Theor Appl Genet (1998) 97: 116–121

R. Bernardo · W. E. Nyquist

Additive and testcross genetic variances in crosses among recombinant inbreds

Received: 23 September 1997 / Accepted: 30 December 1997

Abstract Breeders desire populations with a high mean performance and a large genetic variance. Theory and methods are lacking for predicting additive variance (V_A) and testcross variance (V_T) in biparental populations. Breeders have unsuccessfully attempted to predict V_A based on the coefficient of coancestry (f) or molecular-marker similarity between parents. In this paper, we derive the expected values of V_A and V_T in biparental populations, examine the variability of V_A among biparental crosses, and discuss how V_A and V_T may be predicted in applied breeding programs. Suppose i is a recombinant inbred derived from the cross between inbreds P_1 and P_2, and inbred j is not a direct descendant of i. Let $V_{A(i,j)}$ be the additive variance in the F_2 of the $(i \times j)$ biparental cross. Let $V_{T(i,j)}$ be the variance among testcrosses of F_2 individuals with a specific unrelated inbred or population. Assuming linkage equilibrium and the absence of epistasis, $V_{A(i,j)} = \lambda V_{A(P1,j)} + (1 - \lambda)\ V_{A(P2,j)}$, where λ = parental contribution of P_1 to i. Similarly, $V_{T(i,j)} = \lambda V_{T(P1,j)} + (1 - \lambda) V_{T(P2,j)}$. Additive variance in crosses between recombinant inbreds cannot be modelled as a function of f if, as indicated in the literature, V_A differs among crosses of founder inbreds. If molecular-marker similarity between parents is used as an estimate of f, then a strong linear relationship is likewise not expected between V_A and marker similarity. Differences between the actual and expected λ led to variation in V_A. In applied breeding programs, modelling V_A or V_T in biparental crosses may be feasible with estimates of V_A or V_T in prior crosses and information on λ obtained from molecular-marker data.

Communicated by G. E. Hart

Purdue Agricultural Research Programs Journal Paper no. 15544

R. Bernardo (✉) · W. E. Nyquist
Department of Agronomy, Purdue University, 1150 Lilly Hall of Life Sciences, West Lafayette, IN 47907-1150, USA

Key words Additive variance · Testcross variance · Inbreeding · Recombinant inbreds

Introduction

New inbreds are commonly developed from crosses between elite inbreds. For self-pollinated crops, such as oat (*Avena sativa* L.) and soybean [*Glycine max* (L.) Merr.], progenies are evaluated for their performance as lines *per se*. For hybrid crops, such as maize (*Zea mays* L.), progenies are evaluated for their performance when crossed with an inbred tester. Biparental populations with a high mean performance and a large genetic variance – either on a *per se* or testcross basis – are desired to increase the chance of finding superior recombinants.

The number of potential biparental populations in a breeding program can be prohibitively large. For example, if a breeder has 25 elite inbreds, there are 300 potential biparental populations for developing new inbreds. Methods for predicting both the mean performance and the genetic variance of biparental populations would help the breeder choose the most promising biparental populations for inbred development. The mean performance of recombinant inbreds, selfed from a cross between two parental inbreds, is typically predicted as the average *per se* performance of the two parents, i.e., the midparent value (Panter and Allen 1995). Likewise, the mean performance of a biparental population when crossed to an inbred tester can be predicted as the average performance of the two parents when crossed to the same tester (Bauman 1959). Theory and methods are lacking, however, for predicting *per se* additive variance (denoted V_A) and testcross variance (denoted V_T) in biparental populations.

Falconer and Mackay (1996, p 264) noted that with inbreeding the additive variance in a population is equal to $V_A = V'_A(1 - F)$, where V'_A = additive variance

in the non-inbred base population and F = coefficient of inbreeding. This relationship between V_A and F holds true when dominance is absent or when allele frequencies are 0.5. In a cross between two homozygous parents, F is equal to the coefficient of coancestry (f), i.e., the probability that, at a given locus, the two parents have alleles that are copies of the same ancestral allele. In practice, biparental populations are commonly formed from related parents ($f > 0$). Studies have been conducted to examine the relationship between V_A and both f and molecular-marker similarity between parents in oat (Cowen and Frey 1987; Souza and Sorrells 1991; Moser and Lee 1994) and soybean (Helms et al. 1997; Kisha et al. 1997; Manjarrez-Sandoval et al. 1997). In these studies, V_A for several traits was greater in crosses between unrelated or distantly related parents than in crosses between closely related parents. But, contrary to theoretical expectations, the linear relationship between V_A and f or between V_A and marker similarity was not strong enough to permit routine prediction of V_A.

Our objectives were to: (1) derive the expected values of V_A and V_T in biparental populations, (2) examine the variability of V_A in biparental crosses given different genetic models by computer simulation, and (3) discuss how V_A and V_T may be modelled in applied breeding programs. The results from this study give clear reasons for the lack of relationship, as indicated in the literature, between V_A and both F and marker similarity between parents.

Theory and methods

Additive variance

Suppose inbreds P_1 and P_2 are crossed to form a biparental population. Recombinant inbreds are developed, by continuous selfing until homozygosity, from the $(P_1 \times P_2)F_2$ population or from the bth backcross population where P_1 is the recurrent parent. Let i be a random recombinant inbred line from the $(P_1 \times P_2)$ biparental cross. The parental contribution of P_1 to i is denoted as λ, whereas the parental contribution of P_2 to i is $(1 - \lambda)$. Expected values of λ [i.e., E(λ)] are 0.5 if i is selfed from the F_2, 0.75 if i is selfed from the BC_1, and $(1 - 0.5^{b+1})$ if i is selfed from the bth backcross. Let j be any inbred that is not a direct descendant of i.

Let $V_{A(i,j)}$ be the additive variance in the F_2 of the biparental cross in parentheses.The V_A in the $(i \times j)$ cross can be derived as a function of V_A in the $(P_1 \times j)$ and $(P_2 \times j)$ crosses. Four classes of loci differentiate P_1, P_2, and j (Table 1). The numbers of loci (n_1, n_2, n_3, and n_4) differ among the four classes. Three alleles per locus are present in Class I whereas two alleles per locus are present in Classes II, III, IV. Half the difference between the mean values of the homozygous genotypes is denoted as a_k for the kth locus in Classes II, III, and IV. For Class-I loci, a_k varies according to the parents, i.e., $a_{k(P1,P2)}$ in the $(P_1 \times P_2)F_2$, $a_{k(P1,j)}$ in the $(P_1 \times j)F_2$, and $a_{k(P2,j)}$ in the $(P_2 \times j)F_2$.

The V_A for *per se* performance in the $(P_1 \times j)F_2$ population is

$$\begin{aligned} V_{A(P1,j)} &= \sum_{k=1}^{n_1} 2pq\, a^2_{k(P1,j)} + \sum_{k=n1+1}^{n_1+n_2} 2pq\, a^2_k \\ &\quad + \sum_{k=n1+n2+1}^{n_1+n_2+n_3+n_4} 2pq\, a^2_k \\ &= 1/2 \sum_{k=1}^{n_1} a^2_{k(P1,j)} + 1/2 \sum_{k=n1+1}^{n_1+n_2} a^2_k \\ &\quad + 1/2 \sum_{k=n1+n2+1}^{n_1+n_2+n_3+n_4} a^2_k \\ &= 1/2\, D_1 + 1/2\, D_3 + 1/2\, D_5, \end{aligned}$$

where: $p = 0.5$, the frequency of the favorable allele at every segregating locus in the $(P_1 \times j)F_2$ population; $q = 0.5$, the frequency of the less favorable allele at every segregating locus in the $(P_1 \times j)F_2$ population; and the "D" notations are those used by Mather and Jinks (1982, p 136). Linkage equilibrium and the absence of epistasis are assumed. Dominance may be present because it has no influence on V_A when $p = q = 0.5$. The V_A in the $(P_2 \times j)F_2$ population is:

$$\begin{aligned} V_{A(P2,j)} &= 1/2 \sum_{k=1}^{n_1} a^2_{k(P2,j)} + 1/2 \sum_{k=n1+n2+1}^{n_1+n_2+n_3} a^2_k \\ &\quad + 1/2 \sum_{k=n1+n2+n3+1}^{n_1+n_2+n_3+n_4} a^2_k \\ &= 1/2\, D_2 + 1/2\, D_4 + 1/2\, D_5. \end{aligned}$$

For Class-I loci, which segregate in the $(P_1 \times P_2)$ cross, λ of the recombinant inbreds would inherit the allele from P_1 and $(1 - \lambda)$ of the recombinant inbreds would inherit the allele from P_2. The V_A in the $(i \times j)$ cross at Class-I loci is:

$$\begin{aligned} &[\lambda\, 1/2 \sum_{k=1}^{n_1} a^2_{k(P1,j)} + (1 - \lambda)\, 1/2 \sum_{k=1}^{n_1} a^2_{k(P2,j)}] \\ &\quad = \lambda\, 1/2\, D_1 + (1 - \lambda)\, 1/2\, D_2. \end{aligned}$$

For Class-II loci, which segregate in the $(P_1 \times P_2)$ cross, λ of the recombinant inbreds would inherit the allele from P_1 and would thus segregate in the $(i \times j)$ cross. The remaining $(1 - \lambda)$ of the recombinant inbreds would inherit the allele from P_2 and would not segregate in the $(i \times j)$ cross. The V_A in the $(i \times j)$ cross at Class-II loci is:

$$\lambda\, 1/2 \sum_{k=n1+1}^{n_1+n_2} a^2_k = \lambda\, 1/2\, D_3.$$

Table 1 Classes of loci that differentiate inbreds P_1, P_2, and j

Class of loci	$(P_1 \times P_2)F_2$	$(P_1 \times j)F_2$	$(P_2 \times j)F_2$	Number of loci
I	Segregating $[a_{k(P1,P2)}]$[a]	Segregating $[a_{k(P1,j)}]$	Segregating $[a_{k(P2,j)}]$	n_1 [numbered 1 to n_1]
II	Segregating (a_k)	Segregating (a_k)	Not segregating	n_2 [numbered ($n_1 + 1$) to ($n_1 + n_2$)]
III	Segregating (a_k)	Not segregating	Segregating (a_k)	n_3 [numbered ($n_1 + n_2 + 1$) to ($n_1 + n_2 + n_3$)]
IV	Not segregating	Segregating (a_k)	Segregating (a_k)	n_4 [numbered ($n_1 + n_2 + n_3 + 1$) to ($n_1 + n_2 + n_3 + n_4$)]

[a] Half the difference, for the kth locus in each class, between the mean values of the homozygous genotypes in the F_2 population

In the same manner, for all Class-III loci, the V_A in the $(i \times j)$ cross is:

$$(1-\lambda)\ 1/2 \sum_{k=n1+n2+1}^{n_1+n_2+n_3} a_k^2 = (1-\lambda)\ 1/2\ D_4.$$

For Class-IV loci, all recombinant inbreds from the $(P_1 \times P_2)$ cross would be homozygous for the same allele and all loci would segregate in the $(i \times j)$ cross. The V_A in the $(i \times j)$ cross is:

$$1/2 \sum_{k=n1+n2+n3+1}^{n_1+n_2+n_3+n_4} a_k^2 = 1/2\ D_5.$$

Summing across the four classes, the V_A for *per se* performance in the $(i \times j)F_2$ is:

$$V_{A(i,j)} = \lambda\ 1/2\ D_1 + (1-\lambda)\ 1/2 D_2 + \lambda\ 1/2\ D_3 + (1-\lambda)\ 1/2\ D_4 + 1/2\ D_5$$
$$= \lambda\ V_{A(P1,j)} + (1-\lambda)\ V_{A(P2,j)}. \quad \text{(Eq. 1)}$$

Therefore, the expected V_A in the cross between an inbred (j) and a recombinant inbred from a biparental cross is equal to the weighted (by parental contribution) average of the V_A between j and the parents of the biparental cross.

Testcross variance

Suppose the individuals in the $(i \times j)F_2$ are testcrossed with an unrelated inbred or population. The V_T in the $(i \times j)F_2$ can be derived as a function of the V_T in the $(P_1 \times j)$ and $(P_2 \times j)$ crosses. We assume an arbitrary number of alleles (t_k) at the kth locus in the tester, and $t_k = 1$ with an inbred tester. Two alleles are present at each segregating locus in the F_2 of a biparental cross. At a single locus, the average testcross genotypic value of the favorable allele in the F_2 is $\mu_1 = \Sigma_{m=1}^{t_k} p_m\, \mu_{1m}$, where: p_m = frequency of the mth allele in the tester; and μ_{1m} = value of the genotype formed by the favorable allele from the F_2 and the mth allele from the tester. For the less favorable allele in the F_2, the average testcross genotypic value is $\mu_2 = \Sigma_{m=1}^{t_k} p_m\, \mu_{2m}$, where μ_{2m} = value of the genotype formed by the less favorable allele from the F_2 and the mth allele from the tester. The average effect of an allele substitution in the ($F_2 \times$ tester) population (Melchinger 1987) is $\alpha^T = \mu_1 - \mu_2$. With linkage equilibrium, arbitrary dominance, and the absence of epistasis, the variance among testcrosses (Rawlings and Thompson 1962) in the $(P_1 \times j)F_2$, $(P_2 \times j)F_2$, and $(i \times j)F_2$ populations are:

$$V_{T(P1,j)} = 1/8 \sum_{k=1}^{n_1} [\alpha_{k(P1,j)}^T]^2 + 1/8 \sum_{k=n1+1}^{n_1+n_2} [\alpha_k^T]^2 + 1/8 \sum_{k=n1+n2+n3+1}^{n_1+n_2+n_3+n_4} [\alpha_k^T]^2$$

$$V_{T(P2,j)} = 1/8 \sum_{k=1}^{n_1} [\alpha_{k(P2,j)}^T]^2 + 1/8 \sum_{k=n1+n2+1}^{n_1+n_2+n_3} [\alpha_k^T]^2 + 1/8 \sum_{k=n1+n2+n3+1}^{n_1+n_2+n_3+n_4} [\alpha_k^T]^2$$

$$V_{T(i,j)} = \lambda\, 1/8 \sum_{k=1}^{n_1} [\alpha_{k(P1,j)}^T]^2 + (1-\lambda) 1/8 \sum_{k=1}^{n_1} [\alpha_{k(P2,j)}^T]^2 + \lambda\ 1/8 \sum_{k=n1+1}^{n_1+n_2} [\alpha_k^T]^2 + (1-\lambda) 1/8 \sum_{k=n1+n2+1}^{n_1+n_2+n_3} [\alpha_k^T]^2 + 1/8 \sum_{k=n1+n2+n3+1}^{n_1+n_2+n_3+n_4} [\alpha_k^T]^2$$
$$= \lambda\ V_{T(P1,j)} + (1-\lambda)\ V_{T(P2,j)}, \quad \text{(Eq. 2)}$$

where: $\alpha_{k(P1,j)}^T$ = average effect of an allele substitution at the kth Class-I locus in the [$(P_1 \times j)F_2 \times$ tester] population; $\alpha_{k(P2,j)}^T$ = average effect of an allele substitution at the kth Class-I locus in the [$(P_2 \times j)F_2 \times$ tester] population; and α_k^T = average effect of an allelic substitution at the kth Class-II, -III, or -IV locus segregating in the [$(i \times j)F_2 \times$ tester] population. As indicated by the T in superscript, the $\alpha_{k(P1,j)}^T$, $\alpha_{k(P2,j)}^T$, and α_k^T parameters are dependent on the unrelated tester (Melchinger 1987).

Variability in V_A among biparental crosses

The variability in V_A, caused by deviations of the actual λ from $E(\lambda)$ in biparental crosses (Bernardo et al. 1997), was investigated by computer simulation. Inbreds A, B, and C were founder inbreds that were unrelated to each other and were homozygous for three different alleles at each locus. Recombinant inbred D was randomly derived from the $(A \times B) \times A$ backcross [$E(\lambda_D) = 0.75$, the proportion of alleles received by the inbred in subscript from the first parent listed in the pedigree]. Recombinant inbred E was derived at random from the $(B \times C)$ cross [$E(\lambda_E) = 0.50$]; F from the $(B \times D)$ cross [$E(\lambda_F) = 0.50$]; G from the $(D \times E) \times D$ backcross [$E(\lambda_G) = 0.75$]; and H from the $(F \times G)$ cross [$E(\lambda_H) = 0.50$].

We studied three genetic models that differed in the distribution of allelic effects across n loci. In Model I, allelic effects were equal across $n = 50$ or 200 loci in each founder inbred. The genotypic values at each locus were $30/\sqrt{n}$ in A, $24/\sqrt{n}$ in B, and $20/\sqrt{n}$ in C. Therefore, values of a_k were $0.5(30/\sqrt{n} - 24/\sqrt{n}) = 3/\sqrt{n}$ in the $(A \times B)$ cross, $5/\sqrt{n}$ in the $(A \times C)$ cross, and $2/\sqrt{n}$ in the $(B \times C)$ cross. In Model II, the genotypic values across $n = 50$ or 200 loci were normally-distributed with (1) a mean of $30/\sqrt{n}$ in A, $24/\sqrt{n}$ in B, and $20/\sqrt{n}$ in C; and (2) a variance of $1/n$ in each of the three founder inbreds. Models I and II were characterized by a heterogeneous V_A in crosses among the founder inbreds. In the third model (homogeneous variance), V_A was homogeneous among the $(A \times B)$, $(A \times C)$, and $(B \times C)$ crosses. A homogeneous V_A was simulated with the following values of a_k at $n = 99$ loci: (i) $3/\sqrt{n}$ in the $(A \times B)$ cross, $5/\sqrt{n}$ in the $(A \times C)$ cross, and $2/\sqrt{n}$ in the $(B \times C)$ cross for loci 1 to 33; (2) $2/\sqrt{n}$ in the $(A \times B)$ cross, $3/\sqrt{n}$ in the $(A \times C)$ cross, and $5/\sqrt{n}$ in the $(B \times C)$ cross for loci 34 to 66; and (3) $5/\sqrt{n}$ in the $(A \times B)$ cross, $2/\sqrt{n}$ in the $(A \times C)$ cross, and $3/\sqrt{n}$ in the $(B \times C)$ cross for loci 67 to 99.

Genotypes of A, B, C at each of the n loci were simulated for each genetic model. Genotypes of recombinant inbreds D, E, F, G, and H were simulated 10 000 times, given their pedigrees and the genotypes of A, B, and C. For each of the 10 000 simulations, values of V_A summed across the n loci were calculated for each pair of inbreds. The 10 000 V_A values for each pair of inbreds were sorted in ascending order. The 250th value was considered the lower limit whereas the 9750th value was considered the upper limit of a 95% confidence interval on V_A.

Results and discussion

The relationship between V_A and F was linear only when V_A was homogeneous among crosses of the three founder inbreds (Fig. 1). This result was in accordance with the theoretical relationship between V_A and F given by Falconer and Mackay (1996, p 264). With Models I and II, in which V_A differed in crosses among the founder inbreds, V_A tended to be larger in crosses among distantly related inbreds than among closely related inbreds. However, the inverse linear relationship between V_A and F in biparental crosses was not strong, especially with $F \geqslant 0.25$. Values of V_A were often larger when $F > 0.5$ than when $F = 0.5$. Also, V_A was larger with $F = 0.34$ than with $F = 0.25$. Multiple values of V_A were observed at a given F. For example, V_A was larger in the $(C \times G)$ cross than in the $(D \times E)$ cross although both crosses had $F = 0.13$ (Fig. 2). Three biparental crosses with $F = 0$ differed in V_A for Models I and II (Fig. 1).

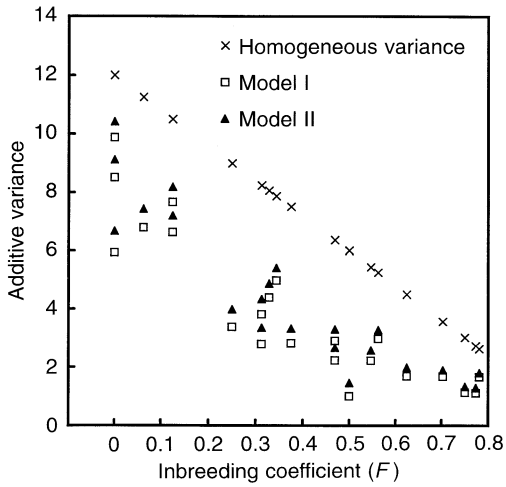

Fig. 1 Relationship between additive variance (V_A) and the inbreeding coefficient (F) in biparental populations when V_A is equal among crosses of three founder inbreds (homogeneous variance), allelic effects are constant across loci in each founder inbred (Model I), and allelic effects are normally distributed across loci in each founder inbred (Model II). Values represent the average V_A with 50 and 200 loci. The V_A in crosses among founder inbreds is excluded. Values of V_A were identical for two biparental populations with $F = 0.50$, two with $F = 0.63$, and two with $F = 0.77$

The simulation results confirmed that the expected V_A in biparental crosses can be determined with Eq. 1, regardless of whether allelic effects were constant (Model I) or variable (Model II) across loci. The results for Model I indicated that differences due to sampling (i.e., genetic drift) between actual λ and E(λ) led to variability in V_A. For each biparental cross involving a recombinant inbred, V_A varied with repeated simulations (Fig. 2). The total V_A for each genetic model was the same regardless of the number of loci controlling the trait. Yet the variation in V_A was larger when the trait was controlled by fewer loci ($n = 50$), each with larger effects, than by more loci ($n = 200$), each with smaller effects. The variation in V_A with repeated simulations generally decreased as F increased. Exceptions to this trend were the (B × E) and (C × E) crosses, which had the least variation in V_A despite having only an intermediate value of F (0.5).

We also investigated the variability in V_A with additional founder inbreds (i.e., five instead of three) and a different number of loci (i.e., 100). The results are not presented because these simulations did not provide any new information, but they confirmed that: (1) the expected V_A can be determined with Eq. 1, and (2) the variation in V_A among biparental crosses decreases as the number of loci increases.

The relationship between V_T in the $(i \times j)F_2$ and in the $(P_1 \times j)$ and $(P_2 \times j)$ crosses is analogous to that for V_A. The lack of a strong linear relationship between F and V_A implies a similar lack of linear relationship between F and V_T when V_T varies among crosses of founder inbreds. Assume the tester is fixed for the less favorable allele. The α_k^T and a_k quantities are equal when dominance is absent (Rawlings and Thompson 1962). At a single locus, $V_T = 1/8(\alpha_k^T)^2 = 1/8a_k^2$ and $V_A = 1/2\ a_k^2$. With equal allelic effects (Model I) and no dominance across all loci, the values of V_T in all of the biparental crosses are equal to one-fourth of the corresponding V_A in Figs. 2 a and b. With equal allelic effects and complete dominance at all loci, α_k^T is equal to $2a_k$, and the values of V_T in all of the biparental crosses are equal to the corresponding V_A in Figs. 2 a and b. But the ratio between V_T and V_A varies among biparental crosses if allelic effects, the level of dominance, or both, vary across loci. Let $c_{P1} = V_{T(P1,j)}/V_{A(P1,j)}$ and $c_{P2} = V_{T(P2,j)}/V_{A(P2,j)}$. In this situation $V_{T(i,j)} = \lambda\, c_{P1} V_{A(P1,j)} + (1 - \lambda)\, c_{P2} V_{A(P2,j)}$. Hence the ratio between V_T and V_A is constant in all biparental crosses only if the ratio between V_T and V_A is constant among all crosses among the founder inbreds, i.e., $c_{P1} = c_{P2}$. But, even if V_T cannot be expressed as a constant proportion of V_A, our simulation results (data not shown) indicated that, as with V_A, (1) the expected V_T can be determined with Eq. 2 and (2) the variation in V_T among biparental crosses decreases as the number of loci increases.

Helms et al. (1997) obtained V_A estimates for soybean yield of 65 000, 29 000, and 78 100 kg ha^{-2} in three biparental crosses with unrelated parents ($F = f = 0$). Such variation in V_A in crosses among unrelated founder inbreds probably caused the lack of a strong linear relationship between V_A and f in the empirical studies by Cowen and Frey (1987), Souza and Sorrells (1991), Moser and Lee (1994), Helms et al. (1997), Kisha et al. (1997), and Manjarrez-Sandoval et al. (1997). If molecular-marker similarity is used merely as a substitute for pedigree-based f, then a strong linear relationship between V_A and molecular-marker similarity is likewise not expected.

Modelling V_A or V_T in biparental crosses among recombinant inbreds requires estimates of (1) V_A or V_T in prior crosses and (2) the parental contribution to recombinant inbreds (λ). One approach is to estimate V_A and V_T for all possible crosses among founder inbreds in a breeding program, and to use these estimates to predict V_A and V_T in all the descendant recombinant inbreds. This procedure may be feasible given the widespread use of second-cycle breeding (Allard 1960, p 276). In maize, for example, most of the inbreds belonging to the Iowa Stiff Stalk Synthetic heterotic group have been derived from B14, B37, or B73 (Baker 1984). In soybean, only ten founder inbreds are estimated to account for 80% of the southern U.S. germplasm (Gizlice et al. 1994). On the other hand, estimates of V_A or V_T among founder inbreds are not needed if estimates are available for more recent biparental crosses. Suppose inbred i was derived from the $(P_1 \times P_2)F_2$, and P_1 and P_2 are not founder inbreds. The V_A in the $(i \times j)$ cross may be predicted directly from the V_A in the $(P_1 \times j)$ and $(P_2 \times j)$ crosses, and estimates of V_A in crosses among the ancestral inbreds of P_1 and

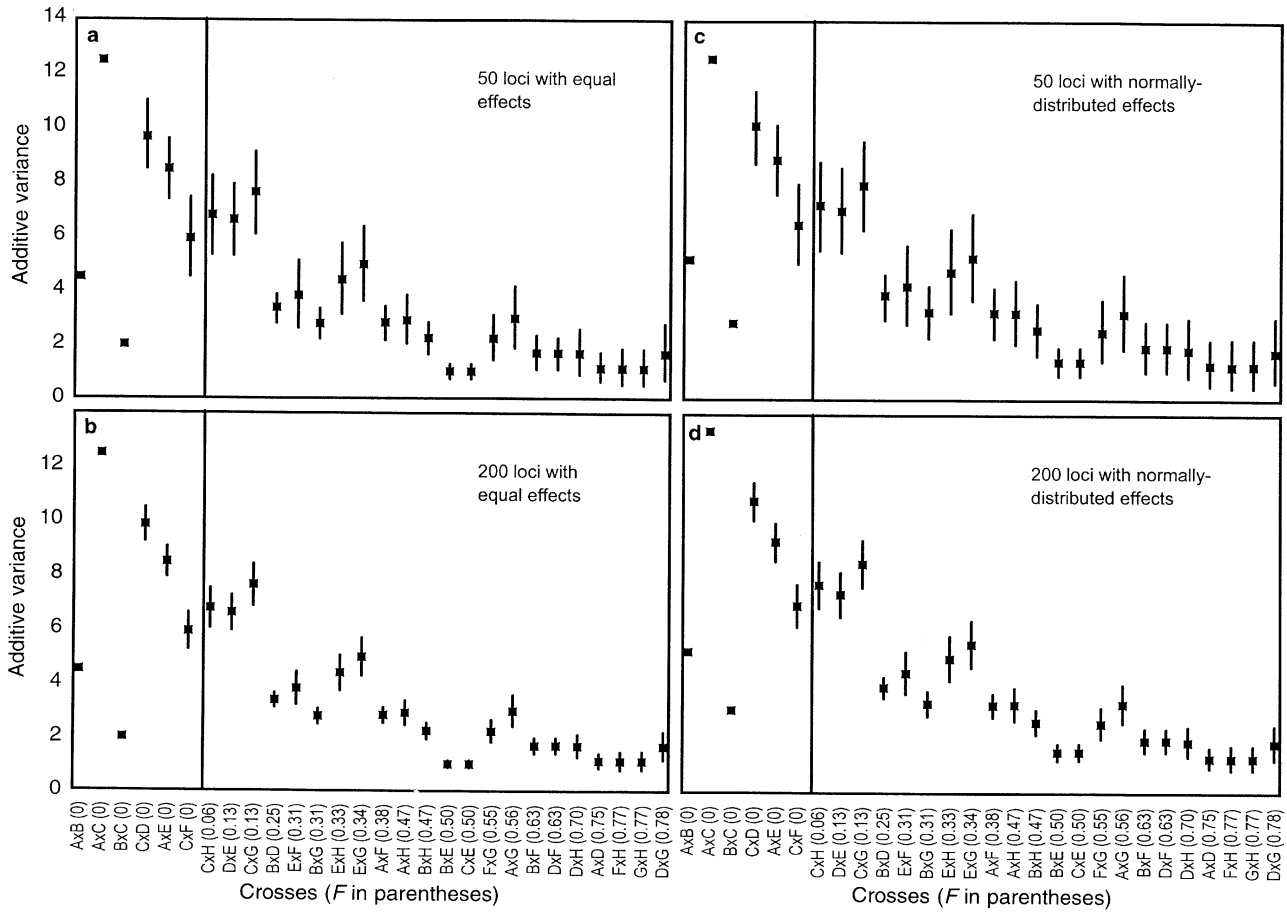

Fig. 2 Variation in additive variance (V_A) for different genetic models (**a, b, c, d**) with unequal V_A among crosses of founder inbreds (A × B, A × C, and B × C). Inbreeding coefficients (F) are in *parentheses*. The *solid marker* indicates the average V_A whereas the *bar* represents a 95% confidence interval

P_2 are not needed. When estimating V_A or V_T, the progenies need to be grown in a large and representative number of environments so that the effects of genotype-by-environment interaction are accounted for.

The simulation results indicated that the use of pedigree-based E(λ) in Eq. 1 may lead to erroneous predicted V_A or V_T values. Molecular markers may account for the effects of drift or selection, or both, on λ (Bernardo et al. 1997) and may lead to better predictions of V_A or V_T. Molecular-marker genotypes of elite inbreds are often, if not routinely, obtained for varietal protection purposes (Smith and Beavis 1996). Consequently, the need for marker data for estimating λ should not be a severe limitation. We will be conducting field studies to compare the predicted and observed V_T in a set of maize biparental crosses, using pedigree or molecular-marker information to estimate λ.

References

Allard RW (1960) Principles of plant breeding. John Wiley and Sons, New York

Baker RJ (1984) Some of the open pollinated varieties that contributed most to modern hybrid corn. Proc Annu Illinois Corn Breeders School 20:1–19

Bauman LF (1959) Evidence of non-allelic gene interaction in determining yield, ear height, and kernel row number in corn. Agron J 51:531–534

Bernardo R, Murigneux A, Maisonneuve JP, Johnsson C, Karaman Z (1997) RFLP-based estimates of parental contribution to F_2- and BC_1-derived maize inbreds. Theor Appl Genet 94:652–656

Cowen NM, Frey KJ (1987) Relationship between genealogical distance breeding behaviour in oats (*Avena sativa* L.). Euphytica 36:413–424

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edn. Longman, London

Gizlice Z, Carter TE Jr, Burton JW (1994) Genetic base for North American public soybean cultivars released between 1947 and 1988. Crop Sci 34:1143–1151

Helms T, Orf J, Vallad G, McLean P (1997) Genetic variance, coefficient of parentage, and genetic distance in six soybean populations. Theor Appl Genet 94:20–26

Kisha TJ, Sneller CH, Diers BW (1997) Relationship between genetic distance among parents and genetic variance in populations of soybean. Crop Sci 37:1317–1325

Manjarrez-Sandoval P, Carter TE Jr, Webb DM, Burton JW (1997) RFLP genetic similarity estimates and coefficient of parentage as genetic variance predictors for soybean yield. Crop Sci 37:698–703

Mather K, Jinks JL (1982) Biometrical genetics, 3rd edn. Chapman and Hall, London

Melchinger AE (1987) Expectation of means and variances of test-crosses produced from F_2 and backcross individuals and their selfed progenies. Heredity 59:105–115

Moser H, Lee M (1994) RFLP variation and genealogical distance, multivariate distance, heterosis, and genetic variance in oats. Theor Appl Genet 87:947–956

Panter DM, Allen FL (1995) Using best linear unbiased predictions to enhance breeding for yield in soybean. I. Choosing parents. Crop Sci 35:397–405

Rawlings JO, Thompson DL (1962) Performance level as a criterion for the choice of maize testers. Crop Sci 2:217–220

Smith JSC, Beavis WD (1996) Molecular marker assisted breeding in a company environment. In: Sobral BWS (ed) The impact of plant molecular genetics. Birkhäusen, Boston, pp 259–272

Souza E, Sorrells ME (1991) Prediction of progeny variation in oat from parental genetic relationships. Theor Appl Genet 82:233–241