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Quantitative genetics of intraspecies hybrids

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Quantitative genetics generally is based on the properties of the randomly fertilized (RF) population or inbred derivatives of it. Simple hybrids and hybrid swarms do not conform to this model; and only some properties of hybrid means appear to have been available. In this paper, several genetical properties are derived, including genotype and allele frequencies, genotypic variance, broad-sense heritability, and outbreeding coefficient. The earlier mean is confirmed, and hybrid vigour is examined critically. These results make it possible to evaluate quantitatively both natural selection and forward selection (in plant breeding) from hybrids. An important finding is that hybrids with maximum hybrid vigour do *not* maximize genetic advance from forward selection, i.e. evolution is unlikely to enhance hybrid vigour. Another finding is that the concepts of *additive genetic variance* and *narrow-sense heritability* are inappropriate for hybrids, owing to the genetic disequilibrium inherent from their origin, and to the ephemeral nature of their population structure.

Keywords: genetic advance, genetic variances, heritability, hybrids, outbreeding, selection.

Introduction

The majority of quantitative genetics is based on the properties of the disomic randomly fertilized population, either as a single panmictic gamodeme in equilibrium or as a dispersed inbred derivative of it (e.g. Wright, 1951, 1952; Crow & Kimura, 1970; Mather & Jinks, 1971; Falconer, 1981). The fundamental quantitative genetic concepts and details are defined with respect to such populations, and include most of the common facts: allele and genotype frequencies, population mean, genotypic variances, heritabilities, selection genetic advance and effects of inbreeding. However, there are other types of populations which are common in nature and in plant breeding for which these properties may not apply. These populations include hybrids (F_1 'hybrid swarms' and simple crosses), and segregating F_2 bulks of either sib-crossed or selfed origin. These are, intrinsically, in disequilibrium by virtue of their very origin. The basic properties arising from the randomly fertilized population (RF) generally may not apply to them. In order to evaluate this, and to account for the effects of such populations in evolution and in plant breeding, it is necessary to reveal their quantitative genetic properties.

The present paper examines the quantitative genetic properties of the bulk hybrid produced by unhindered crossing between two parent populations.[1] Previous work has explored the mean of such an F_1, having been stimulated by interest in hybrid vigour (Falconer, 1981). Also, some knowledge on the genotype frequencies within hybrids is widely extant, but only for the simple case of a hybrid between two complementary pure lines (homozygotes) (Wright, 1952; Kempthorne, 1956). Here, all of the properties mentioned earlier are derived from first principles, including an outbreeding coefficient. The main novel information from this paper is the definition of the hybrid's genotypic variance (σ^2_G), and broad-sense heritability (h^2_B). We will discover that the genic variance (σ^2_A) and dominance variance (σ^2_D) cannot be defined, and are inappropriate for hybrids.

General method

The classical two-allele population gene-model is used (e.g. Falconer, 1981), where p = frequency of A_1 (the *better* allele-expectation, or allele), and q = frequency of A_2 (the *lesser* allele-expectation, or allele), without any omission (i.e. $p + q = 1$).

The genotype effects are deviates from the homozygote midpoint (MP), where a is the A_1A_1 homozygote effect (an expectation), $-a$ is the A_2A_2 effect, and d is the heterozygote effect. The row vector of these effects is $\mathbf{g}' = [a, d, -a]$. Notice that this is a biometrical model and not a single-gene model. In this form, it describes either the *net results* (expectations) of polygenic systems (Mather & Jinks, 1971; Jana, 1972), or the *sensu strictu* single-gene case. It is a *single main-effect* model only,

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[1]Impediments to gene flow, such as species incompatibility, maternal restitution, transgenic instability, organelle dosage, etc., are not considered in this paper.

and does not attempt to define epistasis as interactions amongst factorial main effects. Some forms of epistasis may be accommodated by overdominance ($d > a$). Although this is a simplification, it is a standard approach which has served quantitative genetics well for many decades (Mather & Jinks, 1971; Falconer, 1981).

Alternative models, with factorial main effects and interactions, fall into two categories: biometrical expectations over many loci (Cockerham, 1954; Kempthorne, 1956; Hayman, 1958), or *sensu strictu* polygene specifications (Seyffert, 1966; Jana, 1971). The latter refer to specified loci situations, such as transgenics, mutants, or simply inherited specific phenotypes; they are not considered in this paper. For this initial examination of the properties of the hybrid, we will use the classical, robust, biometrical simple main-effects model which is the foundation of quantitative genetics.

In most of the examples used in this paper, $a = 10$ and $d = 7.5$ (a case of *partial dominance* with $d < a$). When *overdominance* ($d > a$) is being considered, the following values of d are substituted: 15, 22.5 and 30. (In my experience, biometrical overdominance is extremely rare in practice, and allowing for a case of $d = 3a$ probably exceeds any reality.)

One random-fertilizing parent population (P_1) is regarded as *focal*, with frequencies p_1 and q_1. The other random-fertilizing parent population (P_2) is defined as an offset from this where $p_2 = p_1 - y$, and $q_2 = q_1 + y$, with $y = p_1 - p_2$. This follows the procedure of Falconer (1981), and defines the two parental populations within a single system. This is intrinsically better than Kempthorne's approach (Kempthorne, 1956) which is incapable of revealing the interconnectedness arising from hybridization, i.e. the disequilibrium (y). As $p_1 \to 1$ and $p_2 \to 0$ (or vice versa) with $y \to \pm 1$, a simple hybrid between two complementary pure lines is defined.

The methods used actually to derive the hybrid properties form an integral part of the Results of this paper, and are presented in that section.

It is often instructive to compare the F_1 with a random-fertilizing population (RF) based on p_{F1}. The properties of such a population are obtained in the usual way (see, e.g. Falconer, 1981) after incorporating the new allele frequency into the equations:

$$\sigma^2_{A(RF)} = 2p_{F1}q_{F1}\ \alpha^2_{F1} \quad (\text{where } \alpha_{F1} = a + (q_{F1} \quad p_{F1})d),$$

and

$$\sigma^2_{D(RF)} = (2p_{F1}q_{F1})^2 d^2.$$

Results

The frequencies of progeny genotypes following hybridization are obtained as the products between the two parental arrays of allele frequencies $[p_1, q_1]$ and $[p_1 - y, q_1 + y]$, assuming that each parent is contributing equally to the cross. Thus, we are considering the biparental cross (BiP) and hybrid-cultivar in plant breeding; and, in evolution, the mean bidirectional hybrid between two populations. The gamete union is presented in Table 1.

These results lead readily to the following progeny genotype frequencies (row vector $\mathbf{f}'$):

$$\begin{aligned} A_1A_1 \quad & (\mathbf{f}_{11}) = p_1^2 \quad p_1 y \\ A_1A_2 \quad & (\mathbf{f}_{12}) = 2p_1q_1 + y(p_1 \quad q_1) \\ A_2A_2 \quad & (\mathbf{f}_{22}) = q_1^2 + q_1 y. \end{aligned}$$

As discussions of hybrids often focus on their heterozygosity, we examine $\mathbf{f}_{12}$ in Fig. 1, where *complementary opposite* crosses (i.e. $p_2 = 1 - p_1$) are shown,

Table 1 Gamete fertilization outcomes and frequencies between two hybridizing populations

Other parent (P_2)		Focal parent (P_1)			
A_1	$p_1 - y$	A_1A_1	$(p_1 - y)p_1$	A_1A_2	$(p_1 - y)q_1$
A_2	$q_1 + y$	A_2A_1	$(q_1 + y)p_1$	A_2A_2	$(q_1 + y)q_1$

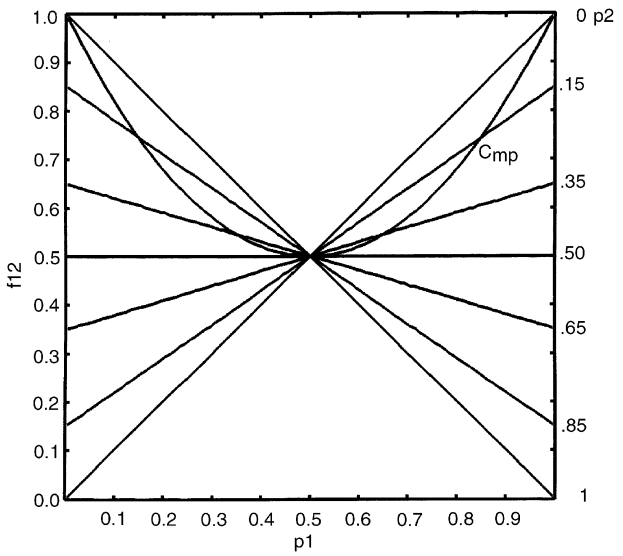

Fig. 1 Frequencies of heterozygotes in the F_1 ($\mathbf{f}_{12}$) from crosses between the *focus* parent (A_1 frequency p_1) and the other parent with various *fixed* p_2. The *complementary-opposite* other parent is compared also.

together with a range of *fixed other parents* (i.e. $p_2 = 0$, 0.15, 0.35, 0.5, 0.65, 0.85 or 1). Notice that a fully heterozygous hybrid occurs only when opposite pure lines ($p_1 = 1$ and $p_2 = 0$, or vice versa) are crossed.

F_1 allele frequency

The hybrid's A_1 'allele' (allele-expectation or actual allele) frequency (p_{F1}) is found as the weighted mean of the progeny (F_1) genotype frequencies $\mathbf{f}'$. The weights reflect the proportions of the *focus* '*allele*' in each genotype in the F_1, i.e. for A_1 the weights are $\mathbf{w}_1' = [1, \frac{1}{2}, 0]$ for the F_1 genotypes $\{A_1A_1, A_1A_2$ and $A_2A_2\}$, respectively. Similarly, for q_{F1}, the frequency of A_2, the weights are $\mathbf{w}_2' = [0, \frac{1}{2}, 1]$ instead. Thus,

$$\begin{aligned} p_{F1} &= \mathbf{w}_1'\mathbf{f} \\ &= 1(p_1^2 \quad p_1 y) + \tfrac{1}{2}(2p_1q_1 + y(p_1 \quad q_1)) \\ &\quad + 0(q_1^2 + q_1 y) \\ &= p_1 \quad \tfrac{1}{2}y. \end{aligned}$$

Similarly, the new A_2 frequency is:

$$\begin{aligned} q_{F1} &= \mathbf{w}_2'\mathbf{f} \\ &= q_1 + \tfrac{1}{2}y. \end{aligned}$$

The frequency p_{F1} is examined in Fig. 2 for the *complementary-opposite* crosses mentioned earlier, and the previous series of *fixed* other-parents. Notice that *complementary-opposite* crosses always result in a hybrid allele frequency of 0.5, as do several other combinations of p_1 and p_2. In general, by rearranging the previous equations, the parental frequency required to obtain any nominated p_{F1} can be estimated from either $p_1 = 2p_{F1} - p_2$, or $p_2 = 2p_{F1} - p_1$, depending on which values are provided and which are sought. For the special case of $p_{F1} = \frac{1}{2}$ these reduce to $p_1 = 1 - p_2$ and $p_2 = 1 - p_1$, respectively.

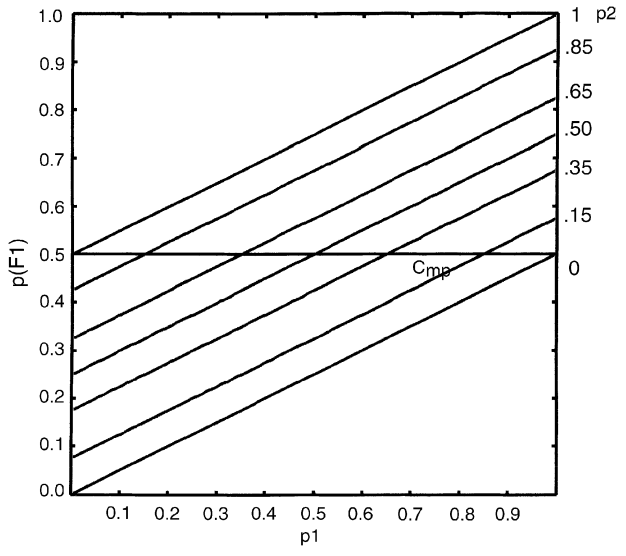

Fig. 2 Frequencies of the A_1 allele in the F_1 (p_{F1}) of crosses between the *focus* parent (A_1 frequency p_1), and the other parent either with *complementary-opposites* p_2 or with various *fixed* p_2.

Hybrid mean

The F_1 mean ($\bar{F}_1$) is $\mu + \bar{G}_{F1}$, where μ is the attribute background mean, and $\bar{G}_{F1}$ ($= \gamma$ also) is the gene-model mean. This is obtained as follows, using the vectors defined earlier.

$$\begin{aligned} \bar{G}_{F1} &= \mathbf{f}'\mathbf{g} \\ &= (p_1^2 \quad p_1 y)a + (2p_1q_1 + y(p_1 \quad q_1))d \\ &\quad + (q_1^2 + q_1 y)(\quad a) \\ &= [(p_1 \quad q_1)a + 2p_1q_1 d] \\ &\quad y[a + (q_1 \quad p_1)d] \\ &= \bar{G}_1 \quad y\alpha_1. \end{aligned}$$

Here, α_1 is the well known *average-allele substitution* effect for the focal parent population (see, e.g. Falconer, 1981), being equal to $a + (q_1 - p_1)\, d$.

This is the same result as obtained by Falconer (1981), but the derivation here is much more direct. The value of this $\bar{F}_1$ is explored in Fig. 3 for *complementary-opposite* crosses and moderate partial dominance ($a = 10$, $d = 7.5$ and $\mu = 10$). It is useful to compare it in Fig. 3 with the equivalent means of both P_1 and P_2, the parental mean (*PM*), and with the RF with $p_{F1} = 0.5$. (In order to save space, we will cease illustrating with *fixed* p_2 crosses from here on.)

Notice that the F_1 mean increases as $p_1 \to 0$ or $p_1 \to 1$, but it is never greater than the mean of the better parent (which is P_2 when $p_1 < \frac{1}{2}$ and P_1 when $p_1 > \frac{1}{2}$) in this example showing partial dominance.

Changes in dominance (particularly *overdominance*, in which $d > a$) elevate the mean considerably, especially as $p_1 \to 0$ or 1.

A common understanding of 'hybrid vigour' is that the 'hybrid is more vigorous than the parents' — i.e. *both* parents. The formal definition does not say that, however, as it defines vigour with respect to the mid-parent (i.e. the parental mean, *PM*). The common *hybrid vigour* definition is $hv = \bar{F}_1 \quad PM$ (Falconer, 1981), who also shows that $hv = y^2 d$ in terms of the gene model. This is a very optimistic view of hybrid vigour, because

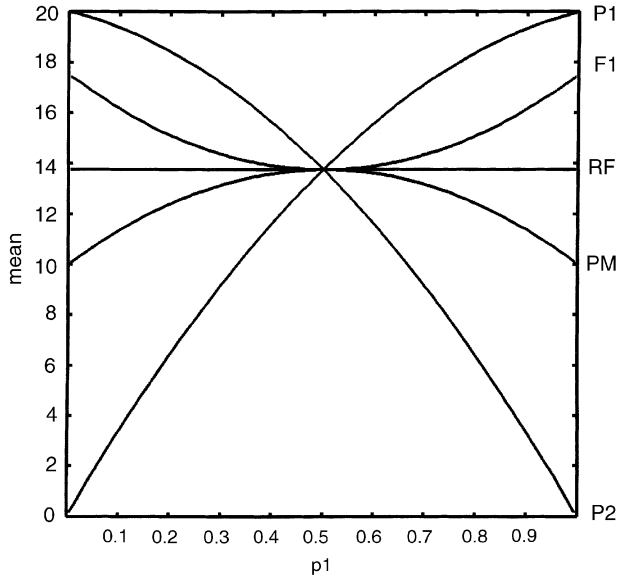

Fig. 3 Population mean of the F_1 of crosses between the *focus* parent (A_1 frequency p_1) and the other parent with *complementary-opposite* p_2. The two parent means (P_1 and P_2) are shown for comparison, along with the bi-parental mean (PM) and RF mean for $p_{F1} = ½$. ($a = 10$, $d = 7.5$, $\mu = 10$.)

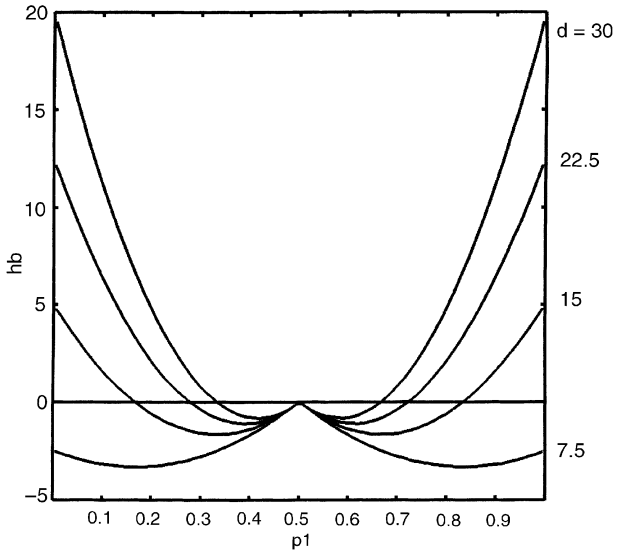

Fig. 4 Heterosis from better parent (hb) in hybrids between a *focus* parent (A_1 frequency p_1) and the other parent with *complementary* p_2. Using $a = 10$, partial dominance has $d = 7.5$; while overdominance increases as $d = 15$, 22.5 and 30.

midparent is never more than the mean of the *better* parent. An alternative view (*hybrid vigour* (*b*): Mather & Jinks, 1971) is more in line with the common concept of hybrid vigour, and is defined as follows:

$$hb = \bar{F}_1 \quad \bar{P}^{\max}, \quad \text{where } \bar{P}^{\max} = {}^{\max}\{\bar{P}_1, \bar{P}_2\}.$$

When $p_1 > p_2$, parent P_1 will be the better parent. We can then derive hybrid vigour (b) (*hb*) in terms of the gene model as follows:

$$\begin{aligned} hb &= \bar{F}_1 \quad \bar{P}_1 \\ &= [a(p_1 \quad q_1 \quad y) + d(2p_1q_1 \quad y(q_1 \quad p_1))] \\ &\quad\; [a(p_1 \quad q_1) + 2p_1q_1d] \\ &= \quad y(a + d(q_1 \quad p_1)) \\ &= \quad y\alpha_1. \end{aligned}$$

With P_1 as the better parent, y is positive: so *hb* will be positive (i.e. real) only when α_1 is negative. The definition of α_1 shows that this will occur when $p_1d > (a + q_1d)$. As y becomes negative, it means that P_2 is now the better parent, and we simply swap our definition base to $hb = -y\alpha_2$. In Fig. 4, the levels of *hb* from several degrees of dominance are examined. Hybrids with *partial dominance* do not express hybrid vigour (b); nor do any hybrids with central values of p_1. Vigour maximizes as $p_1 \to 0$ or 1, and as *overdominance* increases.

Hybrid genotypic variance

The genotypic variance of a hybrid population has the usual expectation:

$$\sigma^2_G = \sum_{i \le i'}^{3} f_{ii'} g^2_{ii'} \quad \gamma^2,$$

where the first right-hand-side term is an unadjusted sum of squares (USS) and the second term is a correction factor $(CF)^2$. The expanded components are as follows.

$$\begin{aligned} \text{USS} &= (p_1^2 \quad p_1y)a^2 + (2p_1q_1 + yp_1 \quad yq_1)d^2 \\ &\quad + (q_1^2 + q_1y)(\quad a)^2. \end{aligned}$$

$$\begin{aligned} \text{CF} &= [(p_1 \quad q_1 \quad y)a + (2p_1q_1 \quad y(q_1 \quad p_1))d]^2 \\ &= p_1^2a^2 \quad 2p_1q_1a^2 + q_1^2a^2 + 4p_1^2q_1ad \quad 4p_1q_1^2ad \\ &\quad + 4p_1^2q_1^2d^2 + y^2a^2 + 2y^2q_1ad \quad 2y^2p_1ad + y^2p_1^2d^2 \\ &\quad y^2 2p_1q_1d^2 + y^2q_1^2d^2 + 2yq_1a^2 \quad 2yp_1a^2 + 2yp_1^2ad \\ &\quad 2y4p_1q_1ad + 2yq_1^2ad + 2y2p_1^2q_1d^2 \quad 2y2p_1q_1^2d^2. \end{aligned}$$

[2] This sum of squares is based on frequencies rather than counts: so it is a mean-square in fact.

After subtracting the CF from the USS and effecting several gathering and factoring of terms[3], the sum of squares becomes:

$$\begin{aligned}
&\mathrm{SS}\left(\sigma^2_{\mathrm{G_{F1}}}\right)\\
&= 2p_1q_1a^2 + (q_1 \quad p_1)4p_1q_1ad + 2p_1q_1d^2(1 \quad 2p_1q_1)\\
&\quad + y\{(p_1 \quad q_1)[a^2 \quad 2ad(p_1 \quad q_1) + d^2 \quad 4p_1q_1d^2]\\
&\quad + 2p_1q_12ad\} \quad y^2\left[a^2 + (q_1 \quad p_1)2ad + (q_1 \quad p_1)^2d^2\right]\\
&= 2p_1q_1\left[a^2 + (q_1 \quad p_1)2ad + (q_1 \quad p_1)^2d^2\right]\\
&\quad + 2p_1q_1(2p_1q_1d^2) + y\{(p_1 \quad q_1)[a^2 + (q_1 \quad p_1)2ad\\
&\quad + d^2(1 \quad 4p_1q_1)] + 4p_1q_1ad\} \quad y^2\alpha_1^2\\
&= 2p_1q_1\alpha_1^2 + (2p_1q_1)^2d^2 + y(p_1 \quad q_1)\alpha_1^2 \quad y^2\alpha_1^2 + y4p_1q_1ad.
\end{aligned}$$

Recalling the classical definitions of σ^2_{A} and of σ^2_{D} (Falconer, 1981), and defining $\mathrm{cov}(a,d) = 4pqad$, we can write:

$$\sigma^2_{\mathrm{G_{F1}}} = \sigma^2_{\mathrm{A_1}}\left(1 + \frac{y(p_1 \quad q_1)}{2p_1q_1} \quad \frac{y^2}{2p_1q_1}\right) + \sigma^2_{\mathrm{D_1}} + y\mathrm{cov}(a,d)_1. \qquad (1)$$

The overall genotypic variance is visualized for our partial dominance and complementary-opposites cross in Fig. 5. There, it is compared also with the genotypic variance of the *focal parent* ($\mathrm{P_1}$), and of the RF population based on $p_{\mathrm{F1}} = ½$ as before.

Notice that simple hybrids between opposite pure lines have no genotypic variance for the gene effect in question, as one would expect. For $p_1 < ½$, the $\mathrm{F_1}$ has smaller genotypic variance than both the focal parent and the equivalent RF. For $p_1 > ½$, its variance lies between that of the other two populations. This pattern is true even for overdominance: which greatly inflates the total amount of genotypic variance in all three population types.

The genic and dominance variances of hybrid populations present a problem of definition, and even of existence. Therefore they will be addressed in the Discussion rather than here in the Results.

[3] Various relations are used to resolve these equations, and are given below.

$(p^2 - 2pq + q^2)$ = either $(p - q)^2$ or $(q - p)^2$;
$(1 - 2pq) = p^2 - 2pq + q^2 + 2pq = (q - p)^2 + 2pq$;
$(1 - 4pq) = (q - p)^2$;
$-2ad(p - q) = (+)\ 2ad(q - p)$.

Also, recall that $\alpha = a + (q - p)d$ (e.g. Falconer, 1981).

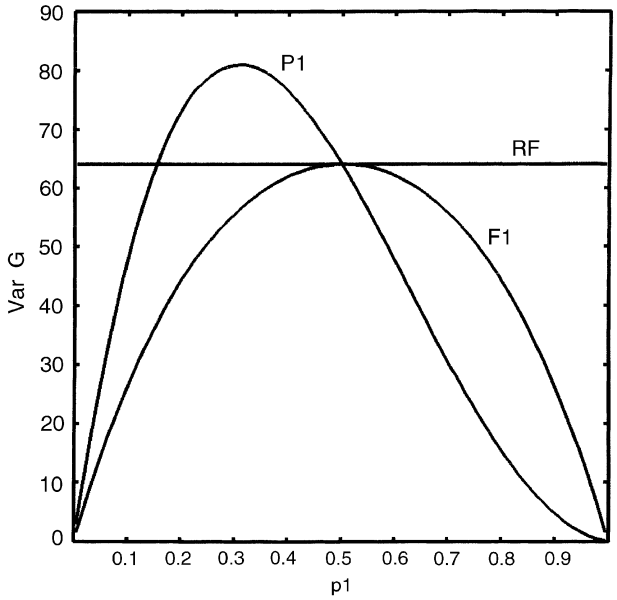

Fig. 5 Genotypic variance (Var G) of hybrids between a *focus* parent (A_1 frequency p_1) and the other parent with *complementary-opposite* p_2. Partial dominance ($a = 10$, $d = 7.5$) is shown. Variance of the focal parent ($\mathrm{P_1}$) and of the RF for $p_{\mathrm{F1}} = ½$ are compared.

Heritability

Having defined a genotypic variance for the $\mathrm{F_1}$, we have a corresponding ratio of σ^2_{G} to σ^2_{P}: that is, a broad-sense heritability. As genic variance is undefined, there is no narrow-sense heritability. The broad-sense heritability (h^2_{B}) is a biometrical parameter, it being the genotypic *determination* of the phenotype (Wright, 1951). This broad-sense heritability would therefore be appropriate for obtaining the genetic advance from forward selection from hybrids. It is shown in Fig. 6, using the various parameter values given elsewhere, and an example environmental variance of $\sigma^2_{\mathrm{E}} = 25$.

Note that the broad-sense heritability attains maximum values for a wide range of hybrids with p_1 of central values, and increases with increasing dominance (d). We would expect therefore to see a maximal result from forward selection in such hybrids, with a minimal response in hybrids between extreme parents (i.e. complementary-opposite parents, and $p_1 \to 0$ or 1). This matter raises interesting discussion (later) about the relative merits of hybrid vigour and selection.

Outbreeding coefficient

The definition is based on the level of heterozygosity in the hybrid as contrasted to a relevant reference population: in this case a RF population with allele frequency p_{F1}. It is as follows:

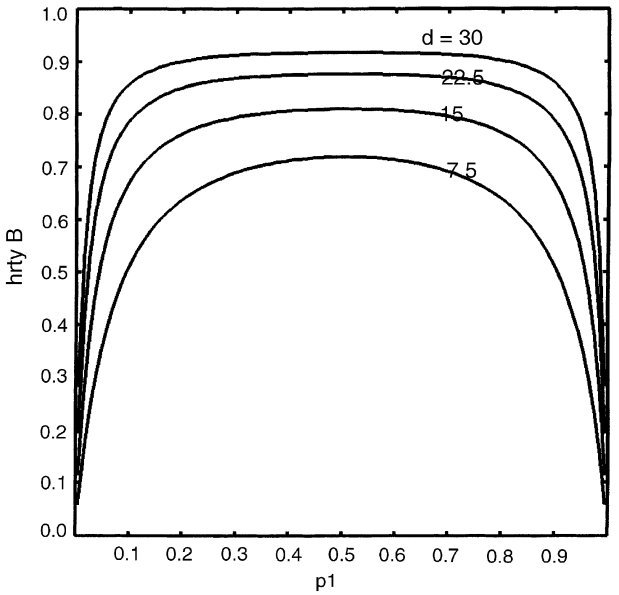

Fig. 6 Broad-sense heritability (h^2_B) under four levels of dominance ($d = 7.5$, 15, 22.5, 30) for hybrids between a focus parent (A_1 frequency p_1) and the other parent with *complementary-opposite* p_2. ($a = 10$, $\sigma^2_E = 25$).

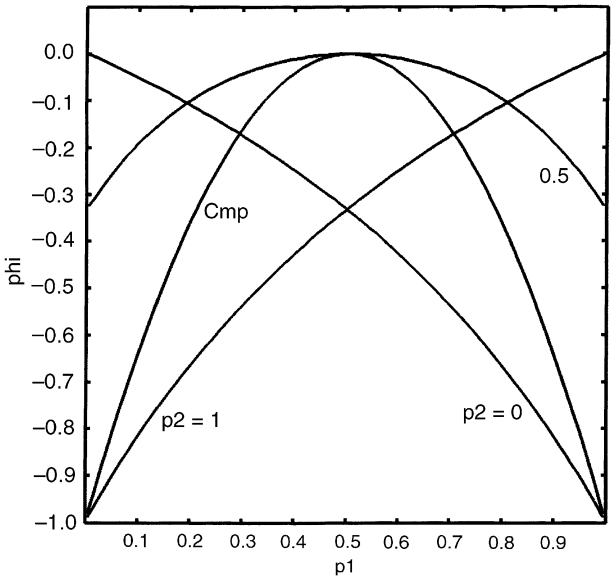

Fig. 7 Outbreeding coefficient (phi (ϕ)) for hybrids between a *focus* parent (A_1 frequency p_1) and the other parent, with $p_2 = 0$, 1, 0.5 and *complementary-opposite*.

$$\phi = \left(1 \quad \frac{f_{12_{F1}}}{f_{12_{RF}}}\right),$$

where all symbols have been defined previously.

This is also one approach to defining an *inbreeding* coefficient: but in this case the higher levels of heterozygosity in the F_1 make it *negative*. This means it indicates 'new heterozygosity relative to a RF population', i.e. outbreeding. Its values for *complementary-opposites* crosses, and for *fixed P_2 crosses* ($p_2 = 0$, 0.5, 1) are shown in Fig. 7. For the *complementary-opposites*, outbreeding maximizes (that is $\phi \to -1$) for extreme values of y ($p_1 \to 0$ or $p_1 \to 1$): in other words, the proportion of heterozygotes approaches twice that of the comparable RF population. When $p_1 = p_2 = ½$, the hybrid has the same heterozygosity as the corresponding RF population, and the outbreeding coefficient is zero.

The situations for *fixed parents* are more variable. Three special cases are shown in Fig. 7. First, for $p_2 = 0.5$, the curve shape across p_1 is similar to that for *complementary-opposite crosses*, with the exception that $\phi_{min} = -0.325$ rather than -1. That is, the level of heterozygosity is never more than a third higher than in the reference RF population. The other two special cases involve the two pure lines ($p_2 = 0$ or 1). In each case, the level of outbreeding changes from -1 (full heterozygosity) to 0 (RF heterozygosity) as the *focus* parent and the *other* parent change from being *complementary-opposite* to nearly identical. At the point of both parents being the same pure lines ($p_1 = p_2 = p_{F1} = 0$, or 1), there is no heterozygosity in any of the three populations, and outcrossing is zero.[4] (The term 'F_1' is, of course, somewhat forced at this juncture.)

Discussion

Genic and dominance variances in the F_1

It is well-known that the classical RF genotypic variance contains the two components: genic and dominance variances. From eqn (1), it is obvious that the F_1 genotypic variance has a different composition. As the hybrid population structure is sexually ephemeral[5], the very concept of *average allele substitution* is questionable. This means that the σ^2_A component (eqn ?tul > 1) should not be interpreted as the F_1 *genic* variance, because such *average allele effect* is the very basis of such a variance (Falconer, 1981). It is simply a function of the *focal parent's genic variance* which forms part of the definition of the F_1 genotypic variance. Furthermore, the F_1 genotypic variance (eqn 1) also contains a third component — excess cov(a,d) — which does not appear in the

[4] The graph covers only the range $p_1 = 0.005$–0.995 in order to avoid division by zero in the computer algorithm.

[5] Following F_1 meiosis and syngamy, it no longer contains the same genotypic frequencies with which it began: it is *not* in equilibrium. In fact, it produces a new kind of population, the F_2.

Table 2 Genetic advance (Δ_G) at selection pressure of 10% ($P = 0.1$), variability (σ^2_P), broad-sense heritability (h^2_B), and mean of the F_1 from *complementary-opposites crosses* for various focus parents (allele frequency p_1) and two dominance levels ($d = 7.5$, 30 with $a = 10$)

d	p_1	Δ_G	σ^2_P	h^2_B	F_1 mean
7.5	0.35	11.34	84.389	0.704	14.09
	0.45	11.84	88.498	0.718	13.79
	0.97	2.68	33.894	0.202	17.06
30.0	0.35	27.49	293.409	0.915	26.35
	0.45	27.81	299.203	0.916	25.15
	0.97	10.80	80.096	0.688	38.25

classical RF case.[6] These observations remind us that a hybrid is profoundly different from a RF population. Therefore, the concepts of genic and dominance variances appear inappropriate with respect to hybrids.

Selection efficiency

Several of the properties (heritability, genotypic variance, mean) have the very important implication that some hybrids will be more efficient for subsequent selection than others. Obviously, those with $h^2_B \to 0$ will be of little value for *forward selection* (i.e. selecting F_1 individuals towards an F_2 nursery).[7] Likewise, those with trivial σ^2_G will be of little utility, because $\sigma^2_P \to \sigma^2_E$. In the case of our illustrative *complementary-opposites* crosses (see Figs 5 and 6), hybrids between 'extremely opposite' parents (i.e. $p_1 < 0.2$ or $p_1 > 0.8$) are undesirable if forward selection is the intention, especially where overdominance prevails. These properties are illustrated in Table 2, where genetic advance (Δ_G) at selection pressure of 10% ($P = 0.1$) in selecting $F_1 \to F_2$ is given, for partial and overdominance ($d = 7.5$ and 30) and *complementary-opposite crosses*, with parental inputs which are *intermediate* ($p_1 = 0.35$), *optimal* ($p_1 = 0.45$), and *extreme* ($p_1 = 0.97$). Background properties are given also, such as hybrid σ^2_P and h^2_B.

All of the trends discussed above are borne out by these values. Notice that the greatest Δ_G occurs at the $p_1 = 0.45$ example within each dominance level; whereas the highest hybrid mean occurs at $p_1 = 0.97$ within each dominance level. The drop in σ^2_P for extreme p_1 is conspicuous; and reduced h^2_B for extreme p_1 is apparent. These hybridization outcomes affect natural selection as well, i.e. adaptation is optimized out of hybrid swarms between *nonextreme* parental populations, rather than those arising from extreme opposites.

For *backward selection*[8], matters are completely different. The relevant property of the hybrid is the mean (or more specifically, its hybrid vigour), which is higher towards extreme ends of the p_1 range (Fig. 3). As we are here using the hybrid's mean performance as a *progeny test* of the parents, and not selecting *F_1 individuals* onwards into the next generation, heritability is not an issue (except insofar as it is biometrically related to the standard error of the mean). So, in this case, the 'most extreme opposites' crosses *would* be the best, just as Falconer (1981) declared when he stated that y should be maximized to maximize hybrid vigour. The last column of Table 2 shows this for the illustrative example. This aspect of using hybrids appears to be entirely anthropomorphic: it is very unlikely to apply to evolution because retrospective re-making of particular crosses requires a discerning control of the programme. Also, we have shown that hybrids which maximize hybrid vigour *do not maximize forward genetic advance*, indicating that natural selection does not operate to maximize hybrid vigour.

[6] The RF genotypic variance can be derived biometrically, in a manner similar to that adopted here for the F_1. Indeed, Mather & Jinks (1971) must surely have done so previously, but it never seems to have been published overtly. By that approach, it can be shown that the original RF $\sigma^2_A = \sigma^2_a + (q \quad p)\mathrm{cov}(a,d) + (q \quad p)^2\sigma^2_d = 2pq\alpha^2$, where $\sigma^2_a = 2pqa^2$ (the gene-model homozygote variance), $\sigma^2_d = 2pqd^2$ (the gene-model heterozygote variance), and other terms are defined previously. For this classical RF situation, all of the covariance is utilized in the absorption into that genic variance. This contrasts strongly with the situation we have revealed for the hybrid.
The so-called dominance variance in the RF population is simply the remnant σ^2_d which could not be absorbed into the genic variance. In fact, $\sigma^2_D = 2pq\sigma^2_d = (2pq)^2d^2$.

[7] $\Delta_{G(F1)} = ih^2_B\sigma_P$, where i = the standardized selection differential (accounting for selection pressure, P), and other symbols have been defined elsewhere in this paper (and in Falconer, 1981).

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[8] i.e. using the hybrid means to identify which parents have given good hybrid combinations of genes as expressed in their progeny (the F_1). The hybrid mean performance is a backward-looking progeny test. Parents identified as having good hybrid combining ability would then be re-crossed to propagate the desirable hybrid.

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