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Heterosis and gene effects of multiplicative characters: theoretical relationships and experimental results from *Vicia faba* L.

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Abstract Theoretical results were derived to relate the heterosis and the hybrid factor (ratio of hybrid performance to parental mean) of a complex character (seed yield) with the respective parameters of com-ponent subcharacters in a multiplicative model. A multiplication factor, which is a function of differences in the parents for subcharecters, was introduced to arrive at multiplicative relationships between the parameters in the model. Under certain assumptions, gene effects of a complex multiplicative trait can be expressed in terms of gene effects for the subcharacters. Data on seed yield and its components in two crosses between *Vicia faba minor* and *major* cultivars were used as a numerical example. Theoretical and experimental results indicate that with large complementary differences for subcharacters in the parents, it is possible to find substantial heterosis in the complex character without significant heterosis in its component traits. However, a review of results from the literature shows that multiplication effects are only of minor importance in most crops. Implications for the use of multiplication effects in the breeding of hybrid, synthetic, and line cultivars are discussed.

Key words Heterosis · Hybrid factor · Multiplication factor · Multiplicative traits · *Vicia faba* L.

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Introduction

Many characters of agronomic interest are the product of subcharacters (components). Examples include yield as a product of yield components, nitrogen-use efficiency as a product of nitrogen uptake and nitrogen-utilization efficiency, disease severity as a product of the number of spores per unit area and infected plant area, and so on (for a review see Sinha and Khanna 1975). According to a hypothesis proposed by Williams (1959), heterosis for complex traits like yield is simply the consequence of multiplicative relationships at the phenotypic level between component characters. Williams (1959, 1960) discounted any genetic explanation for yield heterosis, a notion that was strongly refuted by Hayman (1960a). Geiger and Wahle (1978), following Schnell (1975), suggested an additive partitioning of the heterosis of a complex trait into: (1) multiplicative combination of component heterosis and (2) multiplicative interaction between complementary component differences in the parents.

It is well documented in the literature that multiplication effects between component traits, each having little heterosis, can produce a large amount of heterosis in complex traits (for a review see Schnell and Cockerham 1991). The recent theoretical investigations of these latter authors on the role of multiplicative effects between genes in relation to heterosis stimulated us to further research in this direction.

Using an approach accessible to plant breeders, our objctives were to derive theoretical relationships (1) of relative hybrid performance (F_1 performance compared with parental mean) and midparent heterosis of complex traits with the respective parameters and multiplication effects of subcharacters, retaining their multiplicative functional relationship, and (2) between gene effects for multiplicative complex characters and gene effects for their subcharacters. The theoretically-derived results are illustrated by a numerical example from crosses between small-seeded (*minor*) and large-seeded (*major*) faba bean

(*Vicia faba* L.) lines. This species was chosen because of the substantial amount of heterosis observed in these crosses and the large genetic differences for yield components among the parents (Kittlitz 1986).

Theory

Breakdown of hybrid performance and heterosis for multiplicative characters

Let U, the expression of a complex quantitive character U, be the product of the expressions X and Y of its subcharacters X and Y, i.e.,

$$U = XY. \tag{1}$$

Let $U(\mathrm{P1})$, $U(\mathrm{P2})$, $U(\bar{\mathrm{P}})$, and $U(\mathrm{F}_1)$ denote the performance of the complex character in parent P1, parent P2, for the parental mean, and the F_1 hybrid (P1 × P2), respectively. Similarly, the performance for the subcharacters X and Y, and any other character in these generations is denoted as $X(\mathrm{P1})$, $Y(\mathrm{P1})$, etc.

As earlier used by Immer (1941) and Schnell (1975), and subsequently described by Geiger and Wahle (1978), the hybrid factor (HF) of any character W is defined as

$$HF_W = W(\mathrm{F}_1)/W(\bar{\mathrm{P}}) = 1 + h_W, \tag{2}$$

where h_W is the relative heterosis of W.

Similarly to the hybrid factor, we define a multiplication factor (MF) for subcharacters X and Y by the following equation:

$$HF_U = MF_{XY} HF_X HF_Y \tag{3}$$

or equivalently

$$MF_{XY} = 1/(1 + \Delta_X \Delta_Y) \tag{4}$$

with $\Delta_X = [X(\mathrm{P1}) - X(\mathrm{P2})]/2X(\bar{\mathrm{P}})$ and $\Delta_Y = [Y(\mathrm{P1}) - Y(\mathrm{P2})]/2Y(\bar{\mathrm{P}})$.

The extension of the above relationship to three subcharacters ($U = XYZ$) is straightforward and yields

$$HF_U = MF_{XYZ} HF_X HF_Y HF_Z, \tag{5}$$

where $MF_{XYZ} = 1/(1 + \Delta_X\Delta_Y + \Delta_X\Delta_Z + \Delta_Y\Delta_Z)$.

The relationship to four subcharacters ($U = WXYZ$) becomes

$$HF_U = MF_{WXYZ} HF_W HF_X HF_Y HF_Z, \tag{6}$$

where

$$MF_{WXYZ} = 1/(1 + \Delta_W\Delta_X + \Delta_W\Delta_Y + \Delta_W\Delta_Z + \Delta_X\Delta_Y + \Delta_X\Delta_Z + \Delta_Y\Delta_Z + \Delta_W\Delta_X\Delta_Y\Delta_Z). \tag{7}$$

Generalization to any number of subcharacters is straightforward and shows that MF includes in the nominator only products of Δs between even numbers of subcharacters. By simple algebraic rearrangement, it can be shown that

$$MF_{XYZ} = MF_{X(YZ)} MF_{YZ} \tag{8}$$

and

$$MF_{WXYZ} = MF_{(WX)(YZ)} MF_{WX} MF_{YZ}, \tag{9}$$

if subcharacters (YZ) and (WX) are further partitioned into their subcomponents Y, Z and W, X, respectively.

Considering the relative heterosis of other generations derived by inbreeding the F_1, and assuming absence of epistasis in the component characters, equation (3) can be extended to include the relative heterosis of component characters and the inbreeding coefficient F_t of generation t. Thus, equation (3) then becomes

$$HF_U(F_t) = MF_{XY} + MF_{XY}(h_X + h_Y)(1 - F_t) + MF_{XY} h_X h_Y (1 - F_t)^2. \tag{10}$$

Relationship between gene effects for complex characters and their subcharacters

In the absence of linkage and by using the F_∞-metric, the generation mean of any generation derived from a single cross (P1 × P2) can be expressed as follows (Mather and Jinks 1982):

$$G = c + \gamma a + \eta d + \gamma^2 aa + \gamma\eta ad + \eta^2 dd + \gamma^3 aaa + \ldots, \tag{11}$$

where G is the mean of the generation under consideration, c is the mean of the F_∞ generation, a, d, aa, etc., are the additive, dominance, additive × additive, etc. genetic effects in the F_∞ metric, and γ and η are appropriate coefficients, according to the generation considered, with $\gamma \in [-1, 1]$ and $\eta \in [0, 1]$.

If the subcharacters are uncorrelated, the following equation holds true for any generation mean [compare equation (1)],

$$G_U = G_X G_Y. \tag{12}$$

In the absence of epistasis in subcharacters X and Y, we obtain from equation (11):

$$G_X = c_X + \gamma a_X + \eta d_X$$

and

$$G_Y = c_Y + \gamma a_Y + \eta d_Y, \tag{13}$$

where c_X, a_X, and d_X are the gene effects with respect to subcharacter X, and c_Y, a_Y, and d_Y are the gene effects with respect to subcharacter Y. Inserting equations (13) into (12) yields:

$$G_U = c_X c_Y + \gamma(a_X c_Y + a_Y c_X) + \eta(d_X c_Y + d_Y c_X) + \gamma^2(a_X a_Y) + \gamma\eta(a_X d_Y + a_Y d_X) + \eta^2(d_X d_Y). \tag{14}$$

On the other hand, by applying equation (11) to a complex character U and restricting epistasis to digenic interactions, we obtain:

$$G_U = c_U + \gamma a_U + \eta d_U + \gamma^2 aa_U + \gamma\eta ad_U + \eta^2 dd_U. \tag{15}$$

Considering equations (14) and (15) as polynomials in terms of variables γ and η then, by comparing the coefficient of equal terms (constant, $\gamma, \eta, \gamma^2, \gamma\eta, \eta^2$), we obtain the following identities:

$$c_U = c_X c_Y;\ a_U = a_X c_Y + a_Y c_X;\ d_U = d_X c_Y + d_Y c_X;$$
$$aa_U = a_X a_Y;\ ad_U = a_X d_Y + a_Y d_X;\ dd_U = d_X d_Y. \tag{16}$$

The above method can be extended to allow for epistatic effects in the subcharacters. For example, inclusion of additive × additive epistatic effects for subcharacters X and Y leads not only to digenic but also to higher-order epistatic effects for the multiplicative character U. Thus, we obtain:

$$c_U = c_X c_Y;\ a_U = a_X c_Y + a_Y c_X;\ d_U = d_X c_Y + d_Y c_X;$$
$$aa_U = a_X a_Y + aa_X c_Y + aa_Y c_Y;\ ad_U = a_X d_Y + a_Y d_X;\ dd_U = d_X d_Y;$$
$$aad_U = aa_X d_Y + aa_Y d_X;\ aaa_U = aa_X a_Y + aa_Y a_X;\ aaaa_U = aa_X aa_Y. \tag{17}$$

Extension to more than two subcharacters is straightforward. For example, with multiplicative action between three subcharacters (X, Y, Z) showing no epistasis, the complex trait U will not only exhibit digenic but also trigenic epistatic effects:

$$aaa_U = a_X a_Y a_Z;\ aad_U = a_X a_Y a_Z + a_X a_Z d_Y + a_Y a_Z d_X;$$
$$add_U = a_X d_Y d_Z + a_Y d_X d_Z + a_Z d_X d_Y;\ ddd_U = d_X d_Y d_Z. \tag{18}$$

It is worth mentioning that the above results apply not only to the F_∞ metric but also to the metric of any reference population (with biallelism) defined according to the rules of Hayman (1960b), especially the F_2 metric. This is because equation (11) holds true under a more general setting (Hayman 1960b). Using a different approach, Schnell and Cockerham (1992) derived identities (16) and (18) for gene effects defined with respect to any generalized Hardy-Weinberg equilibrium population with biallelism.

Numerical example

Materials and methods

Plant materials

The investigation is based on six basic generations (P1, P2, F_1 F_2, and first backcrosses B1 and B2) to each plant derived from two crosses of faba bean: cross I = "Felix" (P1) × "Kristall" (P2) and cross II = "Minica" (P1) × "Sving" (P2). "Felix" and "Minica" are two Dutch, large-seeded *V. faba major* cultivars; "Kristall" and "Sving" are two small-seeded *V. faba minor* cultivars from Germany and Sweden, respectively. Generations F_1, F_2, B1, and B2 were evaluated in both reciprocal versions; however, reciprocal differences were ignored here because they were not significant in most cases (Kittlitz 1986).

Field experiments

Cross I was evaluated over 2 years (1982 and 1983) and cross II over 1 year (1982) at Stuttgart-Hohenheim, Germany. A randomized complete block design was used with three replications in 1982 and six replications in 1983. All genotypes were included as duplicate entries except the parents which were entered only as single entries in 1982. One-row plots consisted of 17 plants, 2m long and with a spacing of 50 cm between rows. Observations were recorded on ten randomly-chosen border plants.

Data were recorded for each plant on number of seeds, number of pods, and seed yield in *g*. Seed weight (single-seed weight) in *g* and number of seeds per pod were calculated on the basis of single plants.

Statistical analyses

Breakdown and analysis of heterosis were performed at the plot level. A generation-means analysis was carried out for cross I according to Mather and Jinks (1982). The significance of genetic effects was tested by sequential model fitting and the adequacy of the model was tested by F-tests. Unweighted least-squares estimates of gene effects were calculated using a model incorporating only the significant gene effects for each trait. The trials in 1982 and 1983 were treated as a series and the plot errors, pooled across years, were used for F-tests.

Results

Highly-significant ($P < 0.01$) and complementary differences for yield components existed between the parents of each cross (Table 1). Parent P2 had more than twice the number of seeds per plant, and nearly three times as many pods as compared to parent P1 in each cross. The opposite was true for seed weight. Estimates of midparent heterosis were positive and significant for most traits, apart from a negative estimate for the number of pods in cross I.

Estimates of the hybrid factor (HF) were, as expected, greatest for the complex character, seed yield ($HF = 1.39$ and 1.53 in crosses I and II, respectively) (Fig. 1). Estimates of HF for the subcharacters were considerably smaller and ranged between 1.02 and 1.10, except for a greater HF value (1.21) for the number of seeds per plant in cross II and a smaller HF value (0.91) for the number of seeds per pod in cross I, reflecting negative heterosis. For both crosses, the multiplication factors (MF) contributed most to the hybrid factor of the complex trait, seed yield, and this was even more pronounced, when partitioning the latter into three instead of two subcharacters.

The sequential model fitting in cross I revealed that the additive-dominance model accounted for a major portion of the variation among generations for all characters except seed weight, where additive × additive epistasis was highly significant (Table 2). Reductions in sums of squares due to fitting dominance effects were significant for all characters except the number of seeds per plant. Additive effects were more important than dominance effects for the number of seeds per plant, seed weight, and the number of pods per plant, while the reverse was true for seed yield and the number of seeds per pod. The indirect estimates of gene effects for seed yield obtained through the multiplicative gene effects of two subcharacters [number of seeds per plant and seed weight obtained from equation (17)] agreed well with the direct estimates (Table 2).

Discussion

Heterosis of a complex trait and its components have been studied by many workers without giving due consideration to their multiplicative relationship. In equa-

Table 1 Observed means of generations P1, P2, and F_1 and absolute heterosis ($F_1 - \bar{P}$) for seed yield and its components in two faba bean crosses

Trait	Cross I: Felix × Kristall[a]				Cross II: Minica × Sving[b]			
	P1	P2	F_1	$F_1 - \bar{P}$[c]	P1	P2	F_1	$F_1 - \bar{P}$
Seed yield per plant (g)	20.28	23.29	30.00	8.21**	29.15	20.38	37.91	13.15**
Seed weight (g)	0.83	0.35	0.64	0.05**	0.85	0.28	0.59	0.03
Number of seeds per pod	3.11	2.77	3.24	0.30**	3.79	2.55	3.34	0.17*
Number of pods per plant	8.03	23.96	14.29	− 1.70**	9.13	28.43	19.23	0.45
Number of seeds per plant	23.95	66.08	46.37	1.35	34.27	71.63	64.23	11.28**

[a] Means based on data from 2 years
[b] Means based on data from 1 year
[c] $\bar{P}$ refers to the mean of P1 and P2

*,** Significantly different from zero at the 0.05 and 0.01 probability levels, respectively

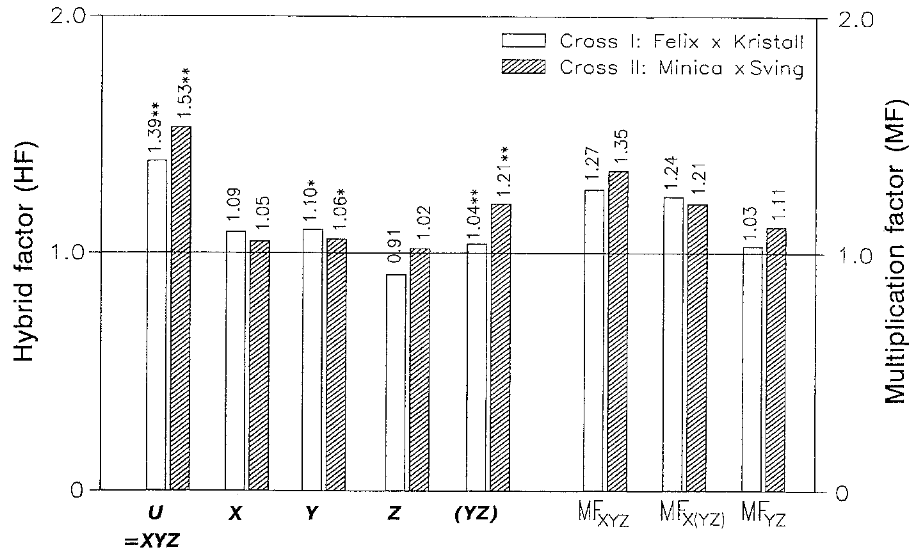

Fig. 1 Hybrid factor and multiplication factor for seed yield *U* and its components seed weight *X*, number of seeds per pod *Y*, number of pods per plant *Z*, and number of seeds per plant (*YZ*), in two faba bean crosses (*, ** significantly different from 1.0 at the 0.05 and 0.01 probability levels respectively)

Table 2 Analyses of variance, estimates of gene effects for seed yield and yield components as well as indirect estimates of gene effects for seed yield calculated from the effects of component traits in the faba bean cross Felix × Kristall

Source	*df*	Seed yield per plant (g)	Single seed weight[a] (g)	Number of seeds per pod[a]	Number of pods per plant	Number of seeds per plant	Indirect estimates of gene effects for seed yield (g)
Mean squares:							
Generations	5	13.07**	2.92**	3.21**	34.29**	243.4**	
a	1	11.89**	14.28**	7.45**	167.14**	1 206.3**	
d	1	48.22**	0.11**	7.24**	2.65*	1.0	
Epistasis	3	1.74	0.06**	0.45	0.55	3.2	
Gen. × year	5	1.77	0.16**	0.94*	3.17**	24.3**	
Error	35	1.50	0.01	0.35	0.39	2.5	
Gene effects:							
m		21.82	0.50	2.97	15.76	45.4	22.60
a		− 2.18	0.24	0.17	− 8.18	− 22.0	− 0.15
d		8.25	0.14	0.32	− 1.93	–	6.35
aa		–[b]	0.09	–	–	–	− 1.17
R^2 (in %)		92.0	99.8	91.5	99.0	99.1	

[a] Mean squares multiplied by 10^2
[b] Estimate not significantly different from zero
*,** Significant at the 0.05 and 0.01 probability levels, respectively

tion (3) to (5), a factorization of the hybrid factor of a complex character was derived in terms of (1) the hybrid factors of its subcharacters and (2) a multiplication factor. This multiplicative breakdown allows an assessment of the contribution of the heterosis in each subcharacter and the multiplication effect to the heterosis of the complex trait. The multiplication effect corresponds to "multiplicative interaction of components at the phenotypic level" as proposed by Williams (1959). The importance of the multiplication factor in our model may further be highlighted by quoting from Williams (1960): "For this (heterosis in a complex trait) to occur the parents must differ as regards the level of expression of each of the components and neither must have a monopoly of high (or low) expression in both the unit characters. Thus, yield heterosis becomes simply an expression of an inequality known to mathematicians as Tchebychev's". Williams arrived at this conclusion by an empirical approach, but failed to quantify it, and also he did not incorporate this into a functional relationship to heterosis. Geiger and Wahle (1978) incorporated a multiplicative factor into a more general model that also accounted for heterosis in subcharacters. However, their model did not fully retain the inherent multiplicative nature of subcharacters and their multiplication factor was not scale-free. A consideration of these aspects is incorporated in the present model.

The multiplication factors defined in our model are completely determined by the parental differences for subcharacters [see equations (4), (5), and (7)]. Thus, parents of hybrids with superior heterosis could be preselected on the basis of their complementarity for subcharacters if (1) *MF* is of great importance relative to the product of *HF* of subcharacters and (2) the parents show a similar performance for the complex trait. On the contrary, if *MF* is small compared to the product of

Table 3 Hybrid and multiplication factors for complex yield characters and their components estimated from published reports in four crop species

Author(s)/crop	No.of crosses	Character	Hybrid factor (*HF*)	Multiplication factor (*MF*)
Grafius (1959); barley	15	Spikes/plant	1.22 ± 0.05^a	
		Kernels/spike	1.06 ± 0.02	
		Kernel/weight	1.03 ± 0.01	
		Grain yield/plant	1.37 ± 0.07	1.03 ± 0.03
Cavicchi and Silvetti (1976); tomato	6	Fruits/plant	1.19 ± 0.04	
		Fruit weight	1.04 ± 0.04	
		Fruit yield/plant	1.25 ± 0.05	1.01 ± 0.01
Williams and Gilbert (1960); tomato	18	Fruits/plant	1.18	
		Fruit weight	1.19	
		Fruit yield/plant	1.48	1.02
Geiger and Wahle (1978); rye	8	Spikes/m^2	0.84 ± 0.11	
		Kernels/spike	2.51 ± 0.13	
		Kernels weight	1.55 ± 0.06	
		Yield/unit area	3.20 ± 0.25	0.98 ± 0.01
Soden-Fraunhofen (1981); maize	13	Ears/plant	1.06	
		Kernel rows/ear	1.05	
		Kernels/row	1.81	
		Kernel weight	1.35	
		Yield/plant	2.73	1.00

[a] Standard error for mean value among crosses

*HF*s, parents of promising hybrids cannot be preselected on the basis of their complementary structure in the subcharacters without evaluating them in cross combinations.

We found only few reports in the literature on the relative importance of *MF* for yield heterosis in various crops (Table 3). In all studies, *MF* was not significantly different from 1.0 and, with a single exception, smaller than *HF* for yield components. In contrast, for the two crosses between small-seeded and large-seeded cultivars of faba bean, the *MF* was significantly greater than 1.0 and explained at least half of the *HF* of yield (Fig. 1). This is due to the fact that the germplasm pools of *V. faba minor* and *V. faba major* have a long history of selection for different yield components. Hence, breeding for hybrid cultivars in faba bean using crosses between *V. faba minor* and *major* parents would not only capitalize on the genetic divergence among these gene pools, causing high heterotic response for each yield component, but would also benefit from multiplication effects due to complementary differences among the parents for the array of yield components.

Heterosis for yield components in autogamous or partially-allogamous species is generally smaller than in allogamous species. Hence, it is more likely that one could exploit multiplication effects in autogamous or partially-allogamous crops if suitable gene pools with complementarity in yield components are available. However, in the absence of such gene pools, selection for a complementary yield structure in the parents will not be rewarding, because Δ_X and Δ_Y must be extremely large to result in a substantial increase in MF_{XY}.

In our numerical example, the magnitude of *MF* was increased if a component of yield (number of seeds per plant) was further split into its subcomponents (number of pods per plant and number of seeds per pod). Equation (8) shows that $MF_{XYZ} > MF_{X(YZ)}$ if, and only if, $MF_{YZ} > 1$, i.e., subcharacters *Y* and *Z* show complementary differences in the parents.

Considering the breeding system and other prerequisites, a plant breeder may not be interested in the commercial production of hybrids but rather in the performance of later generations derived from a cross. For this reason, equation (10) was derived under simplifying assumptions (absence of epistasis, no correlations among subcharacters in segregating generations) to predict the yield performance of partially-inbred generations. A graph based on equation (10) and parameter estimates obtained from cross I is shown in Fig. 2. The yield decline should be a quadratic function of the inbreeding coefficient, F_t, which is not apparent from Fig. 2. However, the deviation of the respective curve from linearity can hardly be detected, unless the product of the relative heterosis for individual traits ($h_X h_Y$) is large. With $MF_{XY} > 1$, the predicted mean of F_∞ lines should always be greater than the midparent value $\bar{P}$ because the ratio of the former to the latter is equal to MF_{XY}. Consequently, under the above assumptions and with non-negative heterosis for each yield component, the mean of any generation derived from inbreeding the F_1 should always exceed the parental mean if the parents are complementary in their yield components. Thus, positive multiplication effects could also be exploited in the breeding of synthetic or line cultivars by using parents with complementary structure in yield components.

In our example, mean yields of the F_2 and B generations in cross I were below the expected relationship based on equation (10) (Fig. 2). Checking the assumptions for equation (10) showed that phenotypic correlations among subcharacters were small ($r^2 < 0.08$) for

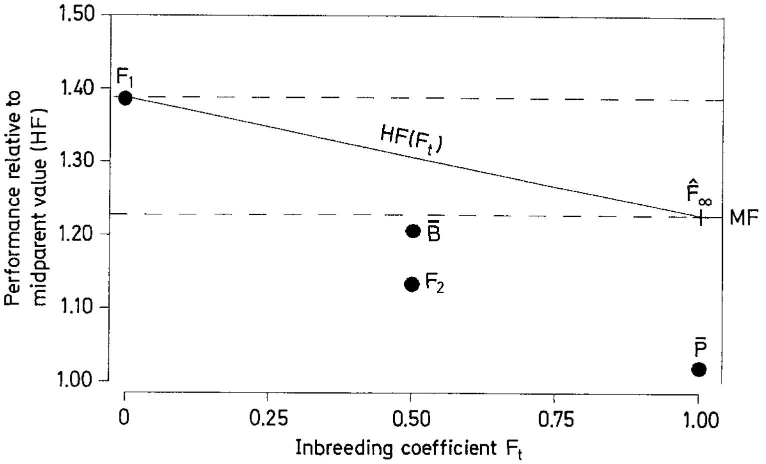

Fig. 2 Mean seed yield in cross I of F_1, F_2, and backcross [$\bar{B} = (B1 + B2)/2$] generations expressed in units of midparent performance $\bar{P}$ and predicted yield performance (*solid line*) of inbred generations as a function of the inbreeding coefficient F_t under equation (10). Assumptions: both component traits (seed weight X and number of seeds per plant Y) display no epistasis and are uncorrelated

both segregating (F_2, B1, B2) and non-segregating generations (P1, P2, F_1). However, the observed deviation could be explained by the presence of significant additive × additive epistasis for one of the subcharacters (seed weight), and this would also result in a lower predicted value for the F_∞ generation.

The theoretical results in equation (16) to (18) were derived to show how multiplicative action between unlinked subsets of loci governing certain subcharacters can give rise to the presence or absence of epistatic effects among the entire set of loci affecting a complex multiplicative trait. Some interesting features emerging from these equations are worth mentioning. Effect dd_U is expected to be positive if d_X and d_Y both have the same sign and dd effects for subcharacters X and Y are equal or close to zero. Likewise, aa_U is expected to be negative if subcharacters show complementary differences among parents and negligible or no aa effects. However, in cross I we found significantly positive aa effects for seed weight. Thus, the negative contribution of $a_X a_Y$ to aa_U was largely cancelled by the positive contribution of $c_X\ aa_Y$ so that the estimate of aa_U was not significantly different from zero.

The models derived in this study incorporate not only the inherent multiplicative nature of subcharacters to the manifestation of heterosis in complex traits but also seek an explanation of this multiplicity in terms of multiplicative gene interaction between the loci of subcharacters. We tested the latter by comparing direct and indirect estimates of gene effects obtained from generation means analyses of the complex trait (yield) and its subcharacters in cross I and found excellent agreement among them. While a generation-means analysis only provides estimates of sums of gene effects of a given type, it has recently become possible to characterize the gene effects of quantitative trait loci (QTLs) with the aid of molecular markers (for a review see Stuber 1992). Using the latter approach, it should be possible to investigate the assumptions underlying our theoretical derivations and conclusions directly at the level of QTLs for multiplicative traits and their subcharacters.

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