

Review Article

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Polyploidy and its implications in plants breeding – A review

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Article Info

Abstract

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Polyploidy is a prominent force of shaping the evolution of in most of ferns and flowering plants. Polyploidy has tremendous contribution in plants improvement program. It is the polyploidy breeding through which new crops can be developed and interspecific genes can be transferred and also the origin of crops can be traced. It is now an interesting field of study to reveal the evolution of crop plants and utilizing their variability in the field of crop breeding. Polyploidy generally differ markedly from their progenitors in morphological, ecological, physiological and cytological characteristics that can contribute both to exploitation of a new niche and to reproductive isolation. As a result, polyploidy is a major mechanism of adaptation and speciation in plants. Another implication of polyploidy is development heterosis in plant breeding. Unlike diploids which may lose heterosis with each consecutive generation due to segregation, polyploidy imposes pairing of homologous chromosomes, thus preventing intergenomic recombination. In this way, heterozygosity is maintained throughout generations. One of the immediate and obvious consequences of polyploidy in plants is an increase in cell size which in turn leads to enlarged plant organs relative to diploids. It is also used in bridge crossing, development of seedless fruits like watermelon and production of apomictic crops.

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Introduction

Plant breeding is being playing significant role for the improvement of the characteristics of the plants. Different types of breeding techniques have been developed for the crop improvement. Hybridization is being utilizing for creating genetic variation (Stebbins, 1958). Beside Mendelian variation, mutation coupled with or without hybridization is used to mutant formation. Moreover, polyploidy is also contributes to the evaluation of crop species.

Polyploidy is an intriguing phenomenon in plants that has provided an important pathway for evolution and speciation (Levin, 1983). Polyploids are organisms with multiple sets of chromosomes in excess of the diploid number (Acquaah, 2007; Chen, 2010; Comai, 2005; Ramsey and Schemske, 1998). Polyploidy is common in nature and provides major mechanism for adaptation and speciation. Approximately 50-70% of angiosperms, which include many crop plants, have undergone polyploidy during their evolutionary process (e.g., cotton, tobacco, wheat, canola, soybean, potato,

sugarcane, cordgrass, and dandelion (Chen et al., 2007). Flowering plants form polyploids at a significantly high frequency of 1 in every 100,000 plants (Comai, 2005).

Many studies have been carried out to understand the nature of polyploidism. To understand polyploidy, a few basic notations need be defined. Though polyploidy got attraction initially due to their unique cytogenetics and their reproductive isolation, it was soon recognized that polyploids also exhibited distinctive phenotypic traits and hybrid vigor useful for agriculture (Ramsey and Schemske, 2002). The polyploidy species formed independently from heterozygous diploid progenitors may provide important source of genetic variation. The basic complete set of chromosomes is designated by “x” while the total number of chromosomes in a somatic cell is designated “2n”. The total number of chromosomes a somatic cell is twice the haploid number (n) in the gametes (Acquaah, 2007; Otto and Whitton, 2000). Even though, the first polyploid was

discovered over a century ago, the genetic and evolutionary implications of polyploidy are still being explained (Bennett, 2004). Therefore, this paper is prepared to over overview and understands different types of polyploidy and their implication on crop plants.

Classification of polyploids

Polyploids may be classified based on their chromosomal composition into euploids and aneuploids. Euploids constitute the majority of polyploids.

Euploids

Euploids are polyploids with multiples of the complete set of chromosomes specific to a species. Depending on the composition of the genome, euploids can be further classified into autopolyploids and allopolyploids. Tetraploidy is the most common class of euploids (Comai, 2005).

Table 1. A list of major crops and their ploidy.

Common Name	Ploidy	Name	Propagation
Maize	2x = 20	Diploid	Outcrossing
Wheat	6x = 42	Hexaploid	Outcrossing
Rice	2x = 24	Diploid	Selfing
Potatoes	4x = 48	Tetraploid	Outcrossing; vegetative
Soybean	2x = 40	Diploid	Selfing
Barley	2x = 14	Diploid	Selfing
Tomatoes	2x = 24	Diploid	Selfing
Bananas	3x = 33	Triploid	Vegetative
Watermelon	2x = 22	Diploid	Outcrossing
Sugarcane	8x = 80	Octaploid	Outcrossing; vegetative
Sugar beet	2x = 18	Diploid	Outcrossing
Cassava	2x = 36	Diploid	Outcrossing; vegetative

Autopolyploids are also referred to as autopoloids. They contain multiple copies of the basic set (x) of chromosomes of the same genome (Acquaah, 2007; Chen, 2010). Autopoloids occur in nature through union of unreduced gametes and at times can be artificially induced (Chen, 2010). Natural autopoloids include tetraploid crops such as alfafa, peanut, potato and coffee and triploid bananas. They occur spontaneously through the process of chromosome doubling. Chromosome doubling in autopoloids has varying effect based on the species. Spontaneous chromosome doubling in ornamentals and forage grasses has led to increased vigour (Acquaah, 2007). Due to the observed advantages in nature, breeders have used the process of

chromosome doubling *in vitro* through induced polyploidy to produce superior crops. For example, induced autotetraploids in the watermelon crop are used for the production of seedless triploid hybrids fruits (Fig 5.1) (Wehner, 2008). Such polyploids are induced through the treatment of diploids with mitotic inhibitors such as dinitroaniles and colchicine (Compton et al., 1996). To determine or identify the ploidy status of induced polyploids, several approaches may be used. These include, chloroplast count in guard cells, morphological features such as leaf, flower or pollen size (gigas effect) and flow cytometry (Brummer et al., 1999; Heping et al., 2008). Examples of Autopolyploidy are Autotriploids, and Autotetraploids.

Autotriploids: Presence of three full sets of chromosomes of the same species. They are highly sterile due to incomplete gamete formation. It is useful for asexually propagated plants like banana, sugarcane, apple, watermelon, sugar beet, etc.

Autotetraploids: Presence of four full set of chromosomes of the same species. They are very stable and fertile as pairing partners are available during meiosis. They are usually larger and more vigour than the diploid species. It is applicable in rye, grasps, alfalfa, groundnut, potato, coffee etc. Autopolyploids may be originated by any one of the following several ways:

Spontaneous: Chromosomes become double occasionally in somatic tissues and also form unreduced gametes in low frequencies due to certain genes, e.g., genes causing complete asynapsis or desynapsis. Spontaneous somatic chromosome doubling is a rare event (Lewis, 1980).

Production of adventitious buds: Callus developed at the cut end of stem due to decapitation may have some polyploidy cells which are commonly found in Solanaceae.

Physical agents: Polyploidy may be occurred due to heat or cold treatments, centrifugation and X-ray or gamma ray irradiation in low frequencies. Development of tetraploid branches in *Datura* is due to cold treatment. Tetraploid progeny of 2-3% may produce due to heat treatment of 38-45 °C on the maize plant or ears. Successful application of heat treatment on barley, wheat, rye and some other crops have been found.

Regeneration *in vitro*: Some of the plants regenerated from callus and suspension culture may be polyploids as found in the *Nicotiana*, *Datura*, *Oryza sativa*, etc.

Colchicine treatment: It is the most effective and widely used treatment for polyploidy production. Colchicine is an alkaloid, which is found in the seeds and bulbs of autumn crocus (*Colchicum autumnale*). It can be used in aqueous solutions, in paste with lanolin, in glycerine or in agar. Low concentrations are applied to the lethal buds or growing tips of the desired plants. Colchicine acts as spindle suppressors at mitosis and results in cells with double number of chromosomes per cell. Some examples of colchicines treatments are as-

Seed treatment: Seeds are treated with colchicines of 0.001-1% for 1-10 days.

Seedling treatment: Shoots of young seedlings are treated with colchicines for 3-24 h.

Growing shoot apices: These are treated with 0.1-1.0% colchicines for once or twice daily for a few days.

Woody plants: About 1% colchicines is generally used for application on shoot buds.

Allopolyploids: Are a kind of Euploidy, they are also called allopolyploids. Allopolyploids are a combination of genomes from different species (Acquaah, 2007). They result from hybridization of two or more genomes followed by chromosome doubling or by the fusion of unreduced gametes between species (Acquaah, 2007; Chen, 2010; Jones et al., 2008; Ramsey and Schemske, 1998). This process is a key in the process of speciation for angiosperms and ferns (Chen, 2010) and occurs often in nature. Important natural allopolyploid crops include strawberry, wheat, oat, upland cotton, oilseed rape, blueberry and mustard (Acquaah, 2007; Chen, 2010). To differentiate between the sources of the genomes in an allopolyploid, each genome is designated by a different letter.

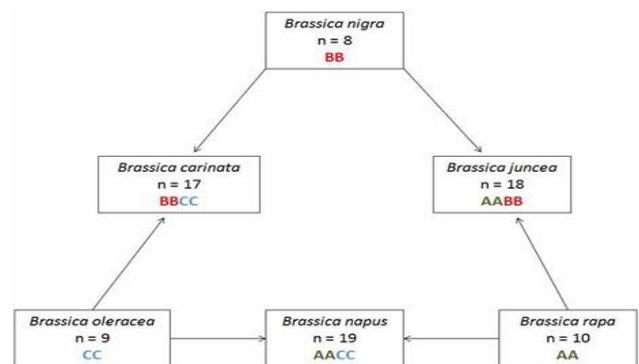


Fig. 1: Triangle of U showing the origin of cultivated mustard.

Aneuploidy

Aneuploids are polyploids that contain either an addition or subtraction of one or more specific chromosome(s) to the total number of chromosomes that usually make up the ploidy of a species (Acquaah, 2007; Ramsey and Schemske, 1998). Aneuploids result from the formation of univalents and multivalents during meiosis of euploids (Acquaah, 2007). For

example, several studies have found that 30-40% of progeny derived from autotetraploid maize are aneuploids (Comai, 2005). With no mechanism of dividing univalents equally among daughter cells during anaphase I, some cells inherit more genetic material than others (Ramsey and Schemske, 1998). Similarly, multivalents such as homologous chromosomes may fail to separate during meiosis leading to unequal migration of chromosomes to opposite poles. This mechanism is called non-disjunction (Acquaah, 2007). These meiotic aberrances result in plants with reduced vigor.

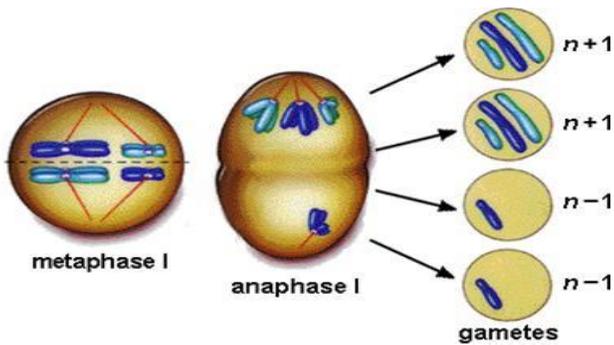


Fig. 2: Non-disjunction.

Aneuploids are classified according to the number of chromosomes gained or lost (Table 2).

Table 2. Classification of aneuploids.

Term	Chromosome number
Monosomy	2n-1
Nullisomy	2n-2
Trisomy	2n+2
Tetrasomy	2n+2
Pentasomy	2n+3

Mechanisms of polyploidy formation

Several cytological mechanisms are known to spontaneously induce polyploidy in plants (Ramsey and Schemske, 1998). One such route involves non-reduction of gametes during meiosis, a process called meiotic nuclear restitution. The formed gametes (2n) contain the somatic nuclear condition of cells. Meiotic aberrations related to spindle formation, spindle function and cytokinesis have been implicated in this process (Ramsey and Schemske, 1998). The subsequent union of reduced and non-reduced gametes leads to the formation of polyploids (Acquaah, 2007; Ramsey and Schemske, 1998). For example, autotetraploids may be formed in a diploid population through the union of two

unreduced (2n) gametes as was found in the F1 progenies of open-pollinated diploid apples (Ramsey and Schemske, 1998). Similarly, spontaneous allotetraploids were formed in 90% of F2 progenies of interspecific crosses between ornamental crop plants (Ramsey and Schemske, 1998). Another example is the formation of autohexaploid *Beta vulgaris* (sugar beet) and alfalfa from cultivated autotetraploid varieties apparently from the union of reduced (2x) and unreduced (4x) gametes (Bingham, 1968; Hornsey, 1973).

Another major route for polyploid formation is through somatic doubling of chromosomes during mitosis. In nature, the formation of polyploids as a result of mitotic aberrations has been reported in the meristematic tissue of several plant species including tomato and in non-meristematic tissues of plants such as bean (Coleman, 1950; Ramsey and Schemske, 1998). Artificial induction of polyploids through the inhibition of mitosis is routine in plant breeding. High temperatures above 40 °C have been used to induce tetraploid and octoploid corn seedlings albeit with low success of 1.8% and 0.8% respectively (Randolph, 1932). Currently, chemical mitotic inhibitory agents such as colchicine or dinitroanilines are used to induce polyploidy in crop plants. A typical example is the production of tetraploid watermelon plants for the production of seedless triploid watermelon (Compton et al., 1996). The major pathways involved in polyploidy formation are represented in Fig. 3.

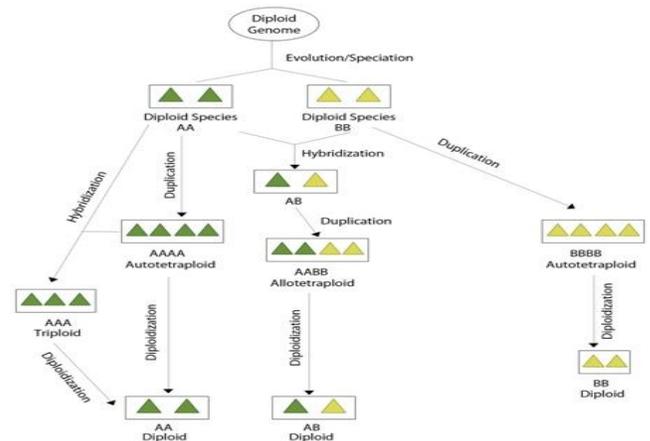


Fig. 3: Major pathways in the formation of polyploidy.

Alterations associated with polyploidy

Several changes in the plant accompany spontaneous or induced polyploidy. These may be changes in genetic

composition, physiological mechanisms, structural composition and vigor.

Genetic changes: following genome duplication involve the rapid loss of chromosomal segments in a process called diploidization. Diploidization describes the process by which a polyploid genome become more 'diploid-like' in character (Fig. 3) (Clarkson et al., 2005; Comai, 2005; Ozkan and Feldman, 2009). It is necessary to eliminate duplicated genes in a newly formed polyploid to avoid gene silencing as well as to stabilize fertility (Chen et al., 2007; Chen, 2010; Clarkson et al., 2005; Comai, 2005).

Morphological change: The increase in nuclear ploidy affects the structural and anatomical characteristics of the plant. In general, polyploidy results in increased leaf and flower size (Fig. 4), stomatal density, cell size and chloroplast count (Dhawan and Lavania, 1996). These phenomena are collectively referred to as the gigas effect (Acquaah, 2007).

Physiological changes are also known to accompany genome duplication. These mainly result from change of metabolism resulting in a general increase in secondary metabolites (Levin, 1983). This property has found application in the breeding of medicinal herbs in the production of pharmaceuticals.



Fig. 4: A comparison between the leaf and flower of a (A) diploid and (B) induced tetraploid watermelon illustrating the gigas effect.

Implications of ploidy in plant breeding

Heterosis in allopolyploids

Heterosis or hybrid vigor is the difference between the hybrid and the mean of the two parents and is characterized by increased vigor and superior qualitative or quantitative traits (Chen, 2010; Dhawan

and Lavania, 1996; Lamkey and Edwards, 1999). However, unlike diploids which may lose heterosis with each consecutive generation due to segregation, allopolyploidy and autopolyploidy imposes pairing of homologous chromosomes, thus preventing intergenomic recombination (Comai, 2005). This concept is called preferential or selective pairing and is the tendency for a doubled set of chromosomes to pair independently of the doubled set of chromosomes of the other species (Acquaah, 2007). In this way, heterozygosity is maintained throughout generations (Acquaah, 2007; Comai, 2005).

Generally, the parents used in hybrid formation should be within subspecies or between subspecies. An example of a man-made interspecies allopolyploid hybrid is triticale. Triticale was developed to combine good qualities of wheat including high yield and grain quality with the hardiness (disease and stress tolerance) of rye (Acquaah, 2007; Chen, 2010). The process of hybrid formation for polyploids is not without setbacks. Many interspecific hybrids have low fertility and viability due to hybrid incompatibilities (Chen, 2010; Orr, 1996). To increase the heterosis, fertility and viability of interspecific hybrids, several factors should be considered. The parents used should be of diverse genetic background and preferably heterozygous (Acquaah, 2007; Chen, 2010).

Inbreeding in polyploids

Self pollination is an important method for attaining homozygosity in breeding. Through this process, it is possible to fix desired alleles in the background of a crop. In general, it takes approximately 3.80 more generations for an autotetraploid to reach the same level of homozygosity as the diploid (Dudley, 1963). Fixing a trait controlled by a single gene in autotetraploid would require four identical alleles to achieve homozygosity.

Effect of polyploidy on sterility

Since autopolyploids contain more than two homologous chromosomes, meiosis results in the formation of univalents and multivalent, unlike in diploids where bivalents are usually formed (Acquaah, 2007). For instance during meiosis, autotetraploids may form bivalents, quadrivalents and univalents (Fig 5). The ratio of these gametes following meiosis determines the fertility of a polyploid individual. Univalents and trivalents result in non-functional sterile gametes and

are the most common in triploids, making them sterile. Rigorous and effective selection strategies for fertile autopolyploids are practiced in the development of inbred

lines. Breeders rogue out autopolyploids with low seed set as well as those with morphological abnormalities (Andrus et al., 1971).

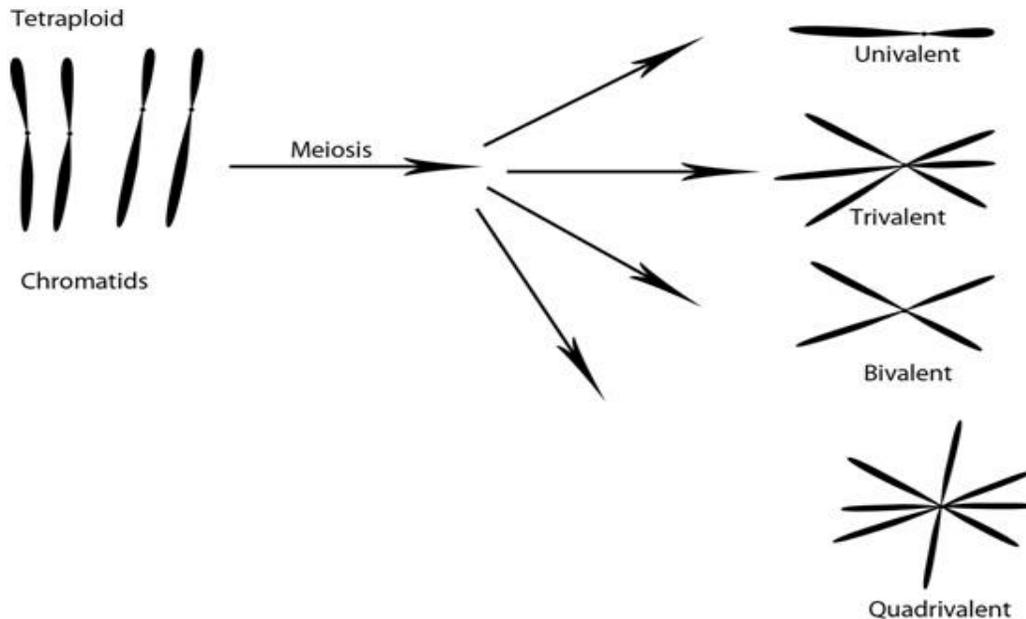


Fig. 5: Gamete formation in autotetraploids. Trivalents and univalents result in sterile gametes while bivalents and quadrivalents result in fertile gametes.

Common applications of ploidy in crop plants

Mutation breeding

High frequencies of chromosome mutations are desirable in modern breeding techniques, as they provide new sources of variation. The multiallelic nature of loci in polyploids has many advantages that are useful in breeding. The masking of deleterious alleles, that may arise from induced mutation, by their dominant forms cushions polyploids from lethal conditions often associated with inbred diploid crops (Gaul, 1958).

Mutation breeding exploits the concept of gene redundancy and mutation tolerance in polyploid crop improvement in two ways. First, polyploids are able to tolerate deleterious allele modifications post-mutation, and secondly, they have increased mutation frequency because of their large genomes resulting from duplicated condition of their genes (Gaul, 1958). The high mutation frequencies observed with polyploids may be exploited when trying to induce mutations in diploid cultivars that do not produce enough genetic variation after a mutagenic treatment. This approach has

been used in mutation breeding of *Achimenes* sp. (nut orchids) by first forming autotetraploids through colchicine treatment followed by the application of fast neutrons and X-rays. In this study, the autotetraploids were found to have 20-40 times higher mutation frequency than the corresponding diploid cultivar due to the large genome (Broertjes, 1976).

Ornamental and forage breeding

One of the immediate and obvious consequences of polyploidy in plants is an increase in cell size which in turn leads to enlarged plant organs, a phenomenon termed gigas effect (Fig. 4) (Acquaah, 2007; Levin, 1983). For example, the volume of tetraploid cells usually is about twice that of their diploid progenitors (Acquaah, 2007; Emsweller and Ruttle, 1941; Levin, 1983; Schepper et al., 2001). The increase in cell volume however is mainly attributed to increased water and not biomass. Therefore, its application is limited for breeding agronomically important crops such as cereals. Although chromosome doubling may result in significantly larger seeds and increased seed-protein content in cereal crops, this advantage is offset by low seed set (Dhawan and Lavania, 1996).

In contrast, the gigas effect has been explored in tree, ornamental, forage crop and fruit breeding (Emsweller and Ruttle, 1941; Schepper et al., 2001). For example, through induced polyploidy, breeders have developed Bouschet tetraploid grapes with more yield and juice content than the diploid progenitor Alicante (Olmo, 1952). A strong inverse correlation between DNA content and development rates in plants has been reported by several authors (Levin, 1983; Smith and Bennett, 1975). It has been attributed to lower auxin levels, reduced surface to volume ratio and altered nuclear surface to cell volume ratio (Acquaah, 2007; Levin, 1983). The slower growth rate of polyploids allows them to flower later and for a longer period of time than their diploid progenitors (Levin, 1983). This quality may be of interest especially in ornamental breeding.

Seedless fruits

The seedless trait of triploids has been desirable especially in fruits. Commercial use of triploid fruits can be found in crops such as watermelons and are produced artificially by first developing tetraploids which are then crossed with diploid watermelon. In order to set fruit, the triploid watermelon is crossed with a desirable diploid pollen donor (Fig. 6).

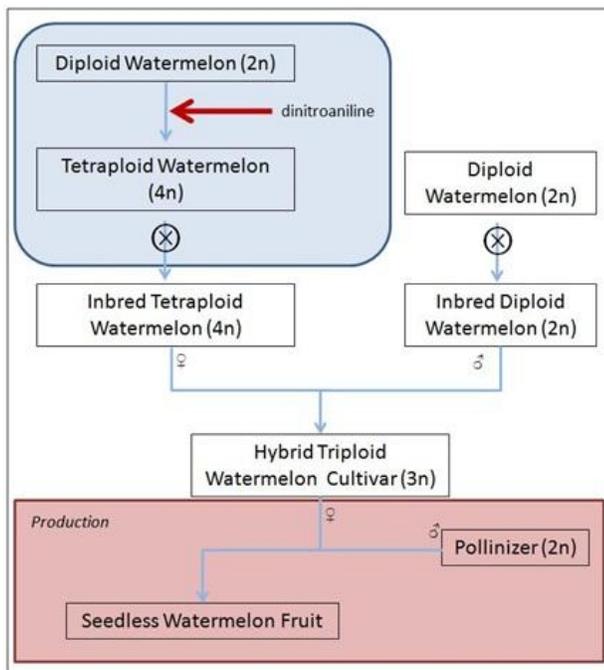


Fig. 6: A flow diagram showing the production of seedless triploid watermelon.

Bridge crossing

Another breeding strategy that utilizes the reproductive superiority of polyploids is bridge crossing. When sexual incompatibilities between two species are due to ploidy levels, transitional crosses can be carried out followed by chromosome doubling to produce fertile bridge hybrids. This method has been used to breed for superior tall fescue grass (*Fescue arundinacea*) from Italian ryegrass ($2n=2x=14$) and tall fescue ($2n=6x=42$) by using meadow grass (*Fescue pratensis*) as a bridge species (Fig. 7) (Acquaah, 2007). The same principle has been applied in fixing heterozygosity in hybrids by doubling the chromosomes in the superior progeny (Comai, 2005).

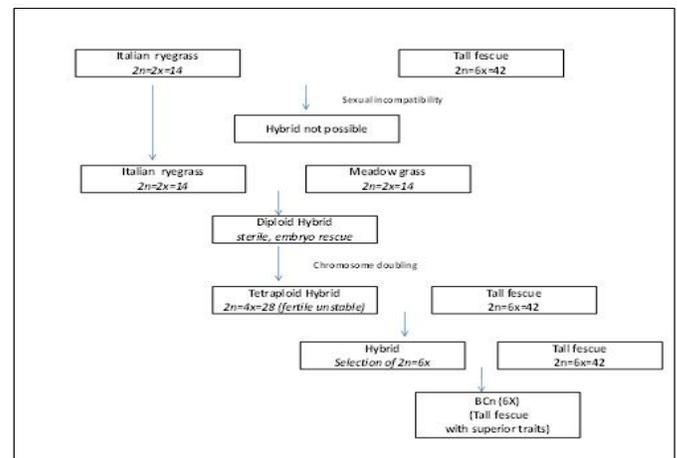


Fig. 7: The development of superior tall fescue grass through bridge crossing and induced tetraploidy.

Production of apomictic crops

Apomixis provides another avenue for use of polyploids in breeding. Apomixis provides an avenue for the production of seeds asexually through parthenogenesis. Most apomictic plants are polyploid but most polyploid plants are not apomictic (Otto and Whitton, 2000). In plants capable of both sexual and asexual reproduction, polyploidy promotes the latter (Dhawan and Lavania, 1996; Levin, 1983). Obligate apomicts are the most desired of hybrids but little gain has been realized towards their development. However, it has been suggested that obligate apomicts may be induced through development of very high ploidy plants (Levin, 1983). An example of an obligate apomict achieved at high ploidy level is the octoploid of the grass, *Themeda triandra* (Levin, 1983).

Conclusions

Polyploidy has significant importance in plant improvement program. Polyploids can be classified into euploids and aneuploids main classes. euploids are originated either through spontaneous, physical agent, regeneration *in vitro* or colchicines treatment. While aneuploids originated through addition or subtraction of one or more specific chromosome(s). Several alterations associated in the plant accompany spontaneous or induced polyploidy may be changes in genetic composition, physiological mechanisms, structural composition and vigor. Generally polyploidy can be utilized to create genetic variation and hybrid vigor in crops which is adaptable to biophysical tolerance/resistance purpose, to produce enlarged plant organs relative to diploids, . It is also used in bridge crossing, development of seedless fruits like watermelon and production of apomictic crops.

Conflict of interest statement

Author declares that there is no conflict of interest.

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