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Sexual Polyploidization and Depolyploidization: Some Terminology and Definitions

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Summary. Sexual polyploidization (deploypIoidization) is the process through which a euploid zygote is formed whose chromosome number is increased above (decreased below) the level that would be expected if each parent contributed a gamete carrying one-half the parental premeiotic chromosome number. One or both gametes may contribute (lack) the extra genome(s) so that these processes may be unilateral or bilateral. Sexual polyploidization has the distinctive characteristic of being a genetically innovative mechanism. This is believed to be its most significant difference with respect to somatic doubling. Sexual depolyploidization, which may be conceived to arise in some rare situations, also has the capacity for innovation. Several cytological mechanisms may be envisioned which give rise to polyploidizing gametes. The genetic consequences of these mechanisms can be markedly different in regards to gene reassortment. Short of a mitotic-like method, FDR (first division restitution) appears to be the most appropriate mechanism to attain such a goal. Other modified meiotic processes generally result in more disturbance of the premeiotic genotypes. Under these circumstances, sexual polyploidization is probably associated with mitigated heterotic responses and a more extensive release of genetic variability.

As a cytological device, FDR has the unique property of producing balanced 2n gametes even after a numerical nondisjunction has occurred. This simple mechanism may restore fertility to, e.g., monoploids and triploids, so that odd-ploids may possess more evolutionary significance by acquiring a means of producing balanced gametes systematically.

Some new terminology is proposed to designate gametes and gametophytes which conserve the parental number of chromosomes, and for polyploids arising in conjunction with their functioning in fertilization.

Introduction

The conservation of the ploidy level of sexually reproducing organisms is commonly insured through the operation of two compensating mechanisms: meiosis and fertilization. The meiotic process normally leads to a reduction in the number of chromosomes to one-half the premeiotic number. This reduction is exactly compensated by fertilization, the process that normally restores the somatic number by adding together the chromosomes of the two uniting gametes. These processes are occasionally altered, however, and so is the ploidy level of the ensuing progeny.

It is the purpose of this account to: (1) Discuss ploidy variations emerging from sexual mechanisms; (2) Describe the genetic consequences of modes of 2n gamete formation; and (3) Propose some new terminology to identify ploidy variants with regards to their origin, both at the gametic (gametophytic) and the zygotic (sporophytic) phases of the life cycle.

Causes of Sexually Mediated Ploidy Variations

Polyploidy has certainly been an important factor in the evolution of higher plants: a significant fraction of them, including more than one-third of the domesticated species, are polyploids. Whether or not a reduction in ploidy has operated in evolution is less apparent, although if it has, it may have involved apomixis, i.e. haploidy, rather than an amphimictic or truly sexual mechanism (de Wet and Harlan 1970; Raven and Thompson 1964).

Much effort has properly been devoted to investigations involving ploidy changes such as polyploidization and haploidization through different agencies. The detection and use of 2n gamets, i.e., gametes with the unreduced number of chromosomes, is rapidly expanding. This is not surprising, since 2n gametes confer enormous versatility to ploidy manipulations. Furthermore, it is increasingly apparent that they could operate in nature to the point where one may surmise their being a most potent polyploidizing agent. In the potato, for example, diploid clones have been found which produce 2n gametes in addition to normal n gametes in one, or the other, or both sexes (Hanneman and Peloquin 1967, 1968). These clones have the potentiality, which has already been experimentally borne out (Mendiburu and Peloquin 1970, 1971), of producing diploid, triploid and tetraploid progeny following 2x - 2x matings, and triploid and tetraploid progeny when they are used in 4x - 2x matings. Similar situations are to be encountered in as distantly related plants as the generic complex *Dichanthium* (de Wet and Harlan 1970), *Medicago* (Bingham 1968, 1969), *Solanum chacoense* (Marks 1966), *Fragaria* (Bringhurst and Gill 1970), *Citrus* (Russo and Torrissi 1951; Esen and Soost 1971, 1972), some *Orchidaceae* (Storey 1956), *Rubus* (Crane and Darlington 1927; Crane 1940a, 1940b), *Sorghum* (Saez and Nunez 1943), *Primula malacoides* (Skiebe 1958), *Cyclamen* (Wellensiek 1955) and many others.

Polyploidization via 2n gametes is indeed a distinctly separable process in comparison to somatic doubling. For the sake of illustration let a cross between two heterozygous diploid clones of constitution A_1A_2 and A_3A_4, both of which are capable of producing 2n gametes, be considered. It is to be expected that such a cross may in general give rise to tetraploids of different genetic constitutions, including tetraploids which are triallelic (e.g. $A_1A_1A_2A_3$) and tetrallelic ($A_1A_2A_3A_4$) at the locus. If one allows selfing, then, a possibility will in general exist of obtaining monoallelic tetraploids as well. Somatic doubling of any one of the two parental clones, on the other hand, would have merely resulted in balanced diallelic, i.e. duplex, tetraploids ($A_1A_1A_2A_2$ or $A_3A_3A_4A_4$). The difference illustrated by this example is considered to be of the utmost importance in breeding and evolution, since it is a difference between a process which is creative and a process which is not. There is room for new interactions which may result in heterotic responses and wider adaptation in the former case but not in the latter. The fundamental difference is one between sexual versus non-sexual polyploidization.

Sexual polyploidization is realized at the moment fertilization takes place, but it is the genomic make-up of the uniting gametes that determines its ocurrence. Ultimately, then, the origin of sexual polyploidization is to be traced back to one or both of the meiotic events which specify the number of chromosomes present in the uniting gametes.

A supplementary mechanism which provides for sexual polyploidization - and depolyploidization - is inherent to meiosis in stocks whose ploidy level is uneven, e.g. triploids producing balanced gametes which have either the x or 2x chromosome number.

There is a distinction to be made between 2n gametes, which conserve the sporophytic chromosome number, and the balanced gametes produced by stocks of uneven ploidy, e.g. x and 2x gametes of a triploid. The former are the consequence of meiosis whose chromosome reduction capacity has been impaired somehow, whereas the latter represent extreme products of conventional meiosis where unbalanced products are less viable. Consequently, the former are strictly polyploidizing agents, whereas the latter can give rise, upon syngamy, to either polyploidization or depolyploidization. Genetically, the consequences of the two meiotic processes are also different. They are non-comparable, though, unless the mode of 2n gamete formation is specified. Since the gametic genotype is determined by a meiotic event in both processes, they are both creative and provide for innovation, thus differing from somatic doubling.

Genetic Consequences of 2n Gamete Formation

1. Diploid (2n = 2x) level

One should avoid considering 2n gametes as a homogeneous group from the genetic point of view, since different methods of 2n gamete formation may lead to entirely different genetic expectations for heterozygous loci.

Lewis and John (1963) as well as Rhoades and Dempsey (1966) have enumerated the ways in which 2n gametes could conceivably arise. These include (1) premeiotic doubling, i.e., somatic doubling resulting in tetraploid germinal tissue, (2) first division restitution (FDR), (3) normal first division followed by chromosomal replication during interphase and a normal second division, (4) second division restitution (SDR), and (5) postmeiotic doubling.

The consequences to be expected may be illustrated by considering a heterozygous diploid of genotype A_1A_2. This notation also serves to stress the fact that homogenic 2n gametes are autozygous and will give ris to inbred polyploids even if the parents are neither inbred nor related. The degree of inbreeding is a function of the mode of 2n gamete formation, the distance between the gene and the centromere and the degree of relationship between parents.

Method (1) leads to tetrasomic inheritance for the balanced diallelic genotype $A_1A_1A_2A_2$. The gametic

Table 1. Some numerical examples of the consequences of 2n gamete formation in a heterozygous diploid A_1A_2

Method Number	$\alpha = p = 0$			$\alpha = 1/7$; $p = 2/3$			$\alpha = 1/6$; $p = 1$		
	A_1A_1	A_1A_2	A_2A_2	A_1A_1	A_1A_2	A_2A_2	A_1A_1	A_1A_2	A_2A_2
1	0.167	0.667	0.167	0.214	0.571	0.214	0.222	0.555	0.222
2	0.0	1.0	0.0	0.167	0.667	0.167	0.25	0.5	0.25
3+4	0.5	0.0	0.5	0.167	0.667	0.167	0.0	1.0	0.0
5	0.5	0.0	0.5	0.5	0.0	0.5	0.5	0.0	0.5

series will be $(1 + 2\alpha)/6\ A_1A_1$; $2(1 - \alpha)/3\ A_1A_2$: $(1 + 2\alpha)/6\ A_2A_2$ where α is the coefficient of double reduction.

Method (2), i.e., FDR, produces $p/4\ A_1A_1$: $1 - (p/2)A_1A_2$: $p/4\ A_2A_2$ 2n gametes, where p is the proportion of single exchange tetrads in relation to the locus A.

Method (3) has the same genetic consequences as method (4).

Method (4), i.e., SDR, yields a proportion of $\frac{1}{2}(1-p)A_1A_1$: pA_1A_2: $\frac{1}{2}(1-p)A_2A_2$ 2n gametes.

Method (5) results in $\frac{1}{2}A_1A_1$: $\frac{1}{2}A_2A_2$, i.e. all homozygous, 2n gametes.

A few extreme numerical examples are presented in Table 1.

An examination of the genetic consequences of these five methods at the monoploid and triploid levels reveals that methods of 2n gamete formation at even ploidy do not necessarily give rise to 2n gametes at uneven levels.

2. Monoploid (2n = x) level

2.1 Premeiotic doubling of the monoploid genotype A_1 will produce a homozygous A_1A_1 germinal tissue. Meiosis will give rise to just one type, A_1, of 2n gamete with the somatic chromosome number.

2.2 FDR will produce nothing but 2n = x gametes, A_1 genotype.

2.3 and 2.5 have the same genetic consequences as 2.4.

2.4 Second division restitution will give rise to a majority of aneuploid gametes. Chromosomes will either be represented twice or not at all. A small proportion of homozygous, A_1A_1, balanced (n = 2x i.e. with twice the somatic chromosome number) gametes may be formed following chance movement of all chromosomes to one pole.

3. Triploid (2n = 3x) level

3.1 Premeiotic doubling of $A_1A_2A_3$ genotype leads to $A_1A_1A_2A_2A_3A_3$ germinal tissue and to 2n(= 3x) gametes whose genotypic constitution is determined by hexasomic inheritance.

3.2 First division restitution will lead neatly to balanced 2n(= 3x) gametes. Triallelic and diallelic 2n gametes are to be expected. In the diallelic gametes (e.g. $A_1A_1A_3$) there are two alleles from sister chromatids, one of these must be a crossover chromatid. The frequency of triallelic loci, i.e. conserving the parental genotype in the 2n gametes, will approach unity for loci near the centromere. Diallelic 2n gametes will increase with map distance from the locus to the centromere.

3.3 Method (3) is again equivalent to second division restitution and leads to mainly unbalanced gametes. The few balanced gametes bear either 2x or 4x chromosomes. The consequences with respect to the position of the locus are likewise similar to SDR.

3.4 When the second division is omitted there will not be 2n(= 3x) gametes produced assuming that two chromosomes go to one pole and one to the other. Mostly unbalanced gametes will result; x/2x disjunctions, however, will produce balanced gametes with 2x and 4x chromosomes, respectively. For genes very near the centromere the 2x gametes will be homozygous (sister chromatids), and the 4x gametes will be of the type $A_1A_1A_2A_2$ (balanced diallelic, two pairs of sister chromatids). For genes farther from the centromere there will be some diallelic 2x gametes (at least one crossover chromatid) and triallelic 4x gametes (e.g. $A_1A_2A_3A_3$).

3.5 Post-meiotic doubling would lead to mostly aneuploid gametes and a few balanced ones. Among the latter, one-half will be 2x and completely homo-

Table 2. Ploidy constitutions following intra- and inter-ploid matings

Row number	Parental somatic chromosome number		Gametic chromosome number		Zygotic chromosome number		Consequences
	♂	♀	♂	♀	actual	expected	
1	2x	2x	x	x	2x	2x	Concordance
2	2x	2x	2x	x	3x	2x	SP-unilateral
3	2x	2x	2x	2x	4x	2x	SP-bilateral
4	x	x	x	x	2x	x	SP-bilateral
5	2x	4x	x	2x	3x	3x	Concordance
6	2x	4x	2x	2x	4x	3x	SP-unilateral
7	4x	4x	2x	2x	4x	4x	Concordance
8	4x	4x	2x	4x	6x	4x	SP-unilateral
9	3x	3x	2x	x	3x	3x	Concordance
10	3x	3x	x	x	2x	3x	SD-bilateral
11	3x	3x	2x	2x	4x	3x	SP-bilateral
12	3x	3x	3x	3x	6x	3x	SP-bilateral
13	3x	x	2x	x	3x	2x	SP-"bilateral"
14	3x	x	x	x	2x	2x	Concordance
15	4x	3x	2x	2x	4x	<4x	SP-unilateral
16	4x	3x	2x	x	3x	>3x	SD-unilateral

zygous and one-half will be 4x and either diallelic (e.g. $A_1A_1A_3A_3$) or monoallelic (e.g. $A_2A_2A_2A_2$).

A Definition of Sexual Polyploidization

The term sexual polyploidization is used to designate the process through which a euploid zygote is formed whose chromosome number is increased above the level that would be expected if each parent contributed a gamete carrying one-half the parental premeiotic chromosome number. Also, sexual depolyploidization is proposed for the corresponding situation when there is a decrease, rather than an increase, in the (euploid) chromosome number of the zygote.

Several examples are presented in Table 2 to illustrate the way the definitions operate. The right most column provides a comparison between the "expected" and the actual chromosome numbers. If there is discordance between these numbers, then either sexual polyploidization (SP) or depolyploidization (SD) has occurred. As it appears from their use in Table 2, both definitions are intended to be operational.

It is also to be noted that sexual polyploidization can be unilateral (Lawrence 1968) when the excess genome(s) are contributed by just one parent, or bilateral, when they are contributed by both.

It is recognized that the "expected" number of chromosomes in Table 2 is somewhat unrealistic when one or both parents are of uneven ploidy. It seems none the less clear, for any particular mating, to discern whether an increase or a decrease in ploidy level has occurred or not.

Another curious feature emerging from Table 2 is a possible sexual polyploidization which does not give rise to polyploids, as is illustrated in row # 4. The converse situation is also possible and is exemplified in row # 16, where a depolyploidized zygote is still polyploid in the conventional sense. These seemingly contradictory consequences of the definition serve to emphasize the fact that only the ploidy level of the progeny relative to that of the parents is considered.

A rather unique situation is created in manipulating gametes with the unreduced number of chromosomes: fertilization invariably results in progeny whose ploidy level is stepped up. It therefore seems advisable to introduce some new terminology so as to better pinpoint the origin of certain gametes and polyploids while avoiding circumlocutions.

The terminology to be introduced is based on the contrast between the processes of haploidization and polyploidization. Whereas the former entails a stepping down in the ploidy level of the progeny with respect to the parent the latter has the reverse effect. Thus, as the term haploid refers to a sporophyte with the gametophytic chromosome number, the noun diplandroid (Gk, *diploos*, twofold; *aner*, man, male; *id*, offspring of; adj. diplandrous) is proposed to describe the converse situation, i.e., that of a male gametophyte or gamete with the sporophytic chromosome number. The noun diplogynoid (adj. diplogynous) would serve to refer to the corresponding situation in the female gametophyte.

Appropriate prefix substitutions suffice to handle the corresponding situations at other ploidy levels. Words are easily generated such as triplandroid and triplandrous, tetrandroid and tetrandrous, etc., to refer to male gametophytes originated from sporophytes with the ploidy level indicated by the prefix and that conserve such ploidy levels. The corresponding words for the opposite sex are triplogynoid and triplogynous, tetragynoid and tetragynous, etc.

Polyploid sporophytes obtained by sexual fertilization will be designated by appropriate adaptations of the suggested words. Thus, a tetraploid produced in 4x × 2x matings through fertilization of a normal (n) egg by a diplandroid (2n sperm) - unilateral sexual polyploidization - will be designated as a diplandrous tetraploid.

When two gametes with the unreduced number of chromosomes function in fertilization - bilateral sexual polyploidization - the proposed words will be used only in their adjectival forms, followed by a noun specifying the ploidy level generated, e.g., triplandro-diplogynous pentaploid (a pentaploid originated by fertilization of a 2n egg produced by a diploid by a 2n sperm produced by a triploid). Most frequently, however, only one gametic ploidy level will need to be considered. Then a small simplification may be obtained by specifying this level only once, e.g., diplandrogynous tetraploid (for a tetraploid originated in an interdiploid mating) is preferred over diplandro-diplogynous tetraploid.

A list of designations is presented in Tables 3 and 4. In Table 4C the sex with highest ploidy level is included first in the designation of the polyploid. When the two gametic ploidy levels are equal the male has been entered first as it seems to result in more euphonious words, e.g., diplandrogynous (tetraploid) is preferred to diplogynandrous (tetraploid). Both of these decisions are, of course, completely arbitrary.

Even though an effort has been made to emphasize the genetic consequences and the significance of the modes of 2n gamete formation, and other meiotic mechanisms which precede polyploidization, no attempt has been made to specify these mechanisms in the proposed terminology. Admitting that any two uniting gametes may have been formed in similar or different ways, and in light of the many different manners in which polyploidizing gametes arise, the incorporation of such specifications in the terminology does not seem to be practically feasible.

Table 3. Designations of gametophytes or gametes conserving the parental sporophytic chromosome number

Chromosome number		Designation	
Parent	Gametophyte or gamete	Noun	Adjective
(a) males			
x	x	monandroid	monandrous
2x	2x	diplandroid	diplandrous
3x	3x	triplandroid	triplandrous
4x	4x	tetrandroid	tetrandrous
5x	5x	pentandroid	pentandrous
6x	6x	hexandroid	hexandrous
7x	7x	heptandroid	heptandrous
8x	8x	octandroid	octandrous
(b) females			
x	x	monogynoid	monogynous
2x	2x	diplogynoid	diplogynous
3x	3x	triplogynoid	triplogynous
4x	4x	tetragynoid	tetragynous
5x	5x	pentagynoid	pentagynous
6x	6x	hexagynoid	hexagynous
7x	7x	heptagynoid	heptagynous
8x	8x	octagynoid	octagynous

Discussion

Sexual polyploidization is unique in that it accomplishes the goals of two fundamental evolutionary processes: sexuality and polyploidy. Its achievements are derived from one or the other of these two phenomena, or from their acting together. Serious consideration should be given to the latter possibility since it may provide for a special type of heterosis, one which is brought about through the combination of two relatively undisturbed and already heterotic divergent genotypes (consider again the synthesis of $A_1A_2A_3A_4$ individuals from the cross $A_1A_2 \times A_3A_4$ as an extreme example; in such a situation the possibilities of intralocus interactions are increased to eleven, 6 of first-order, 4 of second-order and one of third-order - thus providing not only for additivity but also for interaction of interactions).

The level of genetic variability manifested by the progeny will be a function not only of that present in the parents but also of the way the polyploidizing gametes are formed. If the gametes were formed through

Table 4. Designations of sexually-polyploidized sporophytes

Chromosome number			
Female parent	Male parent	Progeny	Designation
A. Fertilization of a 2n-egg by an n-sperm (unilateral sexual polyploidization)			
2x	2x	3x	Diplogynous triploid
2x	4x	4x	Diplogynous tetraploid
2x	6x	5x	Diplogynous pentaploid
3x	2x	4x	Triplogynous tetraploid
3x	4x	5x	Triplogynous pentaploid
3x	6x	6x	Triplogynous hexaploid
4x	2x	5x	Tetragynous pentaploid
4x	4x	6x	Tetragynous hexaploid
4x	6x	7x	Tetragynous heptaploid
5x	2x	6x	Pentagynous hexaploid
5x	4x	7x	Pentagynous heptaploid
5x	6x	8x	Pentagynous octoploid
6x	2x	7x	Hexagynous heptaploid
6x	4x	8x	Hexagynous octoploid
B. Fertilization of an n-egg by a 2n-sperm (unilateral sexual polyploidization)			
2x	2x	3x	Diplandrous triploid
4x	2x	4x	Diplandrous tetraploid
6x	2x	5x	Diplandrous pentaploid
2x	3x	4x	Triplandrous tetraploid
etc.			
C. Fertilization of a 2n-egg by a 2n-sperm (bilateral sexual polyploidization)			
x	x	2x	Monandrogynous diploid
2x	2x	4x	Diplandrogynous tetraploid
2x	3x	5x	Triplandro-diplogynous pentaploid
2x	4x	6x	Tetrandro-diplogynous hexaploid
2x	5x	7x	Pentandro-diplogynous heptaploid
2x	6x	8x	Hexandro-diplogynous octoploid
3x	2x	5x	Triplogynous-diplandrous pentaploid
3x	3x	6x	Triplandrogynous hexaploid
3x	4x	7x	Tetrandro-triplogynous heptaploid
3x	5x	8x	Pentandro-triplogynous octoploid
4x	2x	6x	Tetragyno-diplandrous hexaploid
4x	3x	7x	Tetragyno-triplandrous heptaploid
4x	4x	8x	Tetrandrogynous octoploid
5x	2x	7x	Pentagyno-diplandrous heptaploid
5x	3x	8x	Pentagyno-triplandrous octoploid
6x	2x	8x	Hexagyno-diplandrous octoploid

a mitosis-like process their union would be equivalent to somatic hybridization, which would conceivably result in genetically invariant progeny and maximum heterosis. Short of such an extreme mechanism, first meiotic division restitution (FDR) is associated with highest avoidance of inbreeding. Consequently, it appears to be capable of incorporating the parental genotype into the zygote - through a 2n gamete - with the least amount of gene assortment. Maximum heterosis will closely be approached, and some variability will be released (except in monoploids) as a result of crossing over.

Modified meioses which produce polyploidizing gametes affect the whole genotype. If there is not much disruption of the original genetic constitution at any one locus, the epistatic combinations - if present in the parental genotype - are largely transmitted to the polyploidized progeny. This could have been an important factor in determining heterotic responses in FDR-mediated polyploidization in the potato (Mendiburu, Peloquin and Hanneman 1970; Peloquin and Mendiburu 1972). Favorable epistatic combinations are assumed to be picked up and fixed by an asexual reproductive system at the original (diploid) ploidy level, transmitted through FDR, compounded upon fertilization with an unrelated gamete, and again fixed by vegetative reproduction at the higher (tetraploid) ploidy level.

Sexual polyploidization mediated by meiotic processes which result in more disturbance of the premeiotic genotypes than FDR does, is expected to produce less heterotic response and consequently less concealment of variability.

It is perhaps worth noting that 2n gametes by definition have the parental chromosome number, i.e., independently of the method by which they originate. The converse is not always true, as it may be shown that some meioses that give rise to 2n gametes at one ploidy level are incapable of doing so at a different ploidy level (cf. SDR in diploids and triploids, for example). This qualification does not hold for FDR, since this method has the remarkable property of producing 2n gametes irrespective of the ploidy level. Its unique capacity of overcoming numerical nondisjunction is again best illustrated by considering FDR at uneven ploidy levels. One may conjecture that this capacity of FDR to overcome numerical nondisjunction may be of evolutionary consequence, since it endows monoploids and triploids with the ability to produce balanced gametes in a systematic fashion. This possibility, which has been verified in monoploid peaches (Hesse 1971) may call for a reevaluation of the evolutionary significance of triploidy and other oddploids.

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