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THE POTENTIAL OF MEIOTIC POLYPLOIDIZATION IN BREEDING ALLOGAMOUS CROPS

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ABSTRACT. Meiotic and mitotic polyploidization are compared as to frequency of occurrence in nature and potential for breeding allogamous crops. Meiotic polyploidization via diploid first-division-restitution-gametes is the more powerful approach and can be applied either unilaterally or bilaterally. It is explained how 2n-gametes can be traced by (1) seeking for polyploid plants in diploid populations followed by 4x-2x matings; (2) using colchicine-doubled genotypes in 4x-2x matings; (3) visual discrimination of stained 2n- and n-pollen in diploid plants; (4) establishing the frequency of dyad formation in diploid plants; and (5) large-scale reciprocal crosses between diploids and tetraploids.

Basically all mechanisms leading to FDR gametes can be utilized for breeding through sexual polyploidization, because of the largely intact transfer of the parental genotype to the progeny via such gametes. FDR-genotypes mostly produce both 2n- and n-gametes in various proportions. The common occurrence of lethality of triploid zygotes ("triploid block") is explained and its significance discussed.

Sexual polyploidization is a desirable breeding technique in those crops which at the polyploid level have a better potential performance than at the diploid level. Examples are given. Such better performance of polyploids is based on the larger potential of non-additive gene effects owing to multi-allelism. The highest degree of multi-allelism is obtained with unrelated highly heterozygous parents, the diploid parents producing FDR gametes.

Experimental results are discussed which illustrate the great potential of sexual polyploidization, but at the same time reveal the need of divergent FDR-genotypes with high economic value including resistance to the most important diseases and with a stable mechanism for high-frequency production of 2n (FDR) gametes. An adequate breeding program at the diploid level aimed at breeding such FDR-genotypes is advocated.

Index Descriptors: sexual polyploidization, breeding, 2n-gametes, autopolyploids, ornamentals, maize, and combining ability.

INTRODUCTION

Sexual (Mendiburu and Peloquin, 1977a) or meiotic polyploidization (Skiebe, 1958) is the origin of a polyploid through the fusion of two gametes, one or both of which have the somatic number (= 2n) of chromosomes due to abnormal meiosis. Sexual polyploidization is unilateral or bilateral, when one or both gametes, respectively, contribute the somatic chromosome number. Previously, it was explained that 2n-first-division-restitution-gametes of a plant may transfer up to 100% of the parental heterozygosity and epistatic interactions to the progeny and because of their approximate or complete genetic identity may greatly contribute to the uniformity of that progeny as well. In the ideal situation—100% preservation of the parental genotype in both male and female gametes—the products of bilateral sexual polyploidization are equal to those obtained by somatic hybridization.

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Somatic or mitotic polyploidization arises from inactivation of the spindles during mitotic divisions, each chromosome thus getting an identical partner. Such identical chromosome doubling is a sudden and drastic change of the ideotype of a plant. When applied to diploid outbreeding crops, it may lead to decreased vigor and fertility owing to disturbed meiosis, increased homozygosity, imbalance between genome and plasmon, change of intra- and inter-locus interactions, and of gene dosages. Breeders have to rely upon mitotic doubling when plants are completely sterile owing to nonhomology of their chromosomes, e.g., in F_1 hybrids of remote species and in (amphi)monoploids.

The number of known successful polyploids, that have arisen in nature through mitotic doubling, is small. Yet nature has produced numerous excellent polyploids. In their monograph on colchicine, Eigsti and Dustin (1955) suggested that nearly all natural polyploids originated from unreduced gametes. Systematic investigations on polyploidization in nature have been carried out by several researchers, most comprehensively by Harlan and de Wet (1975). Their experimental results supported the view of Eigsti and Dustin (1955). It was demonstrated that 2n-gametes may occur in every species or ecotype in nature as well as in all kinds of breeding lines and populations. The frequency of 2n-gametes as a rule is extremely low but may vary greatly between genotypes and environments. In the present article, various ways of exploiting 2n-gametes will be indicated. In addition, experimental results will be presented that demonstrate the great potential of meiotic polyploidization for breeding both natural and induced polyploid crops.

HUNTING FOR 2n-GAMETES

Breeders of diploid allogamous crops of which no tetraploid plants or tetraploid related species are available may wish to breed autotetraploid varieties. Sexual polyploidization is to be preferred to mitotic doubling, as explained in the introduction. Following the advice "those who seek find," diploid populations can be grown and screened for the occurrence of polyploids. It is known from numerous reports in the literature that polyploids occur, albeit in low frequencies, in species of various plant families. A few examples are mentioned for illustration: Bauman (cited in Alexander and Beckett, 1963) found 0.06-0.52% triploids in seven single-cross hybrids in maize (*Zea mays*). Morinaga and Fukushima (1934/35) discovered 150 triploids in a field of rice (*Oryza sativa*); Stomps (1912) detected 11 triploids among an unknown number of *Oenothera* seedlings; Einset (1952) reported 17 triploids among 6825 apple (*Malus pumila*) seedlings from a diploid x diploid cross and upon open pollination of these triploids, 148 tetraploids occurred among 5694 progeny plants; Ellerton and Hendriksen (1959) obtained 2.4% triploids in a population from male sterile diploid x normal diploid ugar beets (*Beta vulgare*) but none in a normal diploid cultivar; and Skiebe (1958) screened 8476 F_1 seedlings of diploid *Primula malacoides* and selected four tetraploids and one triploid. When only triploids are found, crosses between triploids and diploids usually produce a reasonable number of tetraploid progeny, as is shown by Einset (1952) and in many other experiments. Once a sufficient number of tetraploids has been obtained, the genetic base can be conveniently broadened by reciprocal tetraploid-diploid crosses, which may produce predominantly tetraploid progeny. This is especially true in those crops where tetraploid and pentaploid endosperms that are associated with triploid embryos from 2x.4x- and 4x.2x-matings, respectively, are defective, whereas only hexaploid endosperm, which occurs in seeds with tetraploid embryos from both 2x.4x and 4x.2x matings, is vital. This phenomenon is called "triploid block" (Marks, 1966). If it is fully effective, it prevents x-gametes from contributing to the progeny, whereas all vital seeds originate from 2x-gametes. Consequently, the number of seeds per fruit obtained from 4x-2x and 2x-4x matings reflects the frequency of 2n-gamete formation on the male and female side, respectively, in the diploid parents.

Hanneman and Peloquin (1967) were the first to apply this approach systematically in potato (*Solanum tuberosum*) for tracing diploid 2n-gamete producers. In their large-scale program, 107 diploid hybrids and 48 tetraploid cultivars were included. Table 1 summarizes their classification of diploid clones on the basis of seeds per fruit from 4x-2x and 2x-4x matings, which because of the effective triploid block in potato is a measure of the frequency of 2n-gametes produced by the diploids on the male and female sides, respectively. The results from reciprocal crosses of four typical diploids presented in Table 2 demonstrate four characteristic types of male and female 2n-gamete production: low-low, low-high, high-low, and high-high, respectively. Seeds per fruit are a good measure of 2n-gamete production capacity, if a triploid block is sufficiently effective. This is clearly demonstrated for potato in Table 3, where the ploidy level distribution is presented in the progenies from reciprocal 4x-2x matings, more than 90% of the plants being tetraploid.

The approach of Hanneman and Peloquin for detecting 2n-gamete producers is applicable to all crops with a sufficiently effective triploid block. As a matter of course, tetraploids—either natural or induced, meiotic or mitotic—should be available or made available.

Jahr et al. (1963) investigated sexual polyploidization in a number of diploid crops using as tetraploid parents varieties obtained by mitotic doubling and improved for 10-20 years. Crosses of the type diploid x tetraploid were made. Table 4 shows the resulting numbers and ploidies in the progenies obtained. The polyploids obtained were predominantly tetraploid. These tetraploids were improved until F_3 in radish (*Raphanus sativus*) and Crimson clover (*Trifolium incarnatum*) and until F_4 in camomile (*Anthemis nobilis*). Then their performance was compared with the colchicine-induced improved tetraploid

Table 1. Distribution of diploid potato hybrids based on average seed set in 4x-2x and in 2x-4x matings (Hanneman and Peloquin, 1967).

Classes of seeds/fruit	Number of diploid hybrids per class	Number of tetraploids used	Average number of seeds/fruit
Tetraploids x diploids			
<2	54	18	0.81
2-5	8	16	2.72
5-10	4	14	6.94
10-20	3	10	12.47
>20	1	11	56.32
Diploids x tetraploids			
<2	49	17	0.43
2-5	6	13	3.84
5-10	7	16	7.50
10-20	3	13	12.92
>20	0	0	0.00

Table 2. Four diploid potato hybrids with a characteristically different capacity of producing male and female 2n-gametes in terms of seeds/fruit (Hanneman and Peloquin, 1967).

	Average seeds per fruit	
Hybrids	diploid x tetraploid	tetraploid x diploid
W 5316-2	0.57 (low)	0.50 (low)
W 5337-3	1.00 (low)	10.00 (high)
W 5720-1	8.22 (high)	1.31 (low)
W 5295-7	6.80 (high)	56.32 (high)

Table 3. Ploidy level distribution in progenies from reciprocal 4x-2x matings in potato.

Type of mating	Number of 4x-2x combinations	Progeny plants (%) 2x	3x	4x	Total plants
Hanneman and Peloquin (1967)					
4x.2x	–	0.6	7.6	91.8	344
2x.4x	–	3.3	1.9	94.8	676
Jacobsen (1980)					
4x.2x	82	1.4	10.8	87.8	510
2x.4x	77	4.3	5.5	90.2	276

Table 4. Meiotic polyploids from diploid x colchicine-tetraploid matings (modified from Jahr et al., 1963): a = hand emasculation + hand pollination; b = hand emasculation + open pollination; and c = no emasculation + open pollination.

Crop (species)	Method	Pollinated flowers	Plants 3x	4x	Remarks
Chinese cabbage (*Brassica chinensis*)	a	300	0	21	–
Radish (*Raphanus sativus*)	a	600	1	8	–
Foxglove (*Digitalis*)	b	230	9	43	–
		Number females			
Camomile (*Anthemis nobilis*)	c	120	1	27	Phenotypic preselection
Red clover (*Trifolium pratense*)	c	—	11	7	Self-incompatible
Crimson clover (*Trifolium incarnatum*)	c	58	0	28	Self-incompatible
Thyme (*Thymus vulgaris*)	c	—	1	48	Gynodioecious

Table 5. Performance of mitotic and meiotic tetraploids in radish, Crimson clover, camomile (Jahr. et al., 1963), and maize (Kristov, 1980).

Origin	Generation	Marketable tubers (%)	
Raphanus sativus			
colchicine (=4x-C)	C21	66.3	
(2x.4x-C).1	F_3	83.6[a]	
(2x.4x-C).2	F_3	81.3[a]	
(2x.4x-C).3	F_3	76.1	
(2x.4x-C).4	F_3	77.1	
Trifolium incarnatum		Fresh weight (kg/ha)	
colchicine (=4x-C)	C11	24,311	
(2x.4x-C).1	F_3	26,427[a]	
(2x.4x-C).2	F_3	25,827[a]	
(2x.4x-C).3	F_3	25,110[a]	
Matricaria chamomilla		Yield dry matter (kg/ha)	
colchicine (=4x-C)	C14	867	
(2x.4x.C).1	F_4	959[a]	
(2x.4x-C).2	F_4	970[a]	
(2x.4x-C).3	F_4	986[a]	
Zea mays		Grain weight (g) per inflorescence	1000-grain weight (g)
diploid singles	F_1	248.30	426.62
colchicine (=4x-C)[b]	C_1	90.80	495.64
2x.4x[b]	F_1	307.00[a]	547.95[a]

[a] significantly higher ($P < 0.05$) than 4x-C.

[b] 4x-C derived from the diploid singles; 2x.4x = tetraploids obtained from crossing diploid inbreds and singles with tetraploid synthetic.

varieties. Table 5 summarizes the results obtained. Some comparable results from Kristov (1980) are added to this table involving diploid maize hybrids and their unimproved mitotic and meiotic tetraploid derivatives. The superiority of meiotic polyploids is evident. Unfortunately, the mechanisms of female 2n-gamete formation in the diploid varieties used was not reported by the authors.

A quick method of estimating the frequency of male 2n-gametes is based on visual size discrimination of stained 2n- and n-pollen. In potato, 2n- and n-pollen have a diameter range of 26-33μ and 18-23μ, respectively. A positive correlation between frequency of big pollen and seed set from 4x.2x-matings has been reported by Quinn et al. (1974) and Jacobsen (1980). The method is suitable for preliminary screening of large populations and has been used as such in potato (Quinn et al., 1974; Den Nijs and Peloquin, 1977; Leue and Peloquin, 1980; Jacobsen, 1980; and Veilleux and Lauer, 1981b), and in alfalfa (*Medicago sativa*) (McCoy, 1982; and Vorsa and Bingham, 1979). The method should be used only with great caution for genetic research on the ability of male 2n-gamete formation or for detecting rather small genetic differences in frequency. In genetic research of qualitative traits, classification of individuals is usually based on presence/absence of a character. As a criterion for presence of the gene for male 2n-gamete formation 5%, 4%, 3%, and even 1% big pollen has been used. However, Veilleux and Lauer (1981b), on the basis of their experiments with *Solanum phureja*, conclude that owing to large environmental variability of the percentage of big pollen in an individual or clone, a consistent classification based on such percentages is not feasible.

The occurrence of dyads in pollen mother cells is a reliable criterion for the ability to produce 2n-pollen. The technique is a little laborious (for description, see Ramanna, 1979) and can be used to trace 2n-gamete producers. However, the frequency of dyads is also subject to large variability owing to micro-environmental (within the anthers) and macro-environmental variation. Ramanna (1979) studied several *Solanum phureja* clones on different dates in 4-6 successive years and found large intra-clonal variation of percentage of dyads (e.g., 12.4-75.1% in clone IVP 10). Therefore, genetic analyses based on percentage of dyads formed should also be considered with caution. The hypothesis by Mok and Peloquin (1975a) of one recessive gene *ps* controlling male 2n-gamete production appears less realistic than the hypothesis by Veilleux and Lauer (1981b) based on an incompletely penetrating gene with a variable expressivity.

The great influence of micro- and macro-environmental conditions on the occurrence and frequency of 2n-gametes in most genotypes largely complicates genetic analysis. On the other hand, it offers a possibility of exploiting environmental variation to increase 2n-gamete frequencies or even to induce 2n-gamete formation. This is particularly important to get a program of sexual polyploidization started in diploid crops lacking tetraploid relatives.

Summarizing this section, it may be concluded that several methods are available to trace or to induce polyploids produced through 2n-gametes, to trace diploid plants with the capacity to produce 2n-gametes, and to select genotypes with a relatively stable high-level production of 2n-gametes.

SEXUAL POLYPLOIDIZATION AND BREEDING

The most desirable mechanisms for sexual polyploidization

For exploiting sexual polyploidization in plant breeding, the breeder must be able to manipulate the capacity of producing 2n-gametes like any other desirable character. He has to have a good knowledge of its inheritance, of its stability under different environments, and of the exact mechanism involved. A few remarks about the most desirable mechanism for practical breeding should be added here. In principle, all FDR-mechanisms can be utilized in breeding. As explained before, all functional gametes are FDR-2n-gametes in those diploids where desynapsis occurs in all spore mother cells and desynapsis + nuclear restitution occurs in a sufficient number of them to warrant a workable level of fertility. The advantages of such diploids for polyploid breeding are obvious. No triploid block is needed, and only tetraploid progeny arise from 4x.2x crosses, from selfing the diploid, and from 2x.2x crosses, if the mechanism is functional in both sexes. Furthermore, a largely intact transfer of the parental genotype to the progeny is warranted as well as a good contribution to its uniformity. However, if vegetative maintenance of such diploid genotypes is impossible, they cannot be maintained as diploids. Neither is it feasible to introduce the mechanism into other valuable parental diploids without upgrading their ploidy level. Only the use of heterozygosity at the locus for desynapsis, as suggested by Hermsen (1980), might be a workable approach, although it would complicate the breeding procedure. An alternative pathway would be to use male desynaptic FDR-diploids as a female parent in crosses with normal agronomically valuable diploids. However, for such an approach, desynapsis on the male side has to be genetically independent from desynapsis on the female side. Peloquin (1982) has reported such independence. If Peloquin's view is correct, the problem of maintenance of desynaptic FDR-diploids remains unsolved for seed-propagated crops. Based on these considerations, the conclusion that diploids producing both functional n-gametes and 2n-(FDR)-gametes are most suitable for breeding purposes seems justified. The proportion of 2n-gametes should be high, that of n-gametes may be low. In order to avoid triploids arising from 4x.2x matings, a triploid block is needed, when the proportion of 2n-gametes in the gametal population is low. This prerequisite is met in practically all crops in which sexual polyploidization is a desirable breeding procedure.

Breeding at the polyploid level is greatly complicated by a number of characteristic features of polyploids. Breeding polyploids at the diploid level offers many new opportunities that will be discussed in the paper on haploids as a tool in breeding. Haploidy in association with sexual polyploidization is the most efficient and promising technique for breeding autopolyploid crops. However, sexual polyploidization has a broader field of application.

Feasibility of sexual polyploidization in different crops

Sexual polyploidization is a desirable breeding technique in those crops which at the polyploid level have a better potential performance than at the diploid level. This may be true for allogamous diploid crops like many grasses and clovers and in autopolyploid crops like potato, alfalfa, orchard grass (*Dactylis glomerata*), crested wheatgrass (*Agropyron cristatum*), birdsfoot trefoil (*Lotus corniculatus*), timothy (*Phleum pratense*), and leek (*Allium porrum*). Also ornamentals should be mentioned, like *Primula*, *Freesia*, cyclamen (*Cyclamen europaeum*), *Gerbera*, *Impatiens*, and *Chrysanthemum*. In diploid ornamentals, the autotetraploid level may be of particular interest because of the increased uniformity at that level, as explained by Sparnaaij (1979).

Synthesis and resynthesis of allopolyploid crops from existing diploid relatives may be more promising through sexual polyploidization than through mitotic doubling, because of a better stability and performance of the products obtained (Skiebe, 1956; Jahr et al., 1965; and Harlan and de Wet, 1975).

SEXUAL POLYPLOIDIZATION AND PERFORMANCE

Most data on performance of autotetraploids produced by unilateral sexual polyploidization have been collected in populations from 4x.2x crosses involving male FDR-gametes. Relatively few data have been reported on 2x.4x-crosses (Kidane-Mariam and Peloquin, 1974, 1975; and Mendiburu and Peloquin, 1977a), because genotypes known to produce a high frequency of female 2n-gametes are few in number and the mechanism is more difficult to identify. For the same reason the data on bilateral sexual polyploidization—tetraploids from 2x.2x crosses—are scanty both in potato (Mendiburu and Peloquin, 1977b) and in alfalfa (Bingham, 1980). The results by Jahr et al. (1963) from 2x.4x matings in radish, trefoil, and camomile and those by Kristov (1980) in maize are presented in Table 5 but will not be discussed in this chapter, because nothing is known about the mechanism of 2n-gamete formation involved.

Theoretical expectations

The genotypic structure at a certain locus in a tetraploid population is defined by the relative frequencies of tetra-allelism, tri-allelism, balanced di-allelism, unbalanced di-allelism, and mono-allelism at that locus in the population. This structure is dependent on the genotypic structure of the parents, their degree of relationship, ploidy level, mechanism of gamete formation, and frequency of crossing over between locus and centromere. Mendiburu et al. (1974) calculated the expected average inbreeding coefficient of tetraploid families obtained from 2x.2x, 4x.2x (FDR), 4x.2x (SDR), and 4x.4x crosses and estimated the transfer of non-additive gene effects to the tetraploid progeny, assuming normal meiosis and $\alpha = 0$ in the tetraploid parents. They reached the following conclusions:

1. FDR-gametes, when compared to SDR-gametes and to reduced gametes of the tetraploid parent, transfer a larger percentage of the parental heterozygosity and epistatic interactions to the progeny.
2. Tetraploid progeny from 2x (FDR) .2x (FDR) crosses are expected to perform better than that from 4x.2x (FDR) crosses and 2x (FDR) .4x crosses, with the 4x.4x crosses ranking lowest.
3. The parents preferably should be unrelated, because then the probability of tetra-allelism in the tetraploid progeny is highest.
4. With absence of homologous pairing and gene recombination the maximum possible performance is expected from 2x(FDR).2x(FDR), with the hybrids being genetically equivalent to the products of somatic hybridization of the same parents.

Experimental results

Mok and Peloquin (1975b) reported data on tuber yield of nine tetraploid cultivars, four 2x-FDR-clones, four 2x-SDR-clones, and average tuber yield of all possible tetraploid hybrid families, viz. 36 each from 4x.4x, 4x.2x (FDR), and 4x.2x (SDR). For each family 20 genotypes were included and grown at two locations with two replications each. The data are presented in a concise way in Table 6. It is apparent that the tetraploid families from 4x.2x (FDR) are significantly superior to the other two family groups. Heterosis in respect to the midparent value has been found not only in this experiment but also by Mendiburu and Peloquin (1977a), de Jong and Tai (1977), de Jong et al. (1981), McHale and Lauer (1981a, 1981b), and Veilleux and Lauer (1981a). Heterosis has been ascribed to the nearly intact transfer of parental heterozygosity and epistatic interactions through FDR-gametes to the progeny, but de Jong and Tai (1977) also think of a favorable combination of tuber number (high in diploid parents) and tuber size (big in tetraploid parents). The degree of heterosis varied considerably in different experiments, being largest with widely-spaced plants. The hybrid plants with large tuber numbers suffer most from inter-plant competition in case of close planting (de Jong and Tai, 1977).

Tetraploid families from 4x.2x (FDR) crosses and their tetraploid parent cultivars were compared by assessing nine quantitative characters (de Jong and

Table 6. Tuber yields (lbs./hill) as averages of family means in two replications at two locations. Number of parents: nine tetraploids, four diploid FDR clones, and four diploid SDR clones of potato. (Pooled data from Mok and Peloquin, 1975b.)[a]

Location	Types of cross		
	4x . 2x (FDR)	4x . 2x (SDR)	4x . 4x
Hancock	7.7	5.1	4.6
Rhinelander	4.3	3.2	3.2
Mean	6.0	4.1	3.9

[a]Average 2x (FDR)-parents	2.7
Average 2x (SDR)-parents	2.4
Average 4x-parents	5.2
LSD (P 0.01, Hancock)	1.45
LSD (P 0.01, Rhinelander)	1.14
LSD (P 0.01, Mean)	1.06

Tai, 1977). The range of variation for most characters was larger in the 4x.2x (FDR) families than in the parent cultivars, independent of the family mean. Thus for nearly all characters, genetic advance could be obtained by selecting the best tetraploid hybrids. De Jong et al. (1981) compared six cultivars and three selected hybrids from 4x.2x (FDR) at four locations with two replications in two successive years. All three hybrids compared well with the cultivars; one hybrid even surpassed the superior cultivar Kennebec in marketable yield and stability of yield. Taking into account that the hybrids were selected from only 10,000 seedlings (200,000 seedlings are needed for one cultivar) from crosses, one parent of which was an unselected diploid, it is apparent that sexual polyploidization is a powerful breeding technique.

Up to now, few data have been published from analogous experiments in alfalfa. There is no reason to assume that the potential of sexual polyploidization in alfalfa would not be similar to that in potato. However, alfalfa is a seed-propagated crop. As indicated briefly by Bingham (1980), FDR-gametes may be used in alfalfa for maximizing heterozygosity to the same degree as in double crosses, but problems related to efficient seed production still have to be solved.

Choice of parents

A rational choice of appropriate parents for prediction of performance upon sexual polyploidization could be based on their qualitative characters and on knowledge of their combining ability in 4x.2x (FDR), 2x (FDR).4x, and 2x (FDR).2x (FDR) crosses. The reported data on combining abilities are rather different. Mok and Peloquin (1975b) found that specific combining ability was significant for average tuber yield of 36 tetraploid families obtained by crossing nine tetraploid cultivars and four slightly related 2x (FDR) clones. The performance of a 4x family could not be predicted from the average test-cross peformance of the parents. Mendiburu and Peloquin (1977a) found significant general combining abilities for the diploid and tetraploid parents used in their experiment. Specific combining abilities were not significant at either location, but they were detected in the analysis combined over locations. The authors concluded that progeny testing is an efficient tool to evaluate the breeding value of both tetraploid and diploid parents for tuber yield in 4x.2x (FDR) crosses.

Also de Jong and Tai (1977), McHale and Lauer (1981b), and Veilleux and Lauer (1981a) found highly significant effects of general combining ability on the between-family differences for several agronomic traits, i.e., total tuber yield, yield of marketable tubers, and maturity. McHale and Lauer (1981b) emphasize the feasibility of selecting superior 2x- and 4x-parents on the basis of average test-cross performance of the parents.

Further research is needed using a larger number of various 2x (FDR)-genotypes than in the aforementioned experiments. Also, FDR-clones should ripen sufficiently early to avoid the necessity for harvesting progeny before they are mature as was done by Veilleux and Lauer (1981b) and McHale and Lauer (1981b).

DISCUSSION

Thorough investigations of the mechanisms of 2n-gamete formation, both male and female, should be continued. Not only the nature and inheritance of these mechanisms should be further elucidated, but also the methods of introducing them into valuable diploid selections should be clarified.

Apart from the potential of FDR-gametes in sexual polyploidization, a set of various superior FDR-genotypes may be an efficient tool in evaluating the breeding value of autotetraploid genotypes, as pointed out by Mok and Peloquin (1975b). The conventional method via analysis of 4x.4x progenies is extremely laborious and less critical because reduced (diploid) gametes from a tetraploid tester are far more heterogeneous than the highly heterozygous but homogeneous 2n-gamete population from diploid FDR-genotypes.

The number and diversity of suitable 2x (FDR)-genotypes is still limited. There is an urgent need for genetically divergent FDR-genotypes with high agronomic value including stable resistance to the most important diseases and a stable mechanism for high-frequency production of 2n (FDR)-gametes. Only an adequate breeding program at the diploid level based upon genetically broad initial material will enable breeders to make an efficient use of sexual polyploidization.

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