

Chapter 2

Genetic Consequences of Polyploidy in Plants

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Abstract Most eukaryotes have a history of whole-genome multiplication events followed by a progressive return to a more diploid state. The initial state of polyploidization, in which more than two copies of the genome are present, is considered here and the various types of genetic consequences that occur depending on the nature of the polyploid formed. The degree of association of chromosomes in meiosis is determined by the relative homology and will affect the segregation of the chromosome which determines the genetic properties. If all the chromosomes are quite similar and form associations of like type, this situation is referred to as autopolyploidy. If the different sets of multiple chromosomes are sufficiently dissimilar to each other, then the homologs will pair in meiosis with themselves and segregate independently of the different but related chromosome pair. This situation is referred to as allopolyploidy. Gene expression in ploidal series typically follows a per cell level correlated more or less with the number of sets of chromosomes present. Variation of individual chromosomes, or aneuploidy, produces a greater number of modulations of gene expression in parallel to classical studies noting that aneuploids have greater impact on the phenotype than changes in the copy number of the whole genome. The genetic properties of odd-number ploidies, such as triploids, are also described as well as higher ploidal levels such as hexaploidy and octoploidy.

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2.1 Introduction

Most eukaryotes have a history of polyploidization followed by fractionation back to a near diploid level (Wolfe and Shields 1997; Simillion et al. 2002; Bowers et al. 2003; Blanc and Wolfe 2004; Chapman et al. 2006; Maere et al. 2005; Blomme et al. 2006; Freeling and Thomas 2006; Barker et al. 2008). Thus, at the least, polyploidy in essence is a matter of degree, and it has played an important role in the composition of the gene repertoire of many species. Typically, it is defined as the presence of more copies of the whole genome than the normal two that constitute a diploid (Stebbins 1947). However, from the standpoint of gene content, the determination of whether a species is a polyploid is somewhat arbitrary and dependent on the time before the present when the copy number of the genome was increased. Nevertheless, for evolutionarily “recent” events, certain principles can apply which will be summarized in this chapter.

In the polyploidy literature, the basic chromosome number is designated by x and consists of the complete set of chromosomes, or a genome. The number of chromosomes in the gametophyte generation and hence the gametes is referred to as the gametic chromosome number or n . In diploids, $x = n$, but at higher levels of polyploidy, this is not the case.

Polyploidy is typically divided into at least two categories that are determined by the type of chromosome pairing in meiosis I and the distribution of chromosomes during this process. Indeed, the type of chromosome pairing that occurs in meiosis affects the genetic properties of the species so such classifications have value. If the increase in genome copy number results from the combination of chromosome sets from divergent species, the different types of chromosomes will usually not pair with each other in prophase of meiosis I. In the case of tetraploids, if both divergent genomes are doubled by whatever means, those sets of chromosomes that are similar or identical will preferentially pair with each other to the exclusion of the other genome. This type of pairing is referred to as “disomic” in analogy with the situation in a diploid. A species with this type of scenario is referred to as an allopolyploid because the contributing genomes are different from each other.

2.2 Allopolyploids

Genetic ratios in an allotetraploid depend on the constitution of each genome (Clausen and Goodspeed 1925; Clausen 1941; Clausen and Cameron 1944). The different sets of related chromosomes are referred to as homoeologues. If both the homoeologues possess the homoeologous gene copies that are expressed similarly, then both would need to be mutant in order to express a recessive phenotype. Under these circumstances, duplicate gene ratios would typically be observed. In other words, recessive phenotypes would be found in $1/16$ ($1/4 \times 1/4$) of the F_2

from a self of an F_1 between parental types that are dominant and recessive. However, if one of the gene copies is missing or expressed in other tissues from one of the homoeologous chromosomes, then genetic ratios typical of a diploid will be found because only one genome will have different alleles in an F_1 , and they will segregate to produce a 3:1 ratio because the single genome will behave as a diploid.

2.3 Autopolyploids

If on the other hand the increase in genome copy number in a polyploid results from the same species such that the chromosomes are all quite similar, the pairing in prophase of meiosis I forms conglomerates that switch pairing partners along the length of the chromosome (Fig. 2.1). This type of pairing is referred to as “quadrivalent” pairing because all four chromosomes present can be involved with each other. However, 3:1 and 2:2 associations are also observed. The segregation in this case will depend on the position of the locus in question in the chromosome and relative to the respective centromere (Blakeslee et al. 1923; Haldane 1930; Bartlett and Haldane 1934; Mather 1935, 1936; Randolph 1935; Little 1945, 1958; Doyle 1973). Those genes near the centromere will be distributed to the diploid gametes based on the usual case that pairs of centromeres will separate from each other at meiosis I and that the two sets from each chromosome of the complement will do so at random. A homozygous dominant autotetraploid (AAAA) is referred to as a quadruplex and the homozygous recessive (aaaa) as a nulliplex. There are three types of heterozygotes: AAAa (triplex), AAaa (duplex), and Aaaa (simplex). If one designates a hybrid autotetraploid as $AA'aa'$, then there are six types of possible gametes that will be formed: AA' , Aa , Aa' , aA , $a'A'$, aa' . The frequency of diploid homozygous gametes under these circumstances is $1/6$ (0.167). A self-pollination will produce 2.77 % of the progeny that are homozygous for the recessive allele (Fig. 2.2). However, as the distance of a gene from the centromere increases, recombination between the locus and the centromere will randomize the distribution of the different alleles into the diploid gametes to the point that the frequency of homozygous diploid gametes will be $(4/8 \times 3/7 = 0.21)$ as a maximum. In this case, a self-pollination will produce 4.41 % of the progeny that are homozygous.

Recombination between the monitored locus and the centromere can also produce homozygous spores from a triplex heterozygote (AAAA) to produce aa gametes (Catcheside 1956). This process is called double reduction. Again, this result is affected by the position of the locus under consideration from the centromere with greater double reduction increasing with distance. Another factor affecting segregation in autotetraploids is aneuploidy, i.e., altered copy number of individual chromosomes. This circumstance would change the pairing and segregation properties of individual chromosomes. Autotetraploids can also generate spontaneous diploid progeny via parthenogenesis (Randolph and Fischer 1939).

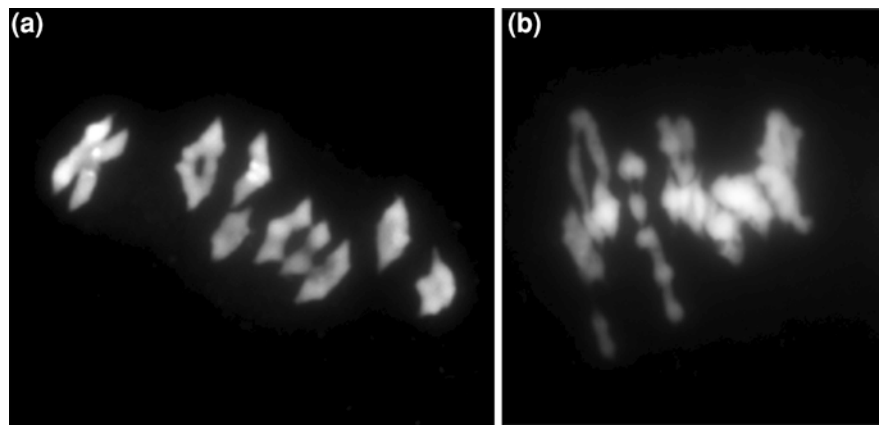


Fig. 2.1 Comparison of meiotic anaphase I in matched diploid and tetraploid maize plants. **a** Gray value image of anaphase I of diploid inbred line B73. Note that members of each pair of homologs separate from each other. Modified from (Birchler 2011). **b** Gray value image of anaphase I of a tetraploid derivative of inbred line B73. Note the multivalent associations of chromosomes. Photos by Zhi Gao and Fangpu Han

	AA	Aa	Aa	Aa	Aa	aa
AA	AA AA	AA Aa	AA Aa	AA Aa	AA Aa	AA aa
Aa	AA Aa	Aa Aa	Aa Aa	Aa Aa	Aa Aa	Aa aa
Aa	AA Aa	Aa Aa	Aa Aa	Aa Aa	Aa Aa	Aa aa
Aa	AA Aa	Aa Aa	Aa Aa	Aa Aa	Aa Aa	Aa aa
Aa	AA Aa	Aa Aa	Aa Aa	Aa Aa	Aa Aa	Aa aa
aa	AA aa	aa Aa	aa Aa	aa Aa	aa Aa	aa aa

Fig. 2.2 Genotypes in a self-pollination of an autotetraploid heterozygote AAaa. In an autotetraploid, the gametes are diploid. With two chromosomes carrying the dominant **A** allele and two carrying the recessive **a** allele, the distribution of gametes from the heterozygote is shown across the *top* and along the *side*. The combinations of these gametes to produce the tetraploid progeny are shown in the grid. Only one out of 36 are homozygous for **A**, and one out of 36 are homozygous for the recessive **a**. Other combinations of **A** and **a** are shown. These conditions hold for genes closely linked to centromeres as described in the text

2.4 Segmental Allopolyploids

A third classification based upon empirical chromosome associations is segmental allopolyploid (Stebbins 1947). In this case, some chromosomes exhibit bivalent pairing and others show quadrivalent pairing. The basis of such behavior was not clear until recently. Xiong and colleagues (Xiong et al. 2011) found that in resynthesized *Brassica napus* derived from the diploid progenitors, *B. oleracea* and *B. rapa*, different lineages could form compensating nullisomic-tetrasomic configurations for different chromosomes. In this case, the tetraploid will have some chromosomes that are basically identical and other members of the set that will be divergent. Similar results were reported for naturally occurring tetraploid *Tragopogon miscellus* (Chester et al. 2012). Such a species will be a composite of allo- and autotetraploid chromosomes for different members of the karyotype and would be expected to exhibit the pairing characterized by a segmental allopolyploid.

2.5 Heterosis and Ploidy

Because of the chromosome pairing considerations noted above, allopolyploids will have a diversity of gene products “fixed” in their genomic structure. This circumstance will basically maintain the essence of hybrid vigor even though technically an otherwise high degree of homozygosity might be present. Thus, allopolyploids typically exhibit robust biomass and excellent fertility compared to the diploid progenitor species. Nevertheless, crosses between different isolates of allopolyploids can show even greater heterotic effects when each genome is heterozygous as well (Gustafson 1946). Autopolyploids, which can have up to four different alleles at one locus, also exhibit hybrid vigor and with increasing diversity of alleles present, a phenomenon known as progressive heterosis, there is increasing biomass and fertility (Busbice and Wilsie 1966; Levings et al. 1967; Mok and Peloquin 1975; Groose et al. 1989). However, autotetraploids can be subject to inbreeding depression in which the potential exists for all copies of a chromosome to become homozygous (Busbice and Wilsie 1966; Sockness and Dudley 1989a, b). Polyploids that are entirely homozygous exhibit extreme depression and reduction of stature and fertility (Busbice and Wilsie 1966; Riddle et al. 2006; Abel and Becker 2007; Stupar et al. 2007; Redei 1964; d’Erfurth et al. 2009; Yao et al. 2011). This situation is unlikely under natural circumstances.

A discussion of the vigor of polyploids needs to consider the intersection with heterosis or hybrid vigor. In recent years, it has been possible to produce ploidy series for completely or highly homozygous materials (Riddle et al. 2006; Abel and Becker 2007; Stupar et al. 2007; d’Erfurth et al. 2009; Yao et al. 2011). The general rule that emerges from these studies is that with increasing ploidy and the maintenance of homozygosity, there is usually a decline in stature and fertility. The cell and pollen size increases with ploidy and the plants typically take on a

“stocky” appearance but with extreme ploidies, the plants are depauperate (Blakeslee 1941; Randolph 1942; Rhoades and Dempsey 1966; d’Erfurth et al. 2009; Yao et al. 2011). In contrast, hybrids with increasing ploidy tend to exhibit greater biomass and in the species in which it has been examined closely, there is an increase in heterosis with increasing diversity of alleles, i.e., progressive heterosis (Busbice and Wilsie 1966; Mok and Peloquin 1975; Levings et al. 1967; Groose et al. 1989; Bingham et al. 1994; Riddle and Birchler 2008). The common view that polyploids exhibit more robust stature derives from experience with allopolyploids or with heterotic autopolyploids, which are the situations most commonly encountered.

2.6 Aneuploidy Relative to Ploidy

In contrast to a ploidy series, changes in dosage of individual chromosomes (or substantial parts of chromosomes) have a more dramatic effect on the phenotype (Blakeslee et al. 1920; Blakeslee 1934). Typically, the removal of a chromosome or chromosomal segment has the strongest effects and is lethal in some cases (Kush and Rick 1968; Vizir and Mulligan 1999). All of the monosomics for each of the ten chromosomes in maize have been recovered and studied (Weber 1983), but this is not the case in other species in which this issue has been examined such as tomato (Kush and Rick 1968) and *Arabidopsis* (Vizir and Mulligan 1999). The addition of a chromosome to produce a trisomic usually also has a detrimental effect on plant vigor but the usual circumstance is that the impact is much less than monosomics (Lee et al. 1996). Indeed, full sets of trisomics have been produced for many plant species (Singh 1993). Tetrasomics for whole chromosome arms, otherwise called secondary trisomics, have been produced in *Datura* by recovery of extra chromosomes that are duplicated for one or the other arm of the progenitor chromosome (Blakeslee 1934). These secondary trisomics usually have more intensified phenotypic effects and are more intensified when present in haploids (Satina et al. 1937a, b).

Extra or missing chromosomes in higher ploidies have less severe phenotypic effects. A comprehensive set of aneuploids was generated in hexaploid wheat (Sears 1944; Sears 1953, 1954). Monosomics and trisomics are regularly produced, and because of the high ploidy state, nullisomics, which are missing both copies of a chromosome, can be produced (Sears 1953, 1954). Nullisomics have a more severe effect than the corresponding monosomic. Tetrasomics can be produced and have a more severe effect than the respective trisomic. Compensating nullisomics for one homoeologue and tetrasomics for another return to a more normal phenotype than exhibited by the nullisomic or tetrasomic alone (Sears 1953, 1954). Newly synthesized *B. napus* (Xiong et al. 2011) and natural neopolyploids of *T. miscellus* (Chester et al. 2012) will exhibit aneuploidy that resolves into compensating 4:0 or 3:1 contributions from different progenitor genomes illustrating that the compensating balanced condition is favored in

laboratory or natural selection. Together, these results further illustrate that the greater the deviation from the standard set of chromosomes, the more severe the impact on the phenotype.

2.7 Gene Expression Studies

Studies on gene expression in ploidy and aneuploid series parallel the phenotypic results. When individual genes are sampled in a ploidy series, the expression level is more or less proportional to the ploidal level, although there are examples of genes whose expression deviates from this trend both positively and negatively (Birchler and Newton 1981; Guo et al. 1996). Genome-wide studies of gene expression in ploidy series demonstrate a similar pattern (Wang et al. 2004; Albertin et al. 2005; Stupar et al. 2007; Riddle et al. 2010; Yu et al. 2010). In contrast, sampling of individual genes or protein patterns in aneuploids reveals a greater set of changes from the diploid level of expression (Birchler 1979; Birchler and Newton 1981; Guo and Birchler 1994). A dosage series for a particular chromosomal region would alter the amount of expression of a portion of the total gene products encoded across the genome. The effects could be positive or negative correlations with the change in dosage. The more common effect especially with trisomics was a negative correlation between the dosage and the target gene expression (Birchler 1979; Birchler and Newton 1981; Guo and Birchler 1994). Thus, the gene expression patterns show changes in a ploidy series but aneuploid series exhibit greater effects in parallel with the phenotypic relationships.

2.8 Genomic Balance

This gene expression relationship led to the suggestion that the stoichiometry of regulatory genes affected the outcome of gene expression (Birchler and Newton 1981) and ultimately the phenotype (Guo and Birchler 1994). Studies to identify single genes that would mimic the aneuploid effects using a partial loss of function mutation in the *white* eye color gene in *Drosophila* produced single-gene mutations that would modulate the target's expression either positively or negatively (Rabinow et al. 1991; Birchler et al. 2001). The molecular identification of many of these genes revealed them to be transcription factors, chromatin modifiers, and components of signal transduction (Birchler et al. 2001).

Interestingly, these same classes of genes are typical of those that exhibit preferential retention following a polyploidization event (Blanc and Wolfe, 2004; Freeling and Thomas, 2006) and underrepresentation in segmental duplications (Maere et al. 2005; Freeling et al. 2008). Thus, this evidence suggests that if these classes of genes are out of register with each other, there is a negative fitness

consequence. Thus, the phenotypic, gene expression and evolutionary studies form a coherent picture that these types of genes form a balance. When individual components exhibit a dosage effect, this will ultimately produce a fitness consequence due to the impact of the altered gene expression on the phenotype (Birchler et al. 2001; Veitia 2002; Veitia 2004; Birchler et al. 2005, 2007; Veitia et al. 2008; Birchler and Veitia 2007, 2010).

2.9 Triploids

Triploids are a polyploid level between diploid and tetraploid. They arise from crosses between diploid and tetraploids of the same or related species or from unreduced gametes from one diploid parent. In meiosis, the chromosomes associate in trivalents, which consists of pairing of any two chromosomes at any one point (McClintock 1929; Punyasingh 1947; Upcott 1935). The distribution of chromosomes is nearly random, resulting in spores that range from $1x$ to $2x$. As a consequence, the gametophytes are mostly highly aneuploid and in some cases abort (Satina and Blakeslee 1937a, b). Fertilization involving gametes of different chromosome numbers in the endosperm will often cause endosperm abortion (Satina et al. 1938; Punyasingh 1947; Brink and Cooper 1947; Cooper 1951). The gametes that are successful tend to be those at or near the $1x$ or $2x$ level. Because of the variability of the chromosome numbers in gametes from triploid individuals, this ploidal level is not stable.

2.10 Higher Ploidal Levels

Ploidal levels above the tetraploid level most commonly involve hexaploids and octoploids although much higher levels have been documented. Chromosome pairing in allohexaploids has been studied in detail, for example in wheat, which is ordinarily disomic in nature (Kihara 1919; Lilienfeld 1951; Dvorak et al. 1988). The Ph system insures pairing of homologs and against pairing of homoeologues but homoeologues can pair in mutant plants (Yousafzai et al. 2010; see Chap. 7, this volume). The wheat genome is composed of three different slightly diverged genomes tracing back through the joining of an allotetraploid composed of two genomes with the third. The Ph system maintains disomic pairing and hence excellent fertility. Octoploids, using sugar cane as an example, have variable chromosome numbers due to the minimal detrimental effects of aneuploidy at this level (Piperidis et al. 2010). In contrast, triticale, which is an octoploid consisting of hexaploid wheat with the addition of a rye genome, exhibits faithful chromosomes numbers.

2.11 Concluding Remarks

The genetics of polyploids depends essentially on the pairing properties of the multiple chromosomes in meiosis. If the multiple copies of a genome are sufficiently dissimilar from each other, they tend to pair among themselves and maintain the genetic variation within each genome. If the multiple copies of a genome are similar to each other, then all copies are free to pair and recombine among themselves. In this circumstance, the genetic behavior of a particular gene is dependent on its position on the chromosome and the fidelity of the pairing of homologs. Aneuploidy, i.e., the variation of a single chromosome or chromosomal segment, can have more severe consequences than varying the whole genome. However, as the background ploidy increases, the effect of the same chromosome change of aneuploidy becomes less. The phenotypic effects, gene expression patterns and the evolutionary results of differential gene retention following whole-genome duplications versus segmental duplication suggest the importance of genomic balance.

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