

Quantitative Genetics of 4x–2x Hybrid Populations With First-Division Restitution and Second-Division Restitution 2n Gametes Produced by Diploid Parents

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ABSTRACT

A model is proposed to describe the genetic value of 4x–2x hybrids resulting from crosses between tetraploid genitors and diploid genitors that produce 2n gametes. The model takes into account the genetic consequences of the First Division Restitution (FDR) and Second Division Restitution (SDR) meiosis, particularly on the homozygosity level that 2n gametes contribute to 4x–2x hybrids. As genes can be identical by descent, numerous parameters are needed in the classical approach to describe the inbreeding effects on the mean and variance of 4x–2x hybrids. Using the concept of test value, the model allows a large decrease in the number of required parameters. The model gives the components of genetic variance and usual covariances between relatives using these synthetic parameters. The model is then used to study the efficiency of a recurrent breeding scheme to improve diploid genitors for their combining ability with tetraploid genitors. It appears that, in presence of dominance, ignoring the meiosis pattern will lead to an overestimation of additive variance and then of genetic advance. Some genetic considerations on the differences between FDR and SDR mechanisms lead us to suggest an experimental comparison of their respective advantages and disadvantages for the type of considered recurrent selection. An experimental crossing design is proposed to obtain estimates of the genetic parameters needed for this comparison.

TO improve commercial varieties, plant breeders need genetic resources that are often less available in the bred material than in the wild ancestral species. Many cultivated tetraploid species evolved from diploid species, and the germplasm of these diploid ancestors can sometimes be integrated in tetraploid breeding programs thanks to diploid progenitors that produce diploid gametes. For example, in potatoes the diploids are a promising way of improving potato varieties, which are tetraploids (MOK and PELOQUIN 1975a).

The meiotic processes responsible for generating 2n gametes have been studied for several species such as alfalfa (VORSA and BINGHAM 1979; PFEIFFER and BINGHAM 1983) and cocksfoot (VAN SANTEN *et al.* 1986). The phenomenon is well described for potatoes (MOK and PELOQUIN 1975b). In this species, diploid genotypes may produce 2n gametes through either of three abnormal meiotic processes, resulting in 2n gametes genetically equivalent to Second-Division Restitution (SDR) or First-Division Restitution (FDR) that are controlled by simple genetic systems. These gametes can fertilize the normal gametes of tetraploids and tetraploid zygotes result from this cross. These progeny are known as 4x–2x hybrids.

FDR 2n gametes show important genetic differences

compared with SDR 2n gametes. When the diploid parent is (*ij*) at a given locus and if *b* is the frequency of single exchange tetrad ($0 \leq b \leq 1$), the FDR process induces the formation of $1 - b/2$ heterozygous 2n gametes (*ij*), and only $b/4$ (*ii*) and $b/4$ (*jj*) gametes (TAI 1982, *b* is called β in his paper). On the contrary, the SDR mechanism permits the same (*ij*) diploid individual to produce homozygous 2n gametes (*ii*) or (*jj*) with a frequency of $(1 - b/2)$ each and heterozygous gametes (*ij*) with the frequency of *b*.

Consequently, 4x–2x FDR progenies benefit by a high level of heterozygosity that transmits nonadditive effects due to favorable interactions between two different alleles (MENDIBURU *et al.* 1974). Furthermore, since SDR gametes are highly homozygous, they largely differ from one another, and the genotypic values of the resulting 4x–2x hybrid progenies are distributed on a larger scale than those coming from FDR gametes. SDR gametes may also decrease the agronomic performances of 4x–2x hybrids since they bring inbreeding effects.

Diploids are tested for their ability to give valuable 4x–2x hybrids. Unfortunately, the value of the diploids, when evaluated at the diploid level, is poorly related to the mean value of their 4x–2x progeny (ORTIZ *et al.* 1991). This latter value can be seen as a *test value* of the diploids that it is essential to improve. To this end, FDR gametes have been considered as having higher potentialities than SDR gametes. Nonetheless, choosing the

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most adapted meiotic process is not easy because the few models that dealt with inbreeding among tetraploid species (BOUFFETTE 1966; GALLAIS 1967, 1977) were not suited to the 4x-2x feature. More recently, BOUDEEC (1988) adapted the classical tetraploid model (KEMPTHORNE 1957) to study quantitative traits in 4x-2x hybrids, and he calculated the correspondent kinship coefficients. HAYNES (1990) described the genetic relationship between a diploid 2n pollen producing genitor and its 4x-2x offspring. HAYNES (1992) then described the relation between a diploid genitor and its 4x-2x offspring taking into account many kinship coefficients in the particular case of the potato, when diploid and tetraploid genetic backgrounds are identical.

Yet the genetic background of cultivated tetraploids often differs widely from that of diploids. Indeed diploids usually come from primitive, sometimes wild species. Consequently, their genetic structures and allele frequencies differ from the tetraploid gene pool. Thus, the variation observed in the 4x-2x hybrids must be allotted separately to the wild diploid origin or to the cultivated tetraploid origin.

This paper proposes a model that describes the genetic value of 4x-2x progenies from tetraploids crossed either with FDR diploids or SDR diploids with nonzero single exchange tetrads. The model takes into account different genetic backgrounds. Using the concept of test value (GALLAIS 1979, 1989), it also considers the inbreeding effects induced by the homozygosity coming from the 2n gametes. This paper also studies the efficiency of a recurrent selection scheme designed to improve the abilities of the diploids to produce valuable 4x-2x progenies.

It therefore provides a method for comparing the breeding efficiency of FDR gametes *vs.* that of SDR over different periods. The paper also proposes particular experimental designs to evaluate the genetic components needed for this latter comparison.

A GENERAL MODEL FOR INTERPOPULATION
CROSSES BETWEEN DIPLOID AND
TETRAPLOID POPULATIONS

The model: Consider the genetic value of a cross between a 4x genitor, being (klmn) at a locus, and a 2x genitor, being (ij) at the same locus. The value $Y_{(klmn \times ij)}$ can be written

$$Y_{(klmn \times ij)} = \frac{1}{6} (RY_{ijkl}^{ddt} + RY_{ijkm}^{ddt} + RY_{ijkn}^{ddt} RY_{ijlm}^{ddt} + RY_{ijnl}^{ddt} + RY_{ijmn}^{ddt}), \quad (1)$$

where RY_{ijkl}^{ddt} represents the mean value of individuals generated by the different gametes from the 2x and the kl gamete from the 4x. R refers to the meiosis pattern. A gene originating from 2x is indexed d, and t when coming from the tetraploid. The 2n gametes from the diploid parent (ij) can be either (ii) (*i.e.*, the two alleles are identical by descent) or (ij) (the alleles are not identical). Let π be the probability, associated to a meiosis pattern R, of having two nonidentical alleles in a 2n gamete. Among

FDR gametes, π equals $1 - b/2$ and among SDR gametes $\pi = b$, where b is the frequency of single exchanging tetrads (TAI 1982). Then the R value, RY_{ijkl}^{ddt} , can be written in terms of the value of the individuals:

$$RY_{ijkl}^{ddt} = \pi Y_{ijkl}^{ddt} + (1 - \pi) (Y_{ikil}^{ddt} + Y_{jjkl}^{ddt}) / 2. \quad (2)$$

Then, RY_{ijkl}^{ddt} can be considered as a test value associated with combinations of i, j, k, and l genes. Using the concept of test value defined by GALLAIS (1979, 1989), RY_{ijkl}^{ddt} can be written as

$$RY_{ijkl}^{ddt} = R\mu + R\alpha_i^d + R\alpha_j^d + R\alpha_k^t + R\alpha_l^t + R\beta_{ij}^{dd} + R\beta_{ik}^{dt} + R\beta_{il}^{dt} + R\beta_{jk}^{dt} + R\beta_{jl}^{dt} + R\beta_{kl}^{tt} + R\gamma_{ijk}^{ddt} + R\gamma_{ijl}^{ddt} + R\gamma_{ikt}^{dt} + R\gamma_{jkl}^{dt} + R\delta_{ijkl}^{ddt}, \quad (3)$$

with $E(R\alpha_i^d) = E(R\alpha_k^t) = 0$, $E(R\beta_{ij}^{dd}) = E(R\beta_{kl}^{tt}) = E(R\beta_{ik}^{dt}) = 0$, $E(R\gamma_{ijk}^{ddt}) = E(R\gamma_{ikt}^{dt}) = 0$, and $E(R\delta_{ijkl}^{ddt}) = 0$.

The different α , β , γ , and δ effects are defined analogously to those defined by KEMPTHORNE (1957): α is the additive effect of each allele, β is the digenic interaction effect, γ is the trigenic interaction effect, and δ is tetragenic interaction effect. We assume that none of the alleles, either in 2x genitors or in 4x genitors, are identical by descent to any of the others. The two pools *a priori* have different genetic backgrounds (this case has been studied for diploids by STUBER and COCKERHAM 1966). The populations are considered to have an infinite size. There is no epistasis and no linkage disequilibrium in either of the two populations. The coefficient of double reduction equals 0. All terms describing the genetic effects are defined for the hybrid 4x-2x population only. Finally, the genotypic value is obtained by summing the elementary effects of each supposed independent locus.

The genetic value is broken down into terms indexed according to the pools. A (d) indexed term describes the effect of alleles coming from the diploid parent. Nevertheless, one must keep in mind that its value also depends on the global background, *i.e.*, it also depends on the allele frequencies among tetraploid genitors. Similarly, the tetraploid origin is noted (t). A (dt), (ddt), (dtt) or (ddt) index means that the effect originates from the interactions between the alleles of the two populations and the number of d's indicates the number of alleles coming from the diploid pool in the interaction terms.

Correspondence with the classical model: Parameters of the previous model can be related to those of the classical model defined for the *per se* value. According to Expression (2) we have to consider the expression required for Y_{ijkl}^{ddt} and Y_{ikil}^{ddt} (KEMPTHORNE 1957).

If i and j are not identical by descent,

$$Y_{ijkl}^{ddt} = \mu + \alpha_i^d + \alpha_j^d + \alpha_k^t + \alpha_l^t + \beta_{ij}^{dd} + \beta_{kl}^{tt} + \beta_{ik}^{dt} + \beta_{il}^{dt} + \beta_{jk}^{dt} + \beta_{jl}^{dt} + \gamma_{ijk}^{ddt} + \gamma_{ijl}^{ddt} + \gamma_{ikt}^{dt} + \gamma_{jkl}^{dt} + \delta_{ijkl}^{ddt}. \quad (4)$$

TABLE 1
Correspondences between the general model
and the R model

Mean	
$R\mu = \mu + (1 - \pi) E(\beta_{ii}^{dd})$	
Additive effects	
$R\alpha_i^d = \alpha_i^d + (1 - \pi)/2(\beta_{ii}^{dd} - E(\beta_{ii}^{dd}))$	Allele from the diploid parent
$R\alpha_k^t = \alpha_k^t$	Allele from the tetraploid parent
Dominance effects	
$R\beta_{ij}^{dd} = \pi \beta_{ij}^{dd}$	2 nonidentical alleles from 2x
$R\beta_{kl}^{tt} = \beta_{kl}^{tt}$	2 alleles from 4x
$R\beta_{ik}^{dt} = \beta_{ik}^{dt} + (1 - \pi)/2\gamma_{ijk}^{dt}$	1 allele from 2x, 1 from 4x
Trigenic effects	
$R\gamma_{ijk}^{ddt} = \pi \gamma_{ijk}^{ddt}$	2 nonidentical alleles from 2x, 1 from 4x
$R\gamma_{ikl}^{dtu} = \gamma_{ikl}^{dtu} + (1 - \pi)/2\delta_{ikl}^{dtu}$	1 allele from 2x, 2 from 4x
Tetragenic effect	
$R\delta_{ijkl}^{ddtu} = \pi \delta_{ijkl}^{ddtu}$	2 nonidentical alleles from 2x, 2 from 4x

π is the probability that the two alleles from the $2n$ gamete are nonidentical by descent knowing that the diploid genitor is itself noninbred.

If i and j are identical by descent,

$$Y_{ijkl}^{ddtu} = \mu + 2\alpha_i^d + \alpha_k^t + \alpha_l^t + \beta_{ii}^{dd} + \beta_{kl}^{tt} + 2\beta_{ik}^{dt} + 2\beta_{il}^{dt} + \gamma_{ijk}^{ddt} + \gamma_{iil}^{ddt} + 2\gamma_{ikl}^{dtu} + \delta_{ijkl}^{ddtu}. \quad (5)$$

Replacing Expressions (4) and (5) in Equation (2) allows a term-to-term identification. Results are given in Table 1 for any value of π . The correspondence for the ideal FDR and SDR cases (*i.e.*, $b = 0$) is expressed in Table 2.

The $R\alpha_i^d$ term contains an $E(\beta_{ii}^{dd})$ term to equate $E(R\alpha_i^d)$ with 0, since $E(\beta_{ii}^{dd})$ has no particular reason for being zero. The terms due to the tetraploid genitor do not depend on the value of π .

For the mean $R\mu$ of the 4x-2x population, as we defined $R\alpha_i$ so that $E(R\alpha_i) = 0$, we have

$$R\mu = \mu + (1 - \pi) E(\beta_{ii}^{dd}). \quad (6)$$

$E(\beta_{ii}^{dd})$ measures the mean inbreeding depression ef-

fect introduced by the homozygosity of the $2n$ gamete. The expectations of other inbred terms, $E(\gamma_{ijk}^{ddt})$ and $E(\delta_{ijkl}^{ddtu})$ equal 0 as demonstrated in the APPENDIX for $E(\gamma_{ijk}^{ddt})$.

Expression of the genetic variance: All R terms are independent and thus the variance of the model can be easily formulated as follows:

$$R\sigma_G^2 = \text{var}(RY_{ijkl}^{ddtu}) = 2E((R\alpha_i^d)^2) + 2E((R\alpha_k^t)^2) + E((R\beta_{ij}^{dd})^2) + E((R\beta_{kl}^{tt})^2) + 4E((R\beta_{ik}^{dt})^2) + 2E((R\gamma_{ijk}^{ddt})^2) + 2E((R\gamma_{ikl}^{dtu})^2) + E((R\delta_{ijkl}^{ddtu})^2). \quad (7)$$

The additive variance splits up into two independent terms: one is entirely due to the contribution of diploid genitors (2x), $2E((R\alpha_i^d)^2)$; the other one is entirely due to the contribution of tetraploid genitors (4x), $2E((R\alpha_k^t)^2)$. Therefore, by analogy with the intrapopulation model, they will be noted as follows:

$$R\sigma_{A,d}^2 = 4E((R\alpha_i^d)^2), \quad \text{additive variance originating from 2x,} \quad (8)$$

$$R\sigma_{A,t}^d = 4E((R\alpha_k^t)^2), \quad \text{additive variance originating from 4x.} \quad (9)$$

The digenic term splits up into three parts:

$$R\sigma_{D,d}^2 = 6E((R\beta_{ij}^{dd})^2) \quad \text{from 2x only,} \quad (10)$$

$$R\sigma_{D,t}^2 = 6E((R\beta_{kl}^{tt})^2) \quad \text{from 4x only,} \quad (11)$$

$$R\sigma_{D,dt}^2 = 6E((R\beta_{ik}^{dt})^2) \quad \text{from the interaction between 2x and 4x.} \quad (12)$$

For the trigenic variance, $R\sigma_{T,ddt}^2 = 4E((R\gamma_{ijk}^{ddt})^2)$ is obtained from the interaction between two alleles coming from 2x and one allele coming from 4x, and $R\sigma_{T,dtu}^2 = 4E((R\gamma_{ikl}^{dtu})^2)$ from the reciprocal situation.

TABLE 2
Models in the ideal FDR case ($\pi = 1$) and in
the ideal SDR case ($\pi = 0$)

Mechanism	FDR	SDR
Mean		
$R\mu$	μ	$\mu + E(\beta_{ii}^{dd})$
Monogenic effects		
$R\alpha_i^d$	α_i^d	$\alpha_i^d + 1/2(\beta_{ii}^{dd} - E(\beta_{ii}^{dd}))$
$R\alpha_k^t$	α_k^t	α_k^t
Digenic effects		
$R\beta_{ij}^{dd}$	β_{ij}^{dd}	β_{ij}^{dd}
$R\beta_{kl}^{tt}$	β_{kl}^{tt}	β_{kl}^{tt}
$R\beta_{ik}^{dt}$	β_{ik}^{dt}	$\beta_{ik}^{dt} + 1/2\gamma_{ijk}^{dt}$
Trigenic effects		
$R\gamma_{ijk}^{ddt}$	γ_{ijk}^{ddt}	γ_{ijk}^{ddt}
$R\gamma_{ikl}^{dtu}$	γ_{ikl}^{dtu}	$\gamma_{ikl}^{dtu} + 1/2\delta_{ikl}^{dtu}$
Tetragenic effect		
$R\delta_{ijkl}^{ddtu}$	δ_{ijkl}^{ddtu}	δ_{ijkl}^{ddtu}

The tetragenic variance is given with $R\sigma_{F,ddt}^2 = E(R\delta_{ijkl}^{ddt})^2$ only.

To sum up, the total genetic variance is given by

$$R\sigma_G^2 = [1/2R\sigma_{A,d}^2 + 1/6R\sigma_{D,d}^2] + [1/2R\sigma_{A,t}^2 + 1/6R\sigma_{D,t}^2] + [2/3R\sigma_{D,d,t}^2 + 1/2R\sigma_{T,ddt}^2 + 1/2R\sigma_{T,dt}^2 + R\sigma_{F,ddt}^2], \quad (13)$$

$$R\sigma_G^2 = R\sigma_{G,d}^2 + R\sigma_{G,t}^2 + R\sigma_{G,dt}^2, \quad (14)$$

where $R\sigma_{G,d}^2$ is the genetic variance due to genes from the 2x, $R\sigma_{G,t}^2$ that one due to genes from the 4x and $R\sigma_{G,dt}^2$ that one due to genes from the 2x and the 4x.

Then, the R model uses eight variance parameters instead of 14 for the usual model since $E(R\alpha_i^d)^2$ includes $E(\alpha_i^d)^2$, $E(\beta_{ii}^{dd})^2$ and $E(\alpha_i^d\beta_{ii}^{dd})$; $E(R\beta_{ik}^{dt})^2$ includes $E(\beta_{ik}^{dt})^2$, $E(\gamma_{iik}^{dt})^2$ and $E(\beta_{ii}^{dd}\gamma_{iik}^{dt})$; and finally, $E(R\gamma_{ikl}^{dt})^2$ includes $E(\gamma_{ikl}^{dt})^2$, $E(\delta_{iikl}^{dt})^2$ and $E(\gamma_{iik}^{dt}\delta_{iikl}^{dt})$. In the digenic case for which only monogenic and digenic effects are used, the R model saves three parameters, *i.e.*, five instead of eight, knowing that the R model partly describes trigenic effects through γ_{iik}^{dt} .

With the given assumptions, the generalization of the expressions of variances and covariances to an arbitrary number of loci is straightforward. The variances due to the contribution of the diploid genitors ($R\sigma_{A,d}^2$ and $R\sigma_{D,d}^2$) are dependent on the frequencies of the genes in the 2x pool only. They take into account the difference of frequencies with the tetraploid pool and the inbreeding effects introduced by the homozygosity of the $2n$ gametes according to the meiosis pattern R . The values of these variance components vary according to π . Given R and R' , two meiosis patterns, respectively associated with probabilities π and π' , there is no particular reason that $R\sigma_{A,d}^2 = R'\sigma_{A,d}^2$ even if these values are correlated. Usually, inbreeding increases the genetic variation among offsprings of heterozygous genitors, so that if $\pi > \pi'$, then one expects that $R\sigma_{A,d}^2 \leq R'\sigma_{A,d}^2$. Furthermore, if $\pi = 0$, as in the case of ideal SDR, then $R\sigma_{D,d}^2$ equals 0 and when $\pi = 1$, as in the case of ideal FDR, $R\sigma_{D,d}^2$ is at its maximum.

The model can be validated by applying it to the intrapopulation case. If the diploid parents are FDR with $b = 0$ [no crossing over, like synaptic individuals in potatoes (IWANAGA 1984)], then $\pi = 1$ and inbreeding terms vanish. In this case only, and if diploids and tetraploids have the same genetic background, (if the 2x pool is extracted from the 4x pool, for instance), then the terms due to 2x are equal to those of 4x.

If $\pi = 1$, then

$$R\sigma_{A,d}^2 = R\sigma_{A,t}^2 = \sigma_A^2 \quad R\sigma_{D,d}^2 = R\sigma_{D,t}^2 = R\sigma_{D,dt}^2 = \sigma_D^2 \\ R\sigma_{T,ddt}^2 = R\sigma_{T,dt}^2 = \sigma_T^2 \quad R\sigma_{F,ddt}^2 = \sigma_F^2.$$

So that the genetic variance (13) becomes

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_T^2 + \sigma_F^2, \quad (15)$$

which is the usual expression of the intrapopulation model (KEMPTHORNE 1957).

Covariances between relatives: A calculation of kinship coefficients adapted to the 4x-2x feature has been partially proposed by BOUDEDEC (1988) and HAYNES (1990, 1992). These authors used different notations. We propose here a generalization. The formulae of covariances between relatives are altered according to the origin of the genes that are identical by descent, *i.e.*, if they come from 2x or from 4x or from both. For example, the half-sib covariance, cov (HS) may differ according to whether the common related individual comes from 2x or 4x. Since the two populations are disjunctive, there is no particular reason that $\text{cov}(\text{HS})_d = \text{cov}(\text{HS})_t$.

Given (Y, Y') , two 4x-2x individuals, and using the R model, the covariance $\text{cov}(Y, Y')$ can be calculated first at the additive level

$$\text{cov}(Y, Y')_{Ad} = \text{cov}(R Y_{ijkl}^{ddt} R Y'_{i'j'k'l'}) \\ = \text{cov}((R\alpha_i^d + R\alpha_j^d + R\alpha_k^t + R\alpha_l^t), \\ (R\alpha_{i'}^d + R\alpha_{j'}^d + R\alpha_{k'}^t + R\alpha_{l'}^t)) = 4E(R\alpha_i^d R\alpha_{i'}^d) \\ + 4E(R\alpha_k^t R\alpha_{k'}^t) + 4E(R\alpha_i^d R\alpha_{k'}^t) \\ + 4E(R\alpha_k^t R\alpha_{i'}^d). \quad (16)$$

It is easy to see that i and k' , also k and i' are two completely independent alleles because they come from two different populations. So, $4E(R\alpha_i^d R\alpha_{k'}^t) = 0$ and, similarly, $4E(R\alpha_k^t R\alpha_{i'}^d) = 0$. Consequently, if φ_1^d is the probability of drawing two identical alleles by descent, one among Y , the other among Y' , knowing they both come from 2x (and φ_1^t if they both come from 4x), $\text{cov}(Y, Y')$ at the additive level becomes

$$\text{cov}(Y, Y')_{Ad} = 4\varphi_1^d E(R\alpha_i^d)^2 + 4\varphi_1^t E(R\alpha_k^t)^2 \\ = \varphi_1^d R\sigma_{A,d}^2 + \varphi_1^t R\sigma_{A,t}^2. \quad (17)$$

These two φ probabilities are conditional on the knowledge of the origin of alleles and are related to their specific variance terms. They are independent and, therefore, easy to calculate. Using the same method at the digenic level, one finally obtains

$$\text{cov}(Y, Y')_{Dom} = \varphi_2^d E(R\beta_{ij}^{dd})^2 \\ + \varphi_2^t E(R\beta_{kl}^{tt})^2 + 16\varphi_1^d \varphi_1^t E(R\beta_{ik}^{dt})^2, \quad (18)$$

where φ_2^d and φ_2^t are the probabilities of drawing among Y and Y' a pair of alleles identical by descent arising either from 2x or 4x. Then, expressed with the variances of the model, $\text{cov}(Y, Y')$ equals for the digenic level

$$\text{cov}(Y, Y')_{Dom} \\ = 1/6[\varphi_2^d R\sigma_{D,d}^2 + \varphi_2^t R\sigma_{D,t}^2] + 8/3 \varphi_1^d \varphi_1^t R\sigma_{D,dt}^2. \quad (19)$$

Similarly, $\text{cov}(Y, Y')$ could be formulated for $R\sigma_T^2$ and $R\sigma_F^2$. To sum up,

$$\text{cov}(Y, Y') = \varphi_1^d R\sigma_{A,d}^2 + \varphi_1^t R\sigma_{A,t}^2 + 1/6 \varphi_2^d R\sigma_{D,d}^2 \\ + 1/6 \varphi_2^t R\sigma_{D,t}^2 + 8/3 \varphi_1^d \varphi_1^t R\sigma_{D,dt}^2 + \varphi_2^d \varphi_1^t R\sigma_T^2 \\ + \varphi_1^d \varphi_2^t R\sigma_T^2 + \varphi_2^d \varphi_2^t R\sigma_F^2. \quad (20)$$

The φ_1^t and φ_2^t coefficients for usual tetraploids (not related and not inbred) are the probabilities of drawing by descent two identical alleles and two identical pairs of alleles, respectively, from Y and Y' (two 4x-2x individuals) knowing that the alleles come from the tetraploid pool, that is to say, that they are drawn from among the (kl) alleles. Thus, when Y and Y' come from the same tetraploid progenitor $\varphi_1^t = 1/4$ and $\varphi_2^t = 1/6$.

The φ_1^d and φ_2^d coefficients are analogous probabilities corresponding to the φ_1^t and φ_2^t coefficients but for probabilities associated with alleles from the diploid pool. When Y and Y' have a common diploid progenitor, φ_1^d does not depend on the type of the 2n gamete the alleles come from, whether ij , ii or jj . That probability equals $1/2$. φ_2^d is the probability that (ij) equals ($i'j'$) knowing that i differs from j among Y , and that i' differs from j' among Y' . If the diploid progenitor is FDR, this means that no crossing over occurred between the centromere and the considered locus, neither among Y nor among Y' . On the other hand, if the 2n gamete was a SDR one, this means that two crossing overs make the gamete heterozygous for the locus both among Y and Y' . Therefore φ_2^d equals 1. The values of φ_2^d and φ_1^d are 0 in other cases. According to (20), half-sib (HS) and full-sib (FS) covariances can be written as follows:

$$\text{cov (HS)}_t = 1/4 R\sigma_{A,t}^2 + 1/36 R\sigma_{D,t}^2, \quad (21)$$

$$\text{cov (HS)}_d = 1/2 R\sigma_{A,d}^2 + 1/6 R\sigma_{D,d}^2, \quad (22)$$

$$\begin{aligned} \text{cov (FS)}_{dt} &= 1/2 R\sigma_{A,d}^2 + 1/4 R\sigma_{A,t}^2 + 1/6 R\sigma_{D,d}^2 + 1/36 R\sigma_{D,t}^2 \\ &+ 1/3 R\sigma_{D,dt}^2 + 1/4 R\sigma_{T,ddt}^2 + 1/12 R\sigma_{T,du}^2 + 1/6 R\sigma_{F,ddu}^2. \end{aligned} \quad (23)$$

APPLICATION TO A RECURRENT SELECTION SCHEME

We can now consider a recurrent selection scheme for improving diploids (or tetraploids) for their 4x-2x combining ability. The 4x-2x value of a diploid (or a tetraploid progenitor) is the averaged value of its 4x-2x progenies when it is intercrossed with a tetraploid tester (or a diploid tester). This mean value is a test value. It can be used to evaluate the genetic advance realized in a recurrent selection scheme.

For the tetraploid pool, there is no difference relative to a classical recurrent scheme. To improve their ability to give good 4x-2x offspring, one only has to intercross the best tetraploid progenitors of 4x-2x hybrids. The new tetraploids will inherit one-half of the additive value and $1/6$ of the dominance value of their parents.

For diploids, the situation may be different from the classical theory. Given a diploid parent being (ij) at a locus, then its 4x-2x test value ${}_R T(ij)$ can be written as follows using the R model.

$$\begin{aligned} {}_R T(i,j) &= {}_R Y_{ij\dots}^{ddt} - {}_R \mu \\ &= E_{kl}({}_R \mu + R\alpha_i^d + R\alpha_j^d + R\alpha_k^t + R\alpha_l^t + \dots), \\ {}_R T(i,j) &= {}_R \mu + R\alpha_i^d + R\alpha_j^d + R\beta_{ij}^{dd}. \end{aligned} \quad (24)$$

The genetic variance of these values is equal to ${}_R \sigma_{G,d}^2$, which is given also by (13)

$${}_R \sigma_{G,d}^2 = 1/2 R\sigma_{A,d}^2 + 1/6 R\sigma_{D,d}^2. \quad (25)$$

As both components of this variance depend on the value of the probability π , large differences exist therefore in the test value between the FDR and the SDR features. For FDR, π is close to 1. Then ${}_R \mu$ is close to μ , the mean of the general model [see (4) and (5)], and a large amount of dominance is transmitted by the 2n gamete. On the other hand, as the SDR feature is very close to $\pi = 0$, ${}_R \sigma_{G,d}^2$ is then almost completely additive and ${}_R \mu$ is greatly altered through inbreeding brought in by $E(\beta_{ii}^{dd})$ [see (6)].

If one assumes that π remains constant over generations, then a diploid progenitor transmits one-half of the 4x-2x additive value, i.e., $1/2 (R\alpha_i^d + R\alpha_j^d)$, to its diploid offspring but not one-half of its own 4x-2x test value, that is to say, one-half of ${}_R T(ij)$. Indeed it does not transmit one-half of ${}_R \beta_{ij}^{dd}$ at the diploid level except if $\pi = 0$. When intercrossing the best diploids, new diploids appear whose 4x-2x value cannot be directly related to the 4x-2x value of their diploid parents when there are interactions between alleles, i.e., dominance. Then, the genetic advance is explained by the parent-offspring covariance that is $1/4 R\sigma_{A,d}^2$.

Ignoring the consequences of the meiosis pattern, the test value T will be considered as an additive value, and then it is assumed that the progeny receives one-half of this value. Then, the parent-offspring covariance for the test value will be $1/2 R\sigma_{G,d}^2 = 1/2 (1/2 R\sigma_{A,d}^2 + 1/6 R\sigma_{D,d}^2)$ instead of $1/4 R\sigma_{A,d}^2$. Consequently, the genetic advance (ΔG) in 4x-2x value among diploid offsprings will be overestimated compared to the real potential advance:

$$\begin{aligned} \frac{\Delta G \text{ Potential}}{\Delta G \text{ Predicted}} &= \frac{1/4 R\sigma_{A,d}^2}{1/2 R\sigma_{G,d}^2} \\ &= \frac{1/4 R\sigma_{A,d}^2}{1/4 R\sigma_{A,d}^2 + 1/12 R\sigma_{D,d}^2} \leq 1. \end{aligned} \quad (26)$$

This overestimation of the genetic advance could be large if $\pi \neq 0$ and if ${}_R \sigma_{D,d}^2$ is high relative to ${}_R \sigma_{A,d}^2$.

ESTIMATION OF THE GENETIC PARAMETERS

The latter considerations stress the need for an estimate of ${}_R \sigma_{D,d}^2$ and ${}_R \sigma_{A,d}^2$. It is, unfortunately, not easily obtained using the usual crossing designs. To this end, a special design is proposed here that could also be very efficient in a recurrent selection scheme.

A population of FS diploid families is crossed with a tetraploid tester (Figure 1). The tested unit is the whole 4x-2x family from a diploid individual coming from one of the FS diploid families. The unit value is the mean of the family. The total genetic variance of diploid individuals for their test value is given by Expression (25).

The variance between FS families is given by the within-family covariance. Using (20) and taking into

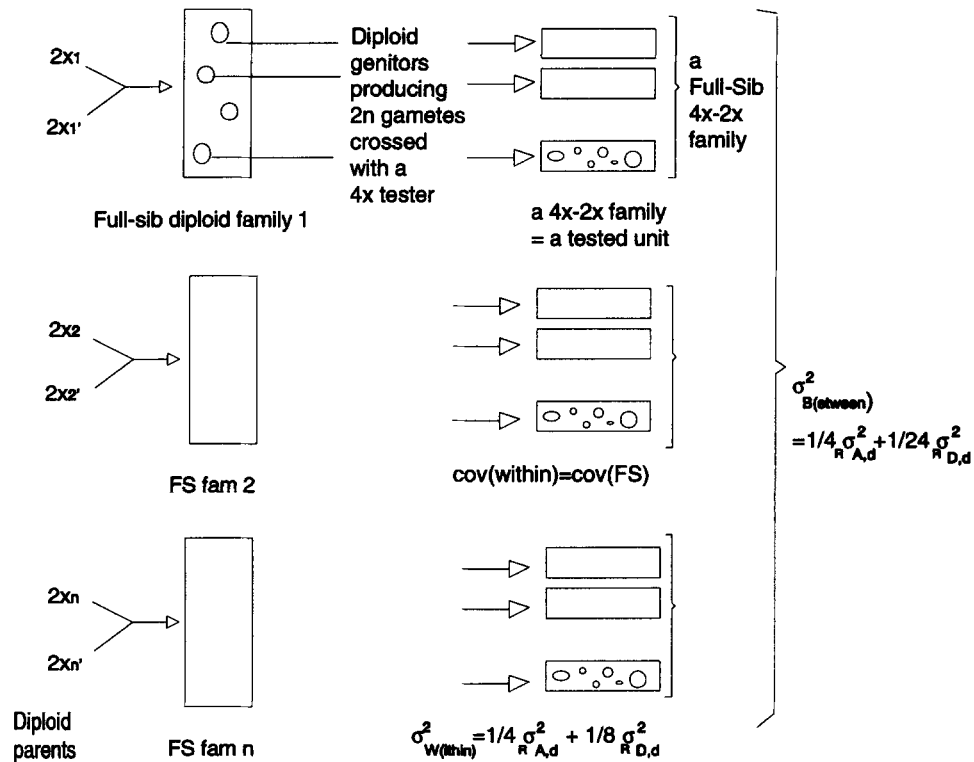


FIGURE 1.—Crossing design using full-sib diploid families in 4x–2x hybrid studies. Diploid progenitors are crossed and give full-sib families of diploid genitors able to produce diploid gametes. Each diploid genitor is crossed with a 4x tester and gives a 4x–2x family, which represents an elementary tested unit. These 4x–2x families are grouped according to the family of their diploid genitor. Two variances could be estimated with this design, σ^2_{within} , which quantifies the mean variation among 4x–2x families of a given diploid full-sib family, and $\sigma^2_{\text{between}}$, which gives the amount of variance at the 4x level between these diploid full-sib families.

account that the gene pool from the tester is the same for each FS family and consequently that all components involving genes from the tester are zero (GALLAIS 1989), we obtain for the additive and dominance variance terms only

$$\text{cov}(Y, Y') = \varphi_1^d R \sigma_{A,d}^2 + \frac{1}{6} \varphi_2^d R \sigma_{D,d}^2. \quad (27)$$

φ_1^d is the probability of drawing out two identical alleles from two different tested units knowing that they both come from the same diploid progenitor.

Since the two units are full-sibs from two nonrelated parents (*ij*) and (*kl*), $\varphi_1^d = \frac{1}{4}$. In the same way, $\varphi_2^d = \frac{1}{4}$. Thus,

$$\begin{aligned} \text{var}(\text{between FS}) &= \sigma_B^2 = \text{cov}(\text{within FS}) \\ &= \frac{1}{4} R \sigma_{A,d}^2 + \frac{1}{24} R \sigma_{D,d}^2. \end{aligned} \quad (28)$$

Subtracting it from the total genetic variance, the following is obtained:

$$\text{var}(\text{within FS}) = \sigma_W^2 = \frac{1}{4} R \sigma_{A,d}^2 + \frac{1}{8} R \sigma_{D,d}^2. \quad (29)$$

By relating (28) and (29) with the variance analysis for the experimental design (Figure 1), the following is obtained

$$\text{FS Family effect } \sigma_B^2 = \frac{1}{4} R \sigma_{A,d}^2 + \frac{1}{24} R \sigma_{D,d}^2, \quad (30)$$

Family unit within FS family effect

$$\sigma_W^2 = \frac{1}{4} R \sigma_{A,d}^2 + \frac{1}{8} R \sigma_{D,d}^2. \quad (31)$$

This way, estimates are obtained for two important terms needed to predict the genetic advance on the 4x–2x value among the diploids:

$$R \sigma_{A,d}^2 = 6 \sigma_B^2 - 2 \sigma_W^2, \quad (32)$$

$$R \sigma_{D,d}^2 = 12 [\sigma_W^2 - \sigma_B^2]. \quad (33)$$

DISCUSSION

The concepts of varietal ability and test value permitted us to simplify the complex expression of the genetic value of 4x–2x inbred individuals. The model provides a way to compare various selection schemes for the integration of diploid germplasm in tetraploid cultivars.

We particularly studied a recurrent selection scheme designed to improve the 4x–2x varietal value of the diploid pool. The best policy appears to be first the comparison of means and variances in 4x–2x test value of SDR diploids with those of FDR diploids coming from the same diploid pool. This step will require adapted crossing designs like those shown in Figure 1. The genetic advance could then be calculated for SDR and FDR. The choice could be discussed according to their respective advantages and failings and according to short- and long-term objectives.

With FDR diploids and with simple recurrent selection schemes, the improvement of the 4x-2x value among diploids could be inefficient if the dominance variance due to diploids ($R\sigma_{D,d}^2$) is large for the main selected traits. The breeding value of SDR diploids are based on their 4x-2x value with little bias, even if dominance plays an important role in the selected characters. In the latter case, the 4x-2x value of the diploid population can be improved by crossing the best diploids revealed by simple 4x-2x progeny tests.

Furthermore, it is expected that homozygosity reveals more variation than does heterozygosity. So, the genetic variance between 4x-2x clones could be greater within the 4x-2x progenies of SDR diploids than within FDR progenies. This variability could be exploited and the efficiency of clonal selection increased.

For these reasons and if inbreeding depression does not excessively alter the mean of the 4x-2x progenies, the genetic advance could be larger and predicted better using the SDR mechanism in such a recurrent selection scheme. In any case, if the inbreeding depression induced by the SDR gametes is too strong to allow their use in breeding, the breeder has to elaborate adapted schemes for FDR diploids. If the dominance variance due to the diploids can be neglected for main breeding traits, a simple intercross of the best diploids is all that is necessary because of its simplicity and efficiency. If dominance effects are found to be strong, two diploid pools could be used in a "reciprocal" recurrent selection pattern, which is a particular case of a three-way cross recurrent selection as proposed by GALLAIS (1991). Two diploid progenitors, one from each pool, will be crossed and give birth to FDR full-sib family, which will be tested for its 4x-2x value. Then, according to the results, within each pool, the diploid parents of the best FDR full-sib family will be selected and intercrossed to found the two new pools. Consequently, the 4x-2x test value of the offspring from the cross of diploid progenitors from the two different pools should increase with the maximum use of the variance of interactions among alleles. Unfortunately, this selection may be difficult to manage.

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APPENDIX

Demonstration that $E(\gamma_{ik}^{ddt}) = 0$.

$$\gamma_{ik}^{ddt} = Y_{ik} - \mu - 2\alpha_i^d - \alpha_k^t - \beta_{ii}^{dd} - 2\beta_{ik}^{dt},$$

where $Y_{ik} = \sum_l p_l Y_{ikl}$, and p_l is the frequency the l allele, and

$$\begin{aligned} E(\gamma_{ik}^{ddt}) &= E(Y_{ik}) - \mu - E(\beta_{ii}^{dd}) \\ &= E(E(Y_{ik})) - \mu - E(\beta_{ii}^{dd}) \\ &= E(Y_{ii..}) - \mu - E(\beta_{ii}^{dd}) \\ &= \mu + E(\beta_{ii}^{dd}) - \mu - E(\beta_{ii}^{dd}) \\ &= 0, \end{aligned}$$

where $E(Y_{ikl}) = \sum_i \sum_k \sum_l p_i p_k p_l Y_{ikl}$.