Polyploidy: Evolution and Crop Improvement

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Abstract

The condition of possessing more than two complete genomes in a cell has intrigued biologists almost a century. Many plant species including flowering plants are polyploids, and we know that it has a significant role in the evolution and crop improvement. It is well tolerated in many groups of eukaryotes. Polyploid ancestors have given rise to a number of flowering plants. Despite its widespread occurrence, the direct effect of polyploidy on evolutionary success of a species is still largely unknown. Many attractive hypotheses have been proposed in order to assign functionality to the increased content of a duplicated genome. Among these hypotheses are the proposals that genome doubling confers various advantages to polyploids which allow them to thrive well in environments that pose challenges to their diploid progenitors. Polyploidy is often accompanied with formation of improved varieties, developing sterile lines, restoring fertility in hybrids, enlargement and enhanced vigor, increasing allelic diversity and heterozygosity, etc. In genome-wide context for optimizing marker-assisted selection and crop plant improvement, all these factors need to be considered. This chapter attempts to give a brief overview of polyploidy, its origin, and role in evolution and crop improvement.

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10.1   Introduction

The organisms with more than two sets of chromosomes are called polyploids (Acquaah 2007; Chen 2010; Comai 2005; Ramsey and Schemske 1998). Polyploidy is widespread in nature and provides a way for adaptation and creation of new species. According to Chen et al. (2007), many crop plants have undergone polyploidy during their evolutionary process. According to Comai (2005), in every 100,000 plants, one plant is formed as polyploid by angiosperms at a significantly higher frequency. For understanding the nature of polyploidy, many studies have been carried out, and the present chapter seeks to throw light on the applications and implications of polyploidy in plant breeding and other commercial ventures. To understand polyploidy a few basic points need to be defined. The complete basic set of chromosomes is designated by "X", while the total number of chromosomes in a somatic cell is denoted by "2n". A somatic cell contains twice the number of chromosomes, while the gametes contain a haploid set only (Acquaah 2007; Otto and Whitton 2000). Three types of polyploidy, namely, autopolyploidy, allopolyploidy, and segmented allopolyploidy, have been distinguished by Stebbins (1947). In the first one, all genomes are identical and arise via genome duplication within the same species (Stebbins 1947; Lewis 1980). Allopolyploids contain two or more different genomes and can arise via hybridization of two different species linked with genome doubling (Stebbins 1947; Grant 1975). The third one, i.e., segmental allopolyploids, carries more than two incompletely distinct genomes which can lead to the formation of both bivalents and multivalents during chromosome pairing (Stebbins 1947; Levin 2002).

During the early part of the twentieth century, the phenomenon of polyploidy gained much more importance. According to Ramsey and Schemske (1998), Hugo De Vries's original mutation of *Oenothera lamarckiana* was one of the earliest examples of natural polyploidy. The occurrence of a fertile-type *Primula kewensis* from a sterile interspecific hybrid through chromosome doubling was discovered by Digby (1912), but the author failed to realize the significance of the same in the context of polyploidy (Stebbins 1971). Many crop plants like wheat, maize, sugarcane, coffee, cotton, and tobacco are polyploids either through intentional hybridization and selective breeding (e.g., some blueberry cultivars) or as a result of polyploidization event taken place in ancient times (e.g., maize) (Ramsey and Schemske 2002). In long-lived perennials that possess various vegetative means of propagation (*Fragaria*, *Rubus*, *Artemisia*, *Potamogeton*, etc.) and in those with frequent occurrences of natural interspecific hybridizations, polyploidy seems to be very favorable (Hilu 1993).

10.2   Changes in Chromosome Number

The changes either in one or a few chromosomes lead to aneuploidy. These changes in chromosome numbers are determined in relation to the somatic chromosome number (2*n*) of the species. Those aneuploid organisms which lack one

Table 10.1 Type of variations in chromosome number

Term	Type of change	Symbol
Aneuploid	One or few chromosomes extra or missing from $2n$	$2n \pm$ few
Nullisomic	One chromosome pair missing	$2n-2$
Monosomic	One chromosome missing	$2n-1$
Double monosomic	One chromosome from each of the two different chromosome pairs missing	$2n-1-1$
Trisomic	One chromosome extra	$2n + 1$
Double trisomic	One chromosome for each of two different chromosome pairs extra	$2n + 1 + 1$
Tetrasomic	One chromosome pair extra	$2n + 2$
Euploid	Number of genomes or copies of a single genome more or less than two	
Monoploid	One copy of a single genome	X
Haploid	Gametic chromosome complement of the species	N
Polyploid	More than two copies of one genome	
Autopolyploid	Genomes identical with each other	
Autotriploid	Three copies of one genome	$3x$
Autotetraploid	Four copies of one genome	$4x$
Autopentaploid	Five copies of one genome	$5x$
Autohexaploid	Six copies of one genome	$6x$
Allopolyploid	Two or more distinct genomes (generally each genome has two copies)	
Allotetraploid	Two distinct genomes	$2x_1 + 2x_2$
Allohexaploid	Three distinct genomes	$2x_1 + 2x_2 + 2x_3$
Allooctoploid	Four distinct genomes	$2x_1 + 2x_2 + 2x_3 + 2x_4$

Source: Singh BD (2012), Plant Breeding Principles and Methods

chromosome pair ($2n-2$) are termed as nullisomic. While those aneuploids that lack a single chromosome ($2n-1$) are known as monosomic. A double monosomic individual lacks two chromosomes which belong to two different chromosome pairs ($2n-1-1$). An aneuploid individual that contains one extra chromosome ($2n + 1$) is known as trisomic and that having two extra chromosomes from two different chromosome pairs is called double trisomic ($2n + 1 + 1$). A tetrasomic individual has one pair of extra chromosomes ($2n + 2$). On the other hand, euploidy involves change in complete set of genome which is an exact multiple of the basic chromosome number of the concerned species. It is generally called polyploidy. A polyploid individual having all the genomes identical is called an autopolyploid. On the other hand, allopolyploids have two or more different genomes present. Euploids may have 3, 4, 5, 6, 7, 8, or more genomes making up their somatic chromosome number. The terminology of heteroploidy in common use is summarized in Table 10.1.

10.3   Origin of Polyploidy

Polyploidy is originated by different means. Somatic doubling during mitosis, non-reduction in meiosis leading to the formation of unreduced gametes, polyspermy (fertilization of the egg by two male nuclei), and endoreduplication (replication of the DNA but no cytokinesis) are some of the basic processes which give rise to polyploidy. According to Grant (1981), some authors have reported endoreduplication and somatic doubling more similar and have not viewed these as separate mechanisms. Chromosome doubling can occur either in the zygote or in some apical meristems to produce complete polyploids and polyploidy chimeras, respectively. Ramsey and Schemske (1998) have reported somatic polyploidy in some nonmeristematic plant tissues (e.g., tetraploid and octoploid cells in the cortex and pith of *Vicia faba*). According to Grant (1981), mitotic nondisjunction is the main cause of somatic doubling. Somatic doubling can occur in purely vegetative tissues, in branches that may produce flowers, or in early embryonic divisions (Grant 1981). Chromosome doubling in the zygotes was best described from heat shock experiments in which young embryos were briefly exposed to high temperatures (Lewis 1980).
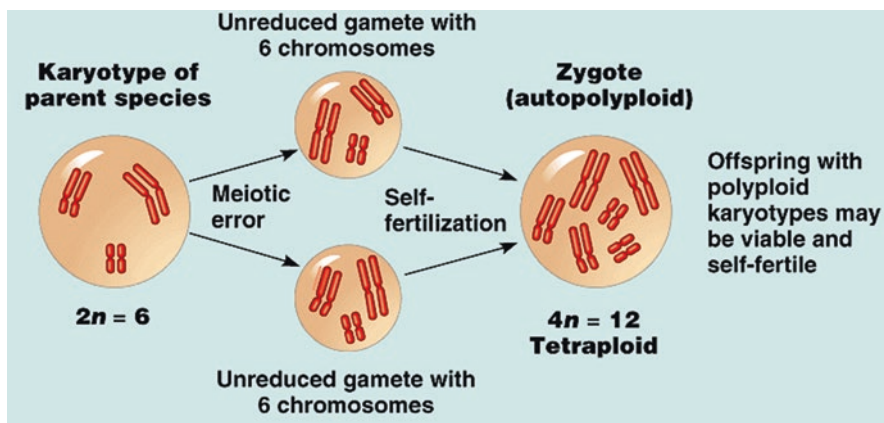
10.3.1 Origin of Autopolyploidy

Autoployploidy can be defined as the individuals with multiple sets of chromosomes derived from a single species. Autopolyploids can occur spontaneously in nature in low frequency and can be artificially induced by various means such as heat and chemical treatments, decapitation, and selection from twin seedlings. In autopolyploidy, the chromosomes fail to separate due to meiotic failure resulting in gametes with twice as many chromosomes as normal (2*n*). Autopolyploids can be formed by unreduced 2*n* gametes which are produced due to gametic nonreduction or meiotic nuclear restitution during micro- and megasporogenesis. Figure 10.1 shows the origin of autopolyploidy from two nonreduced gametes.
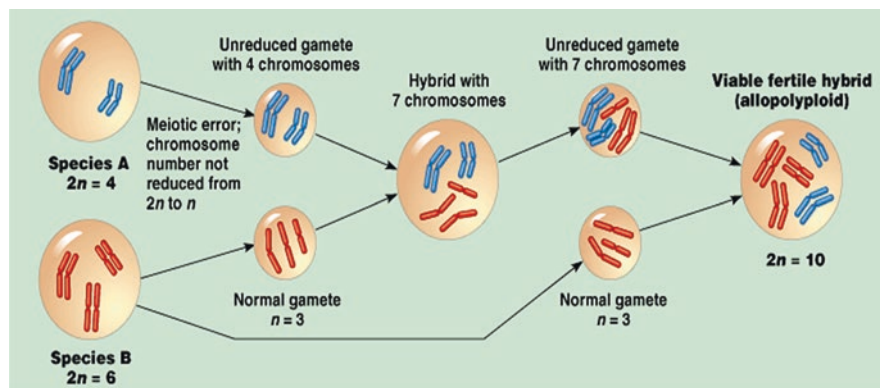
10.3.2 Origin of Allopolyploidy

The polyploids with chromosomes derived from different species are called allopolyploids. The fusion of reduced 1*n* gamete with unreduced 2*n* gamete gives rise to 3*n* zygote followed by the subsequent fusion of 1*n* reduced gamete with 3*n* gamete in the next generation giving rise to a tetraploid individual. This two-step process of allopolyploid production is sometimes referred to as a triploid bridge. The diagrammatic representation of allopolyploid formation is given in Fig. 10.2.

Environment and genotype have the influence on the formation of nonreduced gametes. For example, an increase in the number of nonreduced gametes in *Gilia*

Fig. 10.1 Showing the origin of autopolyploid from unreduced gametes (*Source:* Campbell's Biology, page 454, 5th Edition)

Fig. 10.2 Showing the origin of allopolyploid from unreduced and reduced gametes (*Source*: Campbell's Biology, page 454, 5th Edition)

has been shown to be favored by adverse growing conditions. In case of maize, the gene *elongate* on chromosome 3 was found to increase the proportion of diploid eggs which is an example of genotype in modulating the nonreduced gamete production (Grant 1981; Lewis 1980). The rapid screening techniques like flow cytometry, chromosome pairing, and other genomic techniques are helpful in studies on unreduced gametes in both plants and animals (Mable 2003). According to Ramsey and Schemske (1998), the contribution of polyspermy as a mechanism of polyploidy formation is rare except in some orchids. Endoreduplication has been known to occur in endosperm and the cotyledons of developing seeds, leaves, and stems of bolting plants (Larkins et al. 2001).

10.4   Methods for Inducing Polyploidy

In the1930s it was discovered that colchicine inhibits the formation of spindle fibers and temporarily arrests chromosomes at the anaphase stage (Blakeslee and Avery 1937). At this point, the chromosomes have replicated, but cell division has not yet taken place resulting in the formation of polyploidy cells. Other mitotic inhibitors, namely, oryzalin, trifluralin, amiprophos-methyl, and N_2O gas, have also been identified and used as doubling agents (Bouvier et al. 1994; Van Tuyl et al. 1992; Taylor et al. 1976). There are various methods for applying these doubling agents. One of the easiest and most effective methods is to work with a large number of seedlings having small, actively growing meristems. Seedlings can be soaked or the apical meristems can be submerged with different concentrations, durations, or frequencies of a given doubling agent. Shoots of older plants can be treated, but it is often less successful and results in a greater percentage of cytochimeras. Treatment of smaller axillary or subaxillary meristems is sometimes more effective. Chemical solutions can be applied to buds using cotton, agar, or lanolin or by dipping branch tips into a solution for a few hours or days. Surfactants, wetting agents, and other carriers (dimethyl sulfoxide) are sometimes used to enhance efficacy. Heat or cold treatment, X-ray, or gamma ray irradiation may also induce polyploidy in low frequencies. Triploid branches have been produced in *Datura* by cold treatment. Exposure of maize plants or ears to high temperature (38–45 °C) at the time of first zygotic division produces 2–5 % tetraploid progeny (Randolph 1941). Similarly heat treatments in barley, wheat, rye, and some other crop species have been successfully used for inducing polyploidy.

10.5   Role of Polyploidy in Plant Evolution

In comparison to the gradual evolutionary process whereby species evolve by small spontaneous mutations accumulated over time in the population, new species of plants can also arise rapidly. The most common mechanism for abrupt speciation is through the formation of natural polyploids. Once a tetraploid arises in a population, it can generally hybridize with other tetraploids. However, these tetraploids are reproductively isolated from their parental species. Tetraploids that cross with diploids of the parental species will result in triploids that are typically sterile. This phenomenon provides reproductive barrier between the polyploids and the parental species which is a driving force for speciation. Various estimates suggest that about 47–70 % flowering plants are of polyploidy origin (Grant 1971; Goldblatt 1980; Ramsey and Schemske 1998). For example, the plants in the rosaceous subfamily Maloideae (*Malus*, *Pyrus*, *Photinia*, etc.) are believed to have originated from ancient allopolyploids since they have $n = 17$ basic chromosome number, whereas plants in other subfamilies of Rosaceae have $n = 8$ or 9 (Rowley 1993). In many genera, different species will have different ploidy levels representing a series of polyploids. In *Chrysanthemum* different species have chromosome numbers of $2n = 18, 36, 54, 72, 90$, and 198 – all multiples of a basic chromosome number of 9.

Polyploids have adaptive and evolutionary advantages due to certain factors. They are significantly more heterozygous than their diploid counterparts. The heterozygosity can be a key factor in growth, performance, and adaptability of a polyploidy plant. Allopolyploids can contribute to heterosis or hybrid vigor due to dissimilarity in genes. All polyploid individuals have a certain amount of genetic redundancy; extra copies of genes can mutate and diverge resulting in new traits without compromising essential functions. Polyploid populations often reveal extensive genomic rearrangement including the origin of novel DNA regions (Arnold 1997; Song et al. 1995; Wendel 2000). Ancient polyploids can eventually undergo such changes to the extent that they effectively become diploidized where diploid gene ratios are restored.

Polyploid plants also tend to be more self fertile and apomictic. Since polyploids usually arise at a low frequency, greater self fertility and apomixes would help to compensate for their minority disadvantage (Briggs and Walters 1977) and would provide further benefits in areas where breeding systems are compromised in stressful environments. Furthermore, inbreeding is less harmful for allopolyploid plants due to their greater heterozygous nature. One question that frequently arises is whether polyploids inherently have greater stress tolerance or not. For example, it has often been observed that unequal number of polyploids is found in stressful conditions like cold and dry regions. Some argue that this is a spurious correlation (Sanford 1983) or possibly the result of intermixing of species and formation of allopolyploids during glacial periods (Stebbins 1984). However, polyploids may also have positive characteristics that provide some benefits helpful in adaptation. Molecular studies have confirmed that allopolyploids exhibit enzyme multiplicity (Soltis and Soltis 1993). Since allopolyploids represent a fusion of two different genomes, these polyploids can potentially produce all of the enzymes produced by each parent as well as new hybrid enzymes. This enzyme multiplicity may give polyploids with greater biochemical flexibility, possibly extending the range of environments in which the plant can grow (Roose and Gottlieb 1976). Other changes in expression of genes, altered regulatory interactions, and rapid genetic and epigenetic changes could further contribute to increased variation and new phenotypes (Osborn et al. 2003).

10.5.1 Autopolyploidy and Evolution

Autopolyploidy has played a limited role in evolution of plant species. Some of our present-day crop species are considered to be autopolyploids. Autotetraploids appear to have been more successful as crops than other forms of autopolyploidy. In addition many forage grasses and several ornamentals are most likely autopolyploids. Recent studies using genomic in situ hybridization (GISH), however, have revealed peanut and coffee to be allopolyploids. GISH is a powerful tool for investigation of genome organization and evolutionary relationships. The diploid progenitors (parental species) of *Arachis hypogaea* are *A. villosa* and *A. ipaensis* (Raina and Mukai 1999). Similarly the most likely diploid progenitors of *Coffea arabica*

are the wild species *C. congensis* and *C. eugenioides* (Raina et al. 1998). A similar analysis of other putative autotetraploids may reveal them to be allopolyploid in nature. Molecular analysis like genome sequencing and comparative genomic studies reveal that most species of angiosperms and vertebrates have experienced whole genome duplications, followed by loss of most of the duplicated regions of the genome. In this process, their genomes have retained considerable amounts of duplications, which have expanded the range of genetic diversity in these species. For example, *Oryza sativa* and *Arabidopsis thaliana* have experienced whole genome duplications three times at approximately 70 million years ago, 65 million years ago, and 40 million years ago. A large part of the duplicated genome has been lost since then, but a large number of duplicated genes exist even today. These duplicated genes have diverged to various degrees and become subfunctional, i.e., they show reduced levels of expression as confirmed by transcriptome analyses.

10.5.2 Allopolyploidy and Evolution

Allopolyploidy has played an important role in evolution. Allopolyploidy occurs in various genera of plants and has enjoyed considerable success in natural populations. It is expected that one third of the angiosperms are polyploids, and a huge number of them are allopolyploids. Allopolyploids have been more successful as crop species than autopolyploids. Some of the present-day allopolyploid crop species are given in Table 10.2.

Some naturally occurring allopolyploid crops include wheat, cotton, tobacco, mustard, oat, etc. Interspecific crossing followed by chromosome doubling in nature has resulted in the origin of allopolyploid crop species. The evolutionary origins of some natural allopolyploid crops are described below:

(i) Bread wheat (*Triticum aestivum*)

Evolutionary origin of bread wheat has been the most extensively investigated. Identity of the diploid species contributing the three different genomes (A, B, and D) of *Triticum aestivum* has been investigated by many workers more notably by Sears, Kihara, and others. It is generally accepted that the genome A present in diploid wheat is similar to those present in tetraploid and hexaploid wheat. Further, the genome B of tetraploid emmer wheat is found similar to that in hexaploid wheat. This is evident from chromosome pairing in crosses among diploid, tetraploid, and hexaploid wheat. Hybrid between diploid and tetraploid wheat shows 7^{II} and 7^{I}, while those between tetraploid and hexaploid wheat shows about 14^{II} and 7^{I}. It is believed that A genome of wheat has come from *Triticum monococcum* ($2n = 14$), D genome from *Triticum tauschii* ($2n = 14$), and B genome from unknown source probably from an extinct species ($2n = 14$) (Fig. 10.3).

Table 10.2 Some allopolyploid crop species and their gametic chromosome numbers

Scientific name	Common name	Gametic ch. no.	Cultivated/wild
Avena strigosa	Sand oats	7	Wild
A. barbata	Slender wild oats	14	Wild
A. sativa	Cultivated oats	21	Cultivated
A. byzantine	Cultivated red oats	21	Cultivated
Brassica nigra	Black sarson	8 (B)[a]	Cultivated
B. oleracea	Cabbage, cauliflower, etc.	9 (C)	Cultivated
B. campestris	Turnip rape	10 (A)	Cultivated
B. carinata	Abyssinian cabbage	17	Wild
B. juncea	Rai, Indian mustard	18	Cultivated
B. napus	Rape	19	Cultivated
Gossypium arboreum	Asiatic (desi) cotton	13 (A_2)	Cultivated
G. herbaceum	Asiatic cotton	13 (A_1)	Cultivated
G. thurberi	Wild American cotton	13 (D_1)	Wild
G. barbadense	Sea island (Egyptian) cotton	26 (A_2D_2)	Cultivated
G. hirsutum	American upland cotton	26 (A_1D_1)	Cultivated
Hordeum vulgare	Cultivated barley	7	Cultivated
H. jubatum	Squirrel tail barley	14	Wild
H. nodosum	Foxtail barley	21	Wild
Medicago hispida	California burclover	7	Cultivated
M. lupulina	Black medic	8, 16	Cultivated
M. falcate	Yellow alfalfa	8, 16	Cultivated
Nicotiana sylvestris	Wild tobacco	12	Wild
N. tomentosa	Wild tobacco	12	Wild
N. tabacum	Cultivated tobacco	24	Cultivated
N. rustica	Cultivated tobacco	24	Cultivated
N. bigelovii	Wild tobacco	24	Wild
N. debneyi	Wild tobacco	24	Wild
Prunus americana	American plum	8	Cultivated
P. avium	Sweet cherry	8	Cultivated
P. persica	Peach	8	Cultivated
P. cerasus	Sour cherry	16	Cultivated
P. domestica	European plum	16	Cultivated
Saccharum officinarum	Noble canes	40	Cultivated
S. barberi	Indian canes	41, 45, 46, 58, 62	Cultivated
S. sinensis	Indian canes	58, 59	Cultivated
S. spontaneum	Wild canes	20–64	Wild

Table 10.2 (continued)

Scientific name	Common name	Gametic ch. no.	Cultivated/wild
S. robustum	Wild canes	30–74	Wild
Sorghum versicolor	Wild sorghum	5	Wild
S. bicolor	Jowar	10	Cultivated
S. halepense	Johnson grass	20	Cultivated
Trifolium pratense	Red clover	7	Cultivated
T. alexandrinum	Berseem clover	8	Cultivated
T. repens	White clover	16	Cultivated
T. medium	Zigzag clover	40, 48, 42, 49	Cultivated
Triticcum monococcum	Wild einkorn	7 (A)	Wild
T. turgidum var. dicoccoides	Wild emmer	14 (AB)	Wild
T. turgidum var. dicoccum	Emmer wheat	14 (AB)	Cultivated
T. turgidum var. turgidum	Solid stem wheat	14 (AB)	Cultivated
T. turgidum var. carthlicum	Persian wheat	14 (AB)	Cultivated
T. turgidum var. polonicum	Polish wheat	14 (AB)	Cultivated
T. turgidum var. durum	Durum wheat	14 (AB)	Cultivated
T. timopheevii	–	14 (AG)	Cultivated
T. timopheevii var. americanum	–	14 (AG)	Wild
T. aestivum var. spelta	Spelt wheat	21 (ABD)	Cultivated
T. aestivum var. aestivum	Common bread wheat	21 (ABD)	Cultivated
T. aestivum var. macha	–	21 (ABD)	Wild
T. aestivum var. compactum	Club wheat	21 (ABD)	Cultivated
T. aestivum var. sphaerococcum	Indian dwarf wheat	21 (ABD)	Wild
T. zhukovskyi	–	21 (AAG)	Cultivated

[a]Letters within parentheses denote the genomes present in the species
Source: Singh BD (2012), Plant Breeding, Principles and Methods

(ii) Tobacco (*Nicotiana tabacum*)

The genus *Nicotiana* comprises about 76 currently recognized naturally occurring species that are subdivided into 13 sections (Knapp et al. 2004). *Nicotiana tabacum* ($n = 14$) is a classic amphidiploid species originated from a hybridization event between *Nicotiana sylvestris* and *Nicotiana tomentosa*, both the species are diploid with $n = 12$ (Fig. 10.4). It has been reported that the maternal parent and the other donor of the S genome is *Nicotiana sylvestris* (Bland et al. 1985; Olmstead and Palmer 1991; Aoki and Ito 2000; Yukawa et al. 2006), whereas the section Tomentosae (*Nicotiana tomentosiformis*, *Nicotiana otophora*, or an introgressive hybrid between the two) has contributed the T genome (Kenton et al. 1993; Riechers and Timko 1999; Lim et al. 2000; Kitamura et al. 2001; Ren and Timko 2001).
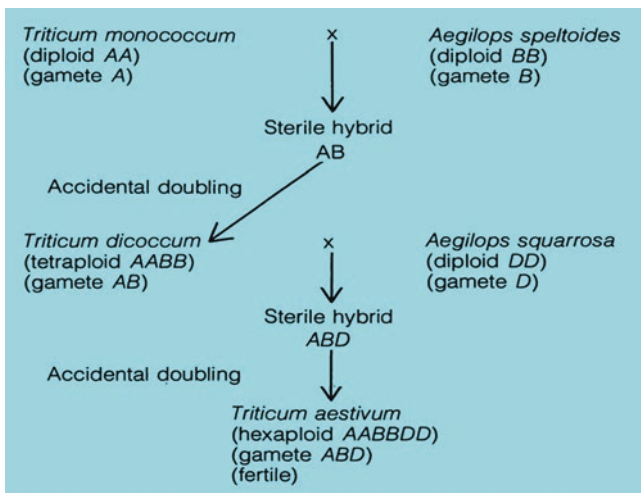
Fig. 10.3 Evolution of bread wheat (*Triticum aestivum*) (Source: http://www.ibri.org/Books/Pun_Evolution/Figures/Fig03-12.gif)
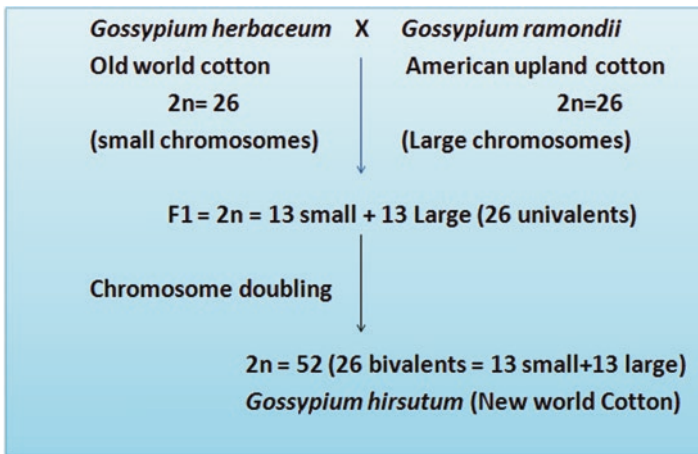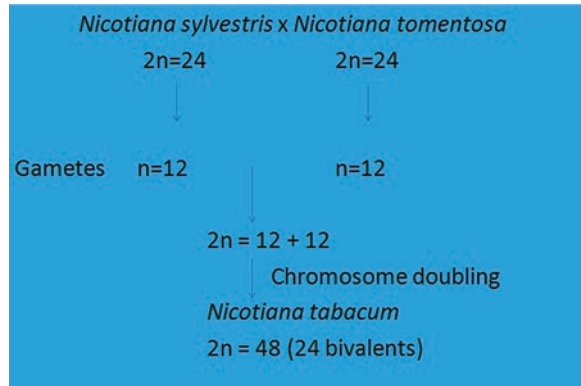
(iii) Cotton (*Gossypium hirsutum*)

All the diploid species of genus *Gossypium* have haploid chromosome number of 13 and fall into seven different genome types, designed A–G based on chromosome pairing relationships (Beasley 1942; Endrizzi et al. 1984). A total of five tetraploid ($n = 2x = 26$) species are recognized in *Gossypium*. According to Kimber (1961), all tetraploid species show disomic chromosome pairing. Chromosome pairing in inter-specific crosses between diploid and tetraploid cotton suggests that tetraploids contain two different genomes, which resemble the A genome of *G. hirsutum* ($n = 13$) and D genome of *G. raimondii* ($n = 13$), respectively. Both the A and D genome species diverged from a common ancestor about 6–11 million years ago (Wendeil 1989). The putative A x D polyploidization event occurred in the New World, about 1.1–1.9 million years ago, in which A genome donor which is native to the old world served as the female parent (Wendeil 1989; Wendeil and Albert 1992). The five allotetraploid species (*G. hirsutum*, *G. barbadense*, *G. darwini*, *G. mustelinum*, and *G. tomentosum*) are thought to have originated by diversification at the polyploidy level (Fig. 10.5).

(iv) Amphidiploid *Brassica* species

An interesting example of the role of allopolyploidy in the evolution of different *Brassica* species is presented in the *Brassica* triangle (Morinaga 1934) (Fig. 10.6). As per the scheme, *Brassica juncea* ($n = 18$) is an amphidiploid from an interspe-cific cross between *Brassica nigra* ($n = 8$) and *Brassica campestris* ($n = 10$), whereas an interspecific cross between *Brassica oleracea* ($n = 9$) and *Brassica campestris* ($n = 10$) has given rise to amphidiploid *Brassica napus* ($n = 19$). On the other hand *Brassica carinata* ($n = 17$) is a result of an interspecific cross between *Brassica nigra* ($n = 8$) and *Brassica oleracea* ($n = 9$).

Fig. 10.4 Evolution of
Nicotiana tabacum

Nicotiana sylvestris x *Nicotiana tomentosa*
2n=24   2n=24

Gametes   n=12   n=12

2n = 12 + 12
Chromosome doubling
Nicotiana tabacum
2n = 48 (24 bivalents)

Gossypium herbaceum   X   *Gossypium ramondii*
Old world cotton   American upland cotton
2n= 26   2n=26
(small chromosomes)   (Large chromosomes)

F1 = 2n = 13 small + 13 Large (26 univalents)

Chromosome doubling

2n = 52 (26 bivalents = 13 small+13 large)
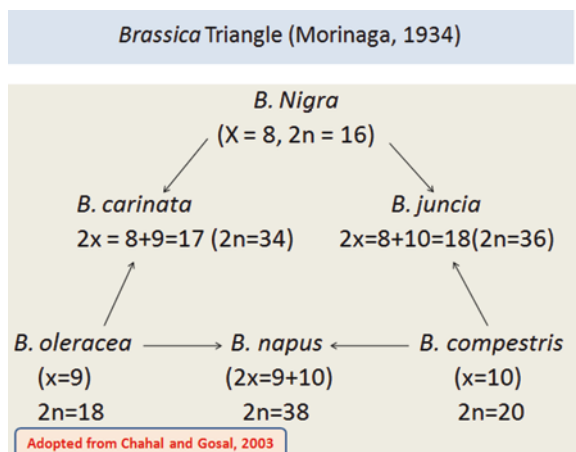*Gossypium hirsutum* (New world Cotton)

Fig. 10.5 Evolution of cotton (*Gossypium hirsutum*)

10.6   Polyploidy and Crop Improvement

Polyploidy has found some practical applications in improvement of crops, includ-
ing the development of commercial varieties in India as well as in some other coun-
tries, utilization as a bridging species, creation of new crop species, widening the
genetic base of existing polyploids, etc. Some important examples are discussed
below.

(a) *Autotetraploids (triploid sugar beet and watermelon):* Triploid sugar beets have
   larger roots as compared to diploids, but they maintain the sugar content of
   diploids and thus yield more sugar per unit area. Such triploids are produced by
   inter planting diploid and tetraploid plants. Autotetraploid sugar beets have

Fig. 10.6 Evolution of *Brassica* species and the relationships between diploid and naturally occurring amphidiploid species of *Brassica*

Brassica Triangle (Morinaga, 1934)

B. Nigra
(X = 8, 2n = 16)

B. carinata
2x = 8+9=17 (2n=34)

B. juncia
2x=8+10=18(2n=36)

B. oleracea ⟶ B. napus ⟵ B. compestris
(x=9)   (2x=9+10)   (x=10)
2n=18   2n=38   2n=20

Adopted from Chahal and Gosal, 2003

smaller roots as compared to diploid. Triploids can be produced when tetraploid and diploid are crossed or when something goes erroneous in meiosis and unreduced gametes are produced (with $2n$ chromosomes) which unite with gametes carrying haploid (n) chromosomes. Triploidy can also be beneficial in watermelons. Diploid watermelons (*Citrullus lanatus*) have 22 chromosomes per somatic cell and are fully fertile and produce a huge number of seeds per fruit. However, natural parthenogenesis is not known for watermelons. Hence Kihara's (1951) technique of producing seedless triploid watermelons can be utilized. The autotetraploid lines are planted alternately with diploids in isolation. Tetraploids are used as seed parent. The seeds produced in triploids from tetraploids are viable. However, when diploid is used as female or seed parent, then the program of triploid seed production is unproductive. Because of meiotic abnormalities, triploids cannot produce true seeds, but rudimentary structures similar to seeds of cucumber (small and white). For raising a commercial successful crop of triploid seedless watermelon, it is necessary to interplant diploid variety because fruit setting on triploids depends upon stimulus provided by the pollen.

(b) *Autotetraploids:* The only successfully developed autotetraploid among the grain crops is the rye (*Secale cereale*). Tetraploid rye has better qualities than diploids like larger kernels, superior ability to emerge under adverse conditions, and higher protein content. It is grown in Sweden and Germany. Similarly tetraploid grapes with larger fruits and fewer seeds per berry than diploids have been developed in California, USA. Tetraploid strains of red clover grown in Sweden have given higher hay yields than corresponding diploids among the forage crops. Pusa giant berseem (a variety of Egyptian clover) has been released in India for higher fodder yield. In cases of ornamental plants like phlox, dahlia, snapdragon, etc., induced autopolyploidy has been most successful as they have bigger flower size, longer blooming period, and rela-

tively longer lasting flowers (Kehr 1996). Autotetraploidy has also been successful in crops like banana, maize, potato, and turnip.

(c) *Overcoming barriers to hybridization*: Due to differences in ploidy levels between prospective parents, the desirable crosses are difficult to obtain. Such interploid barriers appear to arise from abnormal endosperm formation. In species where there is a block at interploid level, seeds will often only develop normally if there is a 1 paternal: 2 maternal ratio in the genomic makeup of the endosperm, which would be the normal case for two diploid parents (Ramsey and Schemske 1998). Seeds that do not meet this criterion are often immature or aborted. In some cases this ratio is not accurate, but the larger the variation, the lower the viability of the seeds (Sanford 1983). In cases where the blocks due to the difference in ploidy level exist, barriers to hybridization may be overcome by manipulating the ploidy levels to match prior to hybridization.

(d) *Developing sterile cultivars:* A significant threat to certain ecosystems is the introduction of invasive species. An ideal approach for addressing this problem is the development of sterile forms of important nursery crops. There are various methods for developing sterile plants. Among them one of the rapid and efficient approaches is to create polyploidy. In most cases, these sterile plants function normally except reproduction particularly meiosis. In spite of these complexities, autotetraploids of some species can produce seeds that are fertile. In such a situation, triploids can be created by hybridizing tetraploids with diploids. In some species triploid development can be complicated due to the interploid block that prevents the normal development of triploid embryo. However, embryo culture is one of the techniques that can be used to produce sterile triploid plants. Another approach for triploid development is the regeneration of plants from endosperm. In most angiospermic seeds, the embryo is diploid, and the adjoining endosperm originates from the fusion of three haploid nuclei (one from male gametophyte and two from female) resulting in triploid tissue. This tissue can be excised from developing seeds and cultured in vitro to eventually give rise to regenerated embryos and plantlets. This method has been successful in various plants like citrus, kiwifruit, loquat, etc.

(e) *Restoring fertility in wide hybrids:* It is not necessary for hybrids between different taxa to be sterile. This often occurs due to failure of the chromosomes to pair correctly during meiosis – referred to as chromosomal sterility. The fertility can be restored by doubling the chromosomes of a wide hybrid. This approach has been used successfully in *Rhododendron* and *Chitalpa tashkentensis* (Contreras 2006; Olsen 2006). However, in some cases this technique has been successful in restoring fertility, as was the case with tetraploid hybrids of *Alstroemeria aurea* × *A. caryophyllaceae* (Lu and Bridgen 1997).

(f) *Enhancing pest resistance and stress tolerance:* Polyploids have played an important role in adaptability and resistance to biotic and abiotic stresses (Levin 1983). In some cases polyploids have demonstrated greater resistance to pests and pathogens, greater nutrient uptake efficiency, better drought resistance, and superior cold tolerance. There are a number of strategies for inducing polyploids as a means of enhancing adaptability. The expression and concentration of cer-

tain secondary metabolites and defense chemicals can be enhanced by increasing the chromosome number and related gene dose. However, this is not always true, and little is generally known about the relationship between gene dose, gene silencing, and expression secondary metabolites. An important method would be to develop allopolyploids between plants with diverse endogenous secondary metabolites. A unique and valuable characteristic of allopolyploids is that they often produce all the enzymes and metabolites (including defense chemicals) of both parents. This could be particularly effective for combining the characteristics of pest resistance of two species and contributing to a much broader and more horizontal form of pest resistance. The same approach may be useful for enhancing tolerance to certain environmental stresses.

(g) *Increased allelic diversity and heterozygosity:* Polyploidy has played an important role in increasing the allelic copy number and heterozygosity leading to novel phenotypes. Allelic diversity also increases during allopolyploidy, when two (or more) different genomes are present in a common nucleus. According to Osborn et al. (2003), the oil seed production in *B. napus* is positively affected by intergenomic heterozygosity. The QTL for seed yield and other traits in other populations of *B. napus* is also affected by intergenomic heterozygosity (Udall et al. 2006; Quijada et al. 2006). The tetraploid cotton also dominates the global market in terms of fiber production because they produce longer, finer, and stronger fiber than do their diploid relatives. According to Jiang et al. (1998), several QTL located on the D genome suggested that D genome loci had been used for the synthesis of fiber subsequent to polyploidy formation.

(h) *Creation of new crop species:* New crop species can be developed by polyploidy as triticale as the best example which is an allopolyploid between *Triticum aestivum* and *Secale cereal*. Poland, Germany, and France mainly cultivate the triticale varieties. An induced polyploid variety *Raphanobrassica* was of no use as the desired traits were not obtained from the cross. Another new autotetraploid variety was produced in kiwi (*Actinidia chinensis*) with the help of colchicine treatment, highlighting the considerable potential of this method to produce new cultivars with satisfactory fruit size (Wu et al. 2012).

10.7 Conclusions

Despite the prevalent occurrence of polyploidy in nature and the occurrence of its footprints in all angiospermic genomes, the question of effects of polyploidy on the evolutionary route of a species is still unclear. Earlier questions about the role of polyploidy in response to environmental stress or whether genome doubling is advantageous or disadvantageous to evolutionary success are being revisited using current genomic tools. Studies based on molecular levels are evident for genomic change on numerous levels of regulation related to polyploidization. However, the effects of polyploidy on fitness under different environmental conditions are not known still in many cases, and there is little evidence that observed transcriptional and genomic changes actually lead to faster evolution or greater adaptation in

natural populations. Polyploids are looking generally different from their progenitors in morphological, ecological, physiological, and cytological characteristics that can contribute both to exploitation of a new niche and to reproductive isolation. Therefore, polyploidy is a major mechanism for adaptation and speciation in plants. The development of new crops and the interspecific gene transfer and also the origin of new crops can be traced with the help of polyploidy breeding. Thus, polyploidy is an interesting field of study to demonstrate the evolution of crop plants and utilize their variability in the field of crop breeding.

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