(384 \times 0.027609 + 384 \times 0.012297 - 196 \times 0.015625 - 294 \times 0.033 - 294 \times 0.013 + 16 \\ &\quad \times 0.017656) = \mathbf{-0.02} \end{aligned}$$

$$i = \frac{32}{49}(\overline{BC}_{31} + \overline{BC}_{32} - 2\bar{F}_4) = \mathbf{0.003}$$

$$i = \frac{32}{49}(0.027609 + 0.012297 - 2 \times 0.017656) = \mathbf{0.003}$$

$$j = \frac{1}{7}(32\overline{BC}_{31} - 32\overline{BC}_{32} - 28\bar{P}_1 + 28\bar{P}_2) = \mathbf{-0.01}$$

$$j = \frac{1}{7}(32 \times 0.027609 - 32 \times 0.012297 - 28 \times 0.033 + 28 \times 0.013) = \mathbf{-0.01}$$

$$L = \frac{16}{49}(98\bar{F}_3 - 68\bar{F}_4 + 49\bar{P}_1 + 49\bar{P}_2 - 64\overline{BC}_{31} - 64\overline{BC}_{32}) = \mathbf{0.01}$$

$$\begin{aligned} L &= \frac{16}{49}(98 \times 0.015625 - 68 \times 0.017656 + 49 \times 0.033 + 49 \times 0.013 - 64 \times 0.027609 - 64 \times 0.012297) \\ &= \mathbf{0.01} \end{aligned}$$

RESULTS

The proposed model in this paper is similar to that model developed by Mather & Jinks (1982) for estimating all types of genetic effects. However, algebraic and mathematical proofs revealed that the proposed model can be applied to estimate all types of genetic effects with different means of advanced populations of $\bar{P}_1, \bar{P}_2, \bar{F}_3, \bar{F}_4, \overline{BC}_{31}$ and \overline{BC}_{32} . The results showed that, if epistasis is absent according to scaling test (A, B, C, D and E) the following equations are used:

$$\text{Mean (m)} = \frac{1}{98}(49\bar{P}_1 + 49\bar{P}_2 - 64\overline{BC}_{31} - 64\overline{BC}_{32} + 128\bar{F}_4)$$

$$\text{Additive effect (d)} = \frac{1}{2}(\bar{P}_1 - \bar{P}_2) \text{ and}$$

$$\text{Dominance effect (h)} = \frac{1}{49}(384\overline{BC}_{31} + 384\overline{BC}_{32} - 196\bar{F}_3 - 294\bar{P}_1 - 294\bar{P}_2 + 16\bar{F}_4)$$

However, if epistasis is present, the following equations are used:

$$\text{Additive * Additive effect (i)} = \frac{32}{49}(\overline{BC}_{31} + \overline{BC}_{32} - 2\bar{F}_4)$$

$$\text{Additive * Dominance effect (j)} = \frac{1}{7}(32\overline{BC}_{31} - 32\overline{BC}_{32} - 28\bar{P}_1 + 28\bar{P}_2) \text{ and}$$

$$\text{Dominance * Dominance effect (L)} = \frac{16}{49}(98\bar{F}_3 - 68\bar{F}_4 + 49\bar{P}_1 + 49\bar{P}_2 - 64\overline{BC}_{31} - 64\overline{BC}_{32})$$

Finally, the real data analysis in soybean (Veronica *et al*, 2017) as an example to validate the equations, suggest that the model can serve as a viable particularly to estimate epistasis, additive and dominance genetic effects using the data generated from advanced filial and backcross populations $\bar{P}_1, \bar{P}_2, \bar{F}_3, \bar{F}_4, \overline{BC}_{31}$ and \overline{BC}_{32} .

CONCLUSION

In this work, an algebraic solution, algebraic and mathematical proof via real data example were used to develop six equations for estimating six types of gene effects as a novel method. The proposed model can utilize the advanced populations for estimating the genetic effects. Thus, the model can help the breeders especially those working with advanced populations of filial and backcross to estimate the genetic effects with simple equations.

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نموذج وراثي احصائي لتقدير التأثيرات الوراثية الاضافية والسيادية والتفوق باستخدام عشائر متقدمة

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العديد من الدراسات تناولت تقدير التأثيرات الوراثية التي تتحكم في الصفات الكمية. معظم طرق التقدير تركز على متوسطات الاجيال المبكرة مثل \bar{F}_1 و \bar{F}_2 والاجيال الرجعية \bar{BC}_{11} و \bar{BC}_{12} . في هذا البحث تم عمل نموذج جديد لتقدير التأثيرات الوراثية باستخدام الاجيال المتقدمة مثل $\bar{F}_3, \bar{F}_4, \dots, \bar{F}_n$ والاجيال الرجعية المتقدمة \bar{BC}_{n1} and \bar{BC}_{n2} . حيث تم اشتقاق المعادلات التالية عن طريق الحل الجبري لمتوسطات اجيال عشائر كلا من $\bar{P}_1, \bar{F}_3, \bar{P}_2, \bar{F}_4, \bar{BC}_{31}$ و \bar{BC}_{32}

$$\frac{1}{98}(49 \bar{P}_1 + 49 \bar{P}_2 - 64 \bar{BC}_{31} - 64 \bar{BC}_{32} + 128 \bar{F}_4) = M \text{ المتوسط}$$

$$\frac{1}{2}(\bar{P}_1 - \bar{P}_2) = (D) \text{ التأثير الاضافي}$$

$$= (H) \text{ التأثير السيادة}$$

$$\frac{1}{49}(384 \bar{BC}_{31} + 384 \bar{BC}_{32} - 196 \bar{F}_3 - 294 \bar{P}_1 - 294 \bar{P}_2 + 16 \bar{F}_4)$$

وثلاثة انواع من التفوق

$$\frac{32}{49}(\bar{BC}_{31} + \bar{BC}_{32} - 2 \bar{F}_4) = (I) \text{ التأثير الاضافي x الاضافي}$$

$$\frac{1}{7}(32 \bar{BC}_{31} - 32 \bar{BC}_{32} - 28 \bar{P}_1 + 28 \bar{P}_2) = (J) \text{ التأثير الاضافي x السيادة}$$

$$= (L) \text{ التأثير السيادة x السيادة}$$

$$\frac{16}{49}(98 \bar{F}_3 - 68 \bar{F}_4 + 49 \bar{P}_1 + 49 \bar{P}_2 - 64 \bar{BC}_{31} - 64 \bar{BC}_{32})$$

هذه المعادلات تم اثباتها بواسطة الحل الجبري لمتوسطات العشائر المتقدمة بالاضافة إلى الاثبات الرياضي باستخدام بيانات حقيقة. اظهرت نتائج هذه الدراسة اقترحت ان النموذج يمكن استخدامه في تقدير التأثيرات الوراثية الاضافية والسيادية والتفوق باستخدام بيانات تم التحصل عليها من عشائر متقدمة مثل $\bar{P}_1, \bar{F}_3, \bar{P}_2, \bar{F}_4, \bar{BC}_{31}$ و \bar{BC}_{32} .