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 PeLooquin 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 PeLooquin 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 ≤ b ≤ 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
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, BOUDEC (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 value of 4x–2x progenies from tetraploids crossed either with FDR diploids or SDR diploids with nonzero single value of 4x–2x progenies from tetraploid. The model takes into account different genetic backgrounds. Using the concept of test value defined by GALWS (1979, 1989), \( R^{Y_{ddtt}} \) can be written as

\[
R^{Y_{ddtt}} = \pi Y_{ddtt} + (1 - \pi) (Y_{ddtt} + Y_{ddtt}) / 2. \tag{2}
\]

Then, \( \mu Y^{ddtt} \) 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), \( R^{Y_{ddtt}} \) can be written as

\[
rY_{ddtt} = \mu R^{Y_{ddtt}} + \mu \alpha_i^d + \mu \alpha_j^d + \mu \alpha_k^d + \mu \alpha_l^d + \mu \beta_{ij}^d + \mu \beta_{kl}^d + \mu \gamma_{ijkl}^d + \mu \delta_{ijkl}^d, \tag{3}
\]

with

\[
E(\mu \alpha_i^d) = E(\mu \alpha_j^d) = E(\mu \alpha_k^d) = E(\mu \beta_{ij}^d) = E(\mu \beta_{kl}^d) = E(\mu \gamma_{ijkl}^d) = E(\mu \gamma_{ijkl}^d) = 0, \text{ and } E(\mu \delta_{ijkl}^d) = 0.
\]

The different \( \alpha, \beta, \gamma, \) and \( \delta \) effects are defined analogously to those defined by KEMPTHORNE (1957): \( \alpha \) is the additive effect of each allele, \( \beta \) is the digenic interaction effect, \( \gamma \) is the trigeneric interaction effect, and \( \delta \) is tetrageneric 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 \( a \) or \( b \) 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 (\( d \)) (\( d \)) or (\( d \)) 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 \( \text{per se} \) value. According to Expression (2) we have to consider the expression required for \( Y_{ddtt} \) and \( Y_{ddtt} \) (KEMPTHORNE 1957).

If \( i \) and \( j \) are not identical by descent, \( Y_{ddtt} = \mu + \alpha_i^d + \alpha_j^d + \alpha_k^d + \alpha_l^d + \beta_{ij}^d + \beta_{ik}^d + \beta_{lj}^d + \beta_{lk}^d + \gamma_{ijkl}\) and \( \delta_{ijkl}^d \).
\[ \pi is the probability that the two alleles from the 2n gamete are nonidentical by descent knowing that the diploid genitor is itself noninbred.\]

\[ Y^{dd}_{iik} = \mu + 2\alpha_i^d + \alpha_i + \alpha_i^d + \beta_{i1} + \beta_{i2}^d + \gamma_{i2} + 2\beta_{i2} + 2\beta_{i1} + \gamma_{i2} + \gamma_{i2}^d + 2\gamma_{i2}^d + \delta_{i2}^dd + \delta_{i2}^dd. \]  

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

\[ E(\beta_{i1}^d) \] measures the mean inbreeding depression effect introduced by the homozygosity of the 2n gamete. The expectations of other inbred terms, \( E(\gamma_{i2}^{dd}) \) and \( E(\delta_{i2}^{dd}) \) equal 0 as demonstrated in the APPENDIX for \( E(\gamma_{i2}^{dd}) \).

\[ \text{Expression of the genetic variance: All } R \text{ terms are independent and thus the variance of the model can be easily formulated as follows:} \]

\[ \sigma_{\beta_{i1}^d}^2 = \var(\mu Y^{dd}_{iik}) = 2E(\mu \alpha_i^d) \]

\[ + 2E((\mu \alpha_i^d)^2) + E(\mu \beta_{i1}^d) + E(\mu \beta_{i1}^d)^2 \]

\[ + 4E(\mu \beta_{i1}^d)^2 + 2E(\mu \gamma_{i2}^{dd}) \]

\[ + 2E(\mu \gamma_{i2}^{dd})^2 + E(\mu \delta_{i2}^{dd})^2. \] 

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

\[ \sigma_{\beta_{i1}^d}^2 = 4E(\mu \alpha_i^d)^2, \]  

additive variance originating from 2x. (8)

\[ \sigma_{\beta_{i1}^d}^4 = 4E(\mu \alpha_i^d)^2, \]  

additive variance originating from 4x. (9)

The digenic term splits up into three parts:

\[ \sigma_{\beta_{i1}^d}^2 = 6E(\mu \beta_{i1}^d)^2 \] from 2x only. (10)

\[ \sigma_{\beta_{i1}^d}^4 = 6E(\mu \beta_{i1}^d)^2 \] from 4x only. (11)

\[ \sigma_{\beta_{i1}^d}^2 = 6E(\mu \beta_{i1}^d)^2 \] from the interaction between 2x and 4x. (12)

For the trigenic variance, \( \sigma_{\beta_{i1}^d}^2 \) is obtained from the interaction between two alleles coming from 2x and one allele coming from 4x, and \( \sigma_{\beta_{i1}^d}^2 \) from the reciprocal situation.
The tetragenic variance is given with \( \mu_2^2 = E(\delta_{2,dt})^2 \) only. To sum up, the total genetic variance is given by

\[
\sigma^2 = \frac{1}{2} \mu_2 \sigma_{\lambda,d}^2 + \frac{1}{2} \mu_2 \sigma_{\lambda,d}^2 + \frac{1}{2} \mu_2 \sigma_{\lambda,d}^2 + \frac{1}{2} \mu_2 \sigma_{\lambda,d}^2,
\]

(13)

where \( \sigma^2_{\lambda,d} \) is the genetic variance due to genes from the 2x, \( \sigma^2_{\lambda,d} \) that one due to genes from the 4x and \( \sigma^2_{\lambda,d} \) that 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 \( E(\delta_{2,dt})^2 \) includes \( E(\delta_{2,dt})^2 \) and \( E(\delta_{4,dt})^2 \); \( E(\sigma_{\lambda,d}^2) \) includes \( E(\sigma_{\lambda,d}^2) \) and \( E(\sigma_{\lambda,d}^2) \); and finally, \( E(\gamma_{2,dt})^2 \) includes \( E(\gamma_{2,dt})^2 \) and \( E(\gamma_{4,dt})^2 \). In the digenic case for which only monogenic and digenic effects are used, the \( R \) model saves three parameters, \( \mu_2 \), five instead of eight, knowing that the \( R \) model partly describes trigenic effects through \( \gamma_{2,dt} \).

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 variation among offsprings of heterozygous genitors, so finally, the contribution of the diploid genitors where the expressions of variances and covariances to an arbitrary inbreeding effects introduced by the homozygosity of correlated. Usually, inbreeding increases the genetic effects are used, the \( R \) model saves three parameters, \( \mu_2 \), five instead of eight, knowing that the \( R \) model partly describes trigenic effects through \( \gamma_{2,dt} \).

Covariances between relatives: A calculation of kinship coefficients adapted to the 4x–2x feature has been partially proposed by Boudec (1988) and Haines (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, \( \text{cov} \) (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 \( \text{cov} \) (HS) = \( \text{cov} \) (HS). 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

\[
\text{cov} \ (Y, Y')_{\lambda d} = \text{cov} \ (\mu_2^2 Y_{2,dt}', H_{1,dt}')
\]

\[
\times \text{cov} \ (H_{1,dt}', \mu_2^2 Y_{2,dt}')
\]

\[
= \text{cov} \ (\mu_2^2 \alpha_1^2 + \mu_2^2 \alpha_2^2 + \mu_2^2 \alpha_1^2 + \mu_2^2 \alpha_2^2)
\]

\[
= 4\text{cov} \ (\mu_2^2 \alpha_1^2 + \mu_2^2 \alpha_2^2) + 4\text{cov} \ (\mu_2^2 \alpha_1^2 + \mu_2^2 \alpha_2^2)
\]

\[
+ 4\text{cov} \ (\mu_2^2 \alpha_1^2 + \mu_2^2 \alpha_2^2).
\]

(16)

It is easy to see that \( i \) and \( k' \), also \( k \) and \( k' \) are two completely independent alleles because they come from two different populations. So, \( 4\text{cov} \ (\mu_2^2 \alpha_1^2) = 0 \) and, similarly, \( 4\text{cov} \ (\mu_2^2 \alpha_1^2) = 0 \). Consequently, if \( \phi^2 \) is the probability of drawing two identical alleles by descent, one among \( Y \), the other among \( Y' \), knowing they both come from 2x (and \( \phi^2 \) if they both come from 4x), \( \text{cov} \ (Y, Y') \) at the additive level becomes

\[
\text{cov} \ (Y, Y')_{\lambda d} = 4\phi^2 \text{cov} \ (\mu_2^2 \alpha_1^2) + 4\phi^2 \text{cov} \ (\mu_2^2 \alpha_2^2)
\]

\[
= \phi^2 \mu_2^2 \sigma_{\lambda,d}^2 + \phi^2 \mu_2^2 \sigma_{\lambda,d}^2.
\]

(17)

These two \( \phi \) 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

\[
\text{cov} \ (Y, Y')_{\text{dom}} = \phi^2 \text{cov} \ (\mu_2^2 \beta_{1,dt}^2)
\]

\[
+ \phi^2 \text{cov} \ (\mu_2^2 \beta_{1,dt}^2) + 10\phi^2 \text{cov} \ (\mu_2^2 \beta_{1,dt}^2),
\]

(18)

where \( \phi^2 \) and \( \phi^2 \) 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

\[
\text{cov} \ (Y, Y')_{\text{dom}} = \phi^2 \text{cov} \ (\mu_2^2 \beta_{1,dt}^2)
\]

\[
+ \phi^2 \text{cov} \ (\mu_2^2 \beta_{1,dt}^2) + 10\phi^2 \text{cov} \ (\mu_2^2 \beta_{1,dt}^2),
\]

(19)

Similarly, \( \text{cov} \ (Y, Y') \) could be formulated for \( \mu_2 \) and \( \mu_2 \). To sum up,

\[
\text{cov} \ (Y, Y') = \phi^2 \text{cov} \ (\mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d})
\]

\[
+ \phi^2 \text{cov} \ (\mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d})
\]

\[
+ \phi^2 \text{cov} \ (\mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d} + \mu_2 \sigma^2_{\lambda,d}).
\]

(20)
The $\phi_1$ and $\phi_2$ 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 corresponding to the $\pi$ and $\sigma_{G,a}$ from, whether the value. It can be used to evaluate the genetic advance of loci, then its $4x-2x$ test value as follows using the $\pi$ and $\sigma_{G,a}$.

Therefore

$$\text{cov} (\text{HS})_t = \frac{1}{4} \text{RT}(\text{i},\text{j}) + \frac{1}{56} \text{RT}(\text{d},\text{i}),$$

$$\text{cov} (\text{HS})_d = \frac{1}{2} \text{RT}(\text{a},\text{d}) + \frac{1}{56} \text{RT}(\text{d},\text{d}),$$

$$\text{cov} (\text{FS})_d = \frac{1}{2} \text{RT}(\text{i},\text{d}) + \frac{1}{56} \text{RT}(\text{d},\text{d}) + \frac{1}{12} \text{RT}(\text{d},\text{d}) + \frac{1}{56} \text{RT}(\text{d},\text{d}).$$

**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 $\text{(i)j}$ at a locus, then its $4x-2x$ test value $\text{RT}(\text{i},\text{j})$ can be written as follows using the $\pi$ model.

$$\text{RT}(\text{i},\text{j}) = \text{RT}(\text{i},\text{j}) - \mu \text{d} = E \text{(RT}(\mu + \mu \text{p}) + \mu \text{p}^2 + \mu \text{p}^3 + \ldots),$$

$$\text{RT}(\text{i},\text{j}) = \mu \text{d} + \mu \text{p}^2 + \mu \text{p}^3 + \mu \text{p}^4 + \ldots.$$ (24)

The genetic variance of these values is equal to $\pi \sigma_{G,a}$, which is given also by (13)

$$\pi \sigma_{G,a} = \frac{1}{2} \mu \text{d} + \frac{1}{6} \mu \text{p}^2.$$ (25)

As both components of this variance depend on the value of the probability $\pi$, large differences exist therefore in the test value between the FDR and the SDR features. For FDR, $\pi$ is close to 1. Then $\mu \text{d}$ is close to $\mu$, 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 $\pi = 0$, $\sigma_{G,a}$ is then almost completely additive and $\mu \text{d}$ is greatly altered through inbreeding brought in by $E(\beta_{ij}^2)$ [see (6)].

If one assumes that $\pi$ remains constant over generations, then a diploid progenitor transmits one-half of the $4x-2x$ additive value, i.e., $\frac{1}{2} (\mu \text{d} + \mu \text{p}^2)$, to its diploid offspring but not one-half of its own $4x-2x$ test value, that is to say, one-half of $\text{RT}(\text{i},\text{j})$. Indeed it does not transmit one-half of $\beta_{ij}^2$ at the diploid level except when $\pi = 0$. 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 $\frac{1}{4} \pi \sigma_{G,a}^2$.

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 $\frac{1}{2} \pi \sigma_{G,a}^2 = \frac{1}{2} \frac{1}{4} \frac{1}{2} \frac{1}{6} \mu \text{d} + \frac{1}{2} \frac{1}{6} \mu \text{p}^2$ instead of $\frac{1}{2} \pi \sigma_{G,a}^2$. Consequently, the genetic advance ($\Delta G$) in $4x-2x$ value among diploid offsprings will be overestimated compared to the real potential advance:

$$\Delta G \text{ Potential} = \frac{\frac{1}{4} \pi \sigma_{G,a}^2}{\frac{1}{2} \pi \sigma_{G,a}^2} = \frac{\frac{1}{4} \pi \sigma_{G,a}^2}{\frac{1}{2} \pi \sigma_{G,a}^2} + \frac{1}{2} \frac{1}{6} \mu \text{p}^2 \leq 1.$$

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

**ESTIMATATION OF THE GENETIC PARAMETERS**

The latter considerations stress the need for an estimate of $\pi \sigma_{G,a}^2$ and $\pi \sigma_{G,a}^2$. 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
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

\[ \text{cov}(Y, Y') = \phi^d_{A,d} \sigma^2_{A,d} + \phi^d_{D,d} \sigma^2_{D,d}. \]

(27)

\( \phi^i \) 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 \((kl)\), \( \phi^i = 1/4 \). In the same way, \( \phi^d = 1/4 \). Thus,

\[ \text{var (between FS)} = \sigma^2_W = \text{cov (within FS)} \]

\[ = \frac{1}{4_4} \sigma^2_{A,d} + \frac{1}{2_4} \sigma^2_{D,d}. \]

(28)

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

\[ \text{var (within FS)} = \sigma^2_W = \frac{1}{4_4} \sigma^2_{A,d} + \frac{1}{2_4} \sigma^2_{D,d}. \]

(29)

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

FS Family effect \( \sigma^2_F = \frac{1}{4_4} \sigma^2_{A,d} + \frac{1}{2_4} \sigma^2_{D,d}. \)

(30)

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 ($\sigma_{d,d}^2$) 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 progeny, 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 actions among alleles. Unfortunately, this selection may be difficult to manage.

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**APPENDIX**

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

$\gamma_{ik}^{dd} = Y_{ik} - \mu - 2 \alpha_i - \beta_1^d - 2 \beta_2^d$, where $Y_{ik} = \sum_1^p Y_{i,dk}$, and $p_i$ is the frequency of the $l$ allele, and

$E(\gamma_{ik}^{dd}) = E(Y_{ik}) - \mu - E(\beta_1^d) - 2 \beta_2^d$

$= E(E(Y_{ik})) - \mu - E(\beta_1^d)$

$= E(Y_{ik}) - \mu - E(\beta_1^d)$

$= \mu + E(\beta_1^d) - \mu - E(\beta_1^d)$

$= 0$,

where $E(Y_{ik}) = \sum_1^p \sum_1^{N_p} p_i p_k Y_{i,dk}$.