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18. Polyploidy Breeding

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Abstract:

Polyploidy breeding, an essential aspect of plant genetics, significantly alters crop development by manipulating the chromosomes. This process includes both euploidy and aneuploidy (the increase of chromosomal sets over the diploid level), which results in improved crop characteristics and variety. The historical relevance of Triticale lies in its critical milestones, such as the synthesis of the crop and the discovery of colchicine's role in inducing polyploidy. Aneuploidy plays a vital function in genetic research, especially in polyploid species such as tobacco and wheat. It helps in the localization of genes and enhances our understanding of their characteristics.

Monoploids and haploids, although less resilient, streamline the process of trait inheritance and the isolation of mutations. The processes of autopolyploidy and allopolyploidy, which include the multiplication of chromosomes or the merging of genomes across different species, have resulted in the production of robust and high-quality crops like wheat, tobacco, and cotton. Polyploidy breeding, despite facing obstacles like as genetic instability and unpredictable phenotypic expression, is nevertheless a highly influential method for improving crop resilience, diversity, and quality. This strategy is crucial for expanding agricultural production and ensuring food security.

Keywords:

Polyploidy, Chromosome Stability, Haploid, Chromosome Aberration, Yield.

18.1 Introduction:

Within the field of plant breeding, it has long been assumed that the number of chromosomes in a species remains constant. The mitotic and meiotic divisions are often precise, ensuring chromosomal stability across different species.

Notwithstanding this consistency, there are occasional anomalies that lead to the appearance of individuals with an abnormal number of chromosomes.

Although rare, these anomalies have had a substantial impact on the development of crops, playing a crucial role in the progress of plant breeding.

This discussion will explore the many forms of chromosomal abnormalities and their significance in improving crop varieties.

18.2 Chromosomal Dynamics in Crop Genetic Enhancement:

Somatic and Gametic Chromosome Numbers:

- The somatic chromosome number is designated as 2n.
- The chromosome number of gametes is denoted by n.

Haploid and Monoploid Definitions:

- An individual with the gametic chromosome number, n, is haploid.
- A monoploid is a haploid of a diploid species with the basic chromosome number, x.

Diploid Species and Genome Composition:

- In a diploid species, nx=x; one x constitutes a genome or chromosome complement.
- Different chromosomes of a single genome are distinct in morphology and/or gene content and homology.

Genome Number in Polyploids:

- A diploid species has two genomes, a triploid has three, and a tetraploid has four, and so on.

Heteroploids and Heteroploidy:

- Chromosome numbers other than diploid (2x, and not 2n) are known as heteroploids.
- The situation of having a chromosome number other than diploid is called heteroploidy.

Aneuploidy:

- Heteroploidy changes determined in relation to the somatic genome are known as aneuploidy.
- Aneuploid changes usually involve one or a few chromosomes of the chromosome number (2n and not 2x).

Euploidy:

- Heteroploidy that involves one or more complete genomes is called euploidy.

Milestones in the History of Heteroploidy and Chromosome Manipulation in Plant Breeding:

- **1907**: Lutz discovered an autotetraploid (4n) in an experimental population of *Oenothera*.
- **1910**: Blakeslee discovered the globe mutant of *Datura stramonium,* which is an autotetraploid.
- **1916**: Winkler produced the first reported case of aneuploidy, an autotetraploid in *Solanum nigrum*, by decapitating shoots and regenerating tetraploid shoot buds from the callus.
- **1917**: Winge suggested that interspecific hybridization followed by chromosome doubling may be important in the evolution of new species.
- **1890**: The first species synthesized experimentally was *Triticale* by Rimpau, from a cross between *Triticum* and *Secale,* although its chromosome number was not studied until 1936.
- **1920**: Belling demonstrated that the globe mutant is trisomic.
- **1925**: Clausen and Goodspeed synthesized *Nicotiana digluta* by spontaneous chromosome doubling of the F1 hybrid from the cross *Nicotiana glutinosa* (n=12 female) × *N. tabacum* (n=24, male).
- **1937**: Blakeslee and Nebel described the action of colchicine treatment for chromosome doubling.
- **1955**: The effect of colchicine on mitosis was discovered.

18.3 Genetic Chromosomal Variations and Notations:

The table presents a thorough categorization of chromosomal variants, each with its distinct notation. Chromosomal variations refer to alterations in the number of chromosomes and the makeup of the genome. These differences are important for comprehending genetic diversity. The table provides a clear guide for researchers and geneticists to navigate through these variations and their related notations.

Table 18.1: Classification of Chromosomal Variations and Corresponding Notations

Classification	Chromosomal variation	Notation
Heteroploid	A change from 2x	-
1. Aneuploid	One or few chromosomes extra or missing from 2n	2n±few
Nullisomic	One chromosome pair missing	2n-2
Monosomic	One chromosome missing	2n-1
Double monosomic	One chromosome from each of 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
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 2 copies of one genome or 2 copies of 2 or more genomes	
a. 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
Autooctaploid	Eight copies of one genome	8x
b. Allopolyploid	Two or more distinct genomes (generally each genome has two copies)	
Allotetraploid	Two distinct genomes	$(2x_1+2x_2)$
Allohexaploid	Three distinct genomes	$(2x_1+2x_2+2x_3)$
Allooctaploid	Four distinct genomes	$(2x_1+2x_2+2x3+2x_4)$

18.3.1 Aneuploidy:

Aneuploidy, particularly monosomics and trisomics, plays a critical role in genetic research involving polyploid species such as tobacco, wheat, and oats. Trisomics are defined by the nature of the extra chromosome relative to the haploid set, categorized as primary when unaltered, secondary when forming an isochromosome, and tertiary when involving a translocated chromosome.

These aneuploid organisms frequently emerge due to meiotic irregularities that lead to the formation of gametes with either an additional or a missing chromosome, a phenomenon observed in species like *Datura*.

Moreover, autotriploid plants are identified as invaluable sources for producing a wide array of aneuploids, as the meiotic anaphase in triploids tends to result in an extensive assortment of aneuploid offspring.

A. The Relationship Between Aneuploidy and Morphogenetic Expression:

- Monosomics often exhibit weaker than normal morphology and typically don’t survive in diploid species.
- Morphology can vary among trisomics, not always indicating chromosome change. Therefore, cytological analysis is essential for aneuploidy confirmation.
- Meiosis in aneuploids shows a deviation from normal chromosome distribution, particularly evident in monosomics and trisomics.
- Aneuploid transmission through pollen is generally inefficient due to creation, with normal pollen outcompeting aneuploid pollen.

B. Mechanisms Underlying Aneuploid Formation:

- Spontaneous Aneuploidy: Aneuploids typically emerge spontaneously at a low rate due to meiotic inconsistencies, resulting in n+1 and n-1 gametes.
- Source from Autotriploids: Autotriploid plants are excellent producers of aneuploids due to irregular meiotic anaphase, offering a full spectrum of aneuploid progenies.
- Role of Tetrasomic Plants: Tetrasomic plants are capable of generating a considerable frequency of n+1 gametes, which is valuable for trisomic production.
- Asynaptic and Desynaptic Mutants: Mutations that lead to asynapsis or desynapsis in meiosis can also result in aneuploids, as these conditions affect chromosome pairing and segregation.
- Translocation Heterozygotes: Plants with translocated chromosomes can produce n+1 and n-1 gametes, which may result in a variable frequency of aneuploid progeny.

C. Applications in Crop Improvement:

- Aneuploids facilitate studies on chromosome loss or gain effects, enhancing understanding of individual gene expression and character.
- They help locate linkage groups and genes on chromosomes, especially when using secondary or tertiary trisomics.

- Aneuploids have revealed homoeology in wheat genomes, aiding in compensatory breeding strategies.
- They are instrumental in identifying chromosomes involved in translocations and in the production of substitution lines for gene transfer.

D. Chromosomal Techniques for Gene Localization in Plant Breeding: A Comprehensive Analysis of Aneuploids

a. Nullisomic Analysis:

- Identifies chromosomes with specific genes in polyploid species by examining plants lacking certain chromosomes.
- Analysis involves studying plants with missing chromosomes to see the effect on phenotype, particularly the absence of dominant traits.
- Essential for understanding gene-chromosome relationships by observing the expression of traits in the F1 and F3 generations and through chromosome substitution.
- Critical for confirming cytologically that plants showing the recessive phenotype are indeed nullisomic.

b. Monosomic Analysis:

- Important for isolating genes in particular chromosomes, first applied in tobacco and extended to other species.
- Involves crossing complete sets of monosomics with disomic strains carrying dominant genes to observe segregation patterns.
- Utilizes chromosome substitution to transfer individual chromosomes or chromosome pairs with desirable genes to different genetic backgrounds.
- Enhances genetic analysis by allowing the study of individual chromosome effects on complex traits.

c. Trisomic Analysis:

- Suitable for diploid species, particularly when monosomic and nullisomic analyses aren't feasible.
- Utilizes trisomic individuals to locate genes on specific chromosomes by observing segregation ratios in progenies.
- Offers insight into gene presence on trisomic chromosomes, differentiating between 3:1 and 1:1 segregation pattern in progeny.
- Applied in various crops like maize, barley, and tomato to map genes and understand chromosome-specific effects.

d. Limitations of Aneuploid Analyses:

- Requires a complete set of aneuploids for analysis, which is often difficult and labor-intensive to produce and maintain.

- Cytogenetic analysis necessary for aneuploid studies is elaborate and time-consuming, adding to the resource demands of such research.
- The phenomenon of univalent shift complicates the maintenance of aneuploids, as progeny of aneuploid plants might become aneuploid for different chromosomes, making the analysis more complex.
- Cytological analysis is a prerequisite for confirming the aneuploid status, adding another layer of complexity to the process.

e. Monoploids and Haploids:

- Monoploids and haploids, while less robust than diploids, offer unique advantages in the realm of agricultural genetics.
- These plant types are pivotal for developing true-breeding lines as they allow for the production of homologous diploid lines through chromosome doubling techniques.
- The utility of monoploids and haploids extends to mutant isolation; mutations expressed in these plants can be instantly observable due to the single dose of genes.
- In genetic studies, the use of monoploids and haploids simplifies the inheritance patterns of traits, making it easier to identify and select for desirable alleles.
- Breeding strategies involving monoploids and haploids are particularly effective in species like asparagus, where male plants can undergo chromosome doubling to produce superior tetraploid varieties with desirable traits.
- The creation of doubled haploids through these plants enhances the frequency of desirable alleles in a population, which is particularly advantageous in selective breeding programs.
- Despite their advantages, the use of monoploids and haploids is not without challenges, as they typically exhibit lower viability and fertility compared to their diploid counterparts.

18.3.2 Autopolyploidy:

Autopolyploidy represents a natural and artificially induced genetic variation in plant breeding that results in the possession of more than two complete sets of chromosomes from a single species. This genetic condition is a key tool in plant breeding as it can lead to increased cell size, larger plant organs, and sometimes novel traits in plants, which can be beneficial for agricultural productivity and quality.

A. Origin and Mechanisms of Chromosome Number Increase:

- Spontaneously: Chromosome doubling may occur occasionally in somatic tissues, and the production of unreduced gametes can happen at low frequencies. This can be due to certain genes that cause complete asynapsis or desynapsis during meiosis.
- Production of Adventitious Buds: This involves the regrowth of tissues or organs in unusual places. For example, the decapitation of some plants can lead to the development of a call us at the cut end of a stem, which may contain polyploid cells.
- Physical Agents: Exposure to heat or cold treatments, centrifugation, and radiation (like X-ray or gamma-ray) can lead to polyploidization. Temperature treatments have been used successfully in barley, wheat, and other crops.

- Regeneration in Vitro: Plants regenerated from cell cultures, such as callus and suspension cultures, may be polyploid. This method has been employed with various crop species including tobacco, rice, and others.
- Colchicine Treatment: Colchicine is the most effective and widely used method for inducing chromosome doubling. It is a chemical that, when applied to plants, disrupts spindle formation during cell division, resulting in doubled chromosome numbers. Colchicine is commonly used on seeds, seedlings, growing shoot apices, woody plants, and cereals to induce polyploidy.
- Other Chemical Agents: Chemicals like acenaphthene, 8-hydroxyquinoline, and nitrous oxide have also been found to have a polyploidizing effect, but they are much less effective than colchicine and are not commonly used.

B. Autopolyploidy and Its Evolutionary Significance:

Autopolyploidy plays a role in the evolution of plant species, contributing to genetic diversity and adaptability. Here's a professional summary of the information provided in the images:

- Autopolyploidy has had a limited but significant impact on the evolution of plant species, enhancing genetic variability and potential for adaptation.
- Present-day crop species such as potatoes (*Solanum tuberosum)* and coffee (*Coffea arabica*) are considered to be autopolyploids, with cultivated forms having higher chromosome numbers than their related wild species.
- Autotetraploids, with four sets of chromosomes, have been notably successful as crops compared to other types of autopolyploids.
- Forage grasses and several ornamental plants are also likely to be autopolyploids, as suggested by recent genomic in situ hybridization studies.
- Genomic in situ hybridization (GISH) has been a powerful tool for understanding the evolutionary relationships and genome organization of autopolyploids.
- For example, GISH studies indicate that the groundnut (*Arachis hypogaea*) and coffee (*Coffea arabica)* are allopolyploids, with *A. villosa* and *A. ipaensis* being the diploid progenitors for groundnut, and *C. congensis* and *C. eugenioides* for coffee.
- Comparative genomic studies have shown that most species of flowering plants and vertebrates have undergone whole genome duplications at some point in their evolutionary history.
- Whole genome duplications expand genetic diversity, with some duplicated genes diverging or becoming subfunctional, as indicated by transcriptome analyses.
- Rice (*Oryza sativa*) and Arabidopsis thaliana have experienced whole genome duplications multiple times in their evolutionary past, which has been key to their adaptability and survival.

C. Enhancing Crop Traits Through Autopolyploidy: Utilization and Outcomes:

- Autopolyploidy contributes to crop improvement by developing commercial varieties with enhanced traits.

- In India, varieties such as TV29 (Tea), Pusa Giant Berseem (Berseem), HMT-1 (*Hyoscyamus niger*), and Sugandha (*Vetiveria zizanoides*) are successful examples of autopolyploidy, showing traits like higher yield, drought tolerance, and increased oil yield.
- Triploids, resulting from hybridization between tetraploid and diploid strains, have advantages like the production of seedless watermelons, which are commercially grown in Japan and the USA.
- Triploid sugarbeets exhibit larger roots and more sugar per unit area than diploids, contributing to higher yields.
- A triploid clone of tea (*Camellia assamica)* produces larger shoots and more cured leaf per unit area, indicating better quality compared to diploid cultivars.

D. Limitations of Autopolyploidy:

- Autopolyploids often have a larger size but may accompany a higher water content, not always advantageous for all types of crop production.
- For seed crops, autopolyploids tend to show high sterility and poor seed set, leading to challenges in seed production.
- Fertility in autotetraploids can be slow to improve through hybridization and selection due to complex segregation patterns.
- Triploids cannot be maintained without clonal propagation due to genetic instability and the production of aneuploid gametes.
- The introduction of autopolyploidy does not guarantee an improvement in agricultural types; often, new polyploids exhibit undesirable features that require further breeding efforts to correct.
- The effects of autopolyploidy are unpredictable, and its utility must be determined experimentally for each crop species.

18.3.3 Allopolyploidy:

- Allopolyploids have genomes from two or more species; many of our crops are allopolyploids.
- A significant number of new allopolyploids have been created to develop new useful species, with the emergence of Triticale and other allopolyploids as evidence of successful breeding.

A. Origin and Production of Allopolyploids:

- Modern allopolyploids most likely resulted from chromosome doubling in F1 hybrids between two species from the same genus or different genera.
- Chromosome doubling could occur due to irregular mitotic cell division in somatic tissues, leading to allopolyploid sectors.
- Sexual progeny from branches with allopolyploid cells would themselves be allopolyploids.
- Another method involves irregular meiosis, where a complete failure of chromosome pairing could result in all chromosomes being included in one nucleus at telophase I, potentially leading to unreduced gametes and allopolyploid offspring.

B. Experimental Production of Allopolyploids:

- In some experimentally produced distant hybrids that were largely sterile, some branches were observed to be highly fertile with double the chromosome number of the F1 hybrid, resulting in fertile allopolyploid progeny.
- An example of this is the cross between Primula verticillata and P. floribunda, which led to an allotetraploid offspring.
- Another example is the cross between B. oleracea var. capitata (cabbage) and Raphanus sativus (radish), producing seeds that gave rise to the allotetraploid Raphanobrassica.

C. Synthetic Allopolyploids:

- Allopolyploids can be artificially produced by doubling the chromosome number with agents like colchicine, leading to synthetic allopolyploids.
- The process involves two main steps: (1) producing an F1 hybrid by crossing two species, and (2) chromosome doubling of this F1 hybrid, with many successful crosses achieved through in vitro techniques.
- Chromosome doubling generally is not a significant issue since most species respond to colchicine, but for those that do not, other agents may be used for chromosome doubling.

D. The Role of Allopolyploidy in Evolutionary Dynamics:

The concept of allopolyploidy serves as a cornerstone in understanding the evolutionary success of numerous plant species. This genetic phenomenon, where two or more distinct sets of chromosomes come together to forge a new polyploid species, has been a catalyst for innovation in the natural world and in agricultural practices.

As we look closely at the origin stories of our most valuable crops, we uncover the allopolyploid chapters that have not only enriched biodiversity but also provided us with the means to cultivate resilience and abundance in our fields. This fusion of genetics has not only stood the test of time but also promises a fertile future for plant breeding and genetic enhancement.

E. Fundamental Role in Plant Evolution:

- Allopolyploidy acts as a driving force in plant evolution by combining genomes from different species, leading to new genetic combinations and increased biodiversity.
- Approximately one-third of all flowering plants are believed to be allopolyploids, demonstrating the widespread occurrence of this phenomenon in nature.

F. Genetic and Phenotypic Advantages:

- Allopolyploids often exhibit greater vigor and adaptability than their diploid progenitors due to the merging of diverse genetic traits.

- These organisms are typically more resilient to environmental stresses, diseases, and pests, which is a direct benefit of their hybrid genetic backgrounds.

G. Identification and Analysis of Allopolyploids:

- Chromosome pairing during meiosis is a key indicator for identifying allopolyploid species. Homologous chromosomes from different species pair up, showing the hybrid nature of the organism.
- Modern molecular techniques, including DNA sequencing and genomic in situ hybridization (GISH), allow for the detailed analysis of allopolyploid genomes, shedding light on their complex ancestries.

Examples:

a. Wheat (*Triticum Aestivum*):

- Wheat is an allohexaploid, meaning it contains six sets of chromosomes, two sets from each of three different species.
- The evolutionary history of bread wheat began with a hybridization between a wild wheat, *Triticum urartu* (AA genome), and a relative of modern-day *Aegilops speltoides* (BB genome) to form *Triticum dicoccoides* (AABB genome).
- A subsequent cross with *Aegilops tauschii* (DD genome) led to the current allohexaploid wheat with a genome composition of AABBDD.
- This genetic composition has provided wheat with a rich gene pool, leading to traits like improved grain quality, disease resistance, and environmental adaptability.

b. Tobacco (*Nicotiana Tabacum*):

- Tobacco is an allotetraploid with a genome composition indicated as (SSBB). It originated from the natural hybridization of two diploid ancestors, *Nicotiana sylvestris* (SS genome) and *Nicotiana tomentosiformis* (BB genome).
- The combination of these genomes has resulted in a plant with the favorable attributes of both ancestors, such as increased alkaloid content, which is important for the plant's defense and for its use as a commercial product.

c. Cotton (*Gossypium* Species):

- Cultivated cotton species like *Gossypium hirsutum* (upland cotton) and *Gossypium barbadense* (Pima cotton) are allotetraploids with AD genomes, originating from a cross between a diploid African species with an A genome (such as *Gossypium herbaceum* or *Gossypium arboreum*) and a diploid American species with a D genome (*Gossypium raimondii*).
- The allopolyploid cotton has high fiber quality due to the combination of the fiber length from the D-genome parent and the fiber strength from the A-genome parent, making it one of the world's most valuable natural fibers.

d. Brassica Species:

- Many crops within the Brassica genus are allopolyploids, including *Brassica napus* (canola/rapeseed), *Brassica juncea* (mustard), and *Brassica carinata* (Ethiopian mustard).
- *Brassica napus* (canola/rapeseed) is an allotetraploid (AACC genome) formed from the hybridization of *Brassica rapa* (AA genome) and *Brassica oleracea* (CC genome).
- These species have been bred for various traits such as oil content and quality in canola, and disease resistance in mustard crops.
- The allopolyploid nature of these crops has been exploited to create hybrids that are more vigorous and productive than their parental species, providing valuable oils and vegetables for human consumption.

H. Implications for Plant Breeding:

- Plant breeders utilize the principles of allopolyploidy to create superior crop varieties by artificially inducing polyploidy, thus combining desirable traits from different species.
- This technique has been instrumental in developing crops with specific attributes such as increased size, better nutritional content, and resistance to adverse conditions.

I. Evolutionary and Breeding Challenges:

- While allopolyploidy can lead to beneficial traits, it also introduces complexities in genome organization and function those researchers and breeder need to understand and manage.
- The challenge lies in unravelling the intricate relationships between the inherited traits from multiple parental species and how they express in the allopolyploid offspring.

J. Strategic Utilization of Allopolyploidy in Crop Breeding:

- Allopolyploidy serves as a bridge in transferring characteristics from one species to another, especially from wild progenitors to cultivated varieties. This transfer often results in the creation of amphiploids, which are then backcrossed with recipient species to introduce desirable genes or groups of genes.
- Notable examples include the use of synthetic *N. digluta* as a bridging species to transfer rust resistance from *Ailanthus grovei* to wheat and from *Nicotiana plumbaginifolia* to *Nicotiana tabacum.*
- The creation of new crop species through allopolyploidy has been less successful due to high sterility and genetic instability. However, allopolyploids such as Triticale, a wheat-rye hybrid, have shown success in some environments due to their hardiness and yield.
- Allopolyploidy aids in widening the genetic base of existing allopolyploids by introducing variability. This is crucial for species with a narrow genetic base, such as *Brassica napus* (canola), where new genetic material is introduced from related species.

K. Challenges and Limitations of Allopolyploidy:

- The outcomes of allopolyploidy are unpredictable and may include undesirable traits such as low fertility, cytogenetic and genetic instability, and poor seed set.
- Newly synthesized allopolyploids often possess many defects and require considerable improvement through intensive breeding efforts.
- Only a small proportion of allopolyploids prove to be agriculturally promising, necessitating a process of trial and error to identify beneficial allopolyploids that can be developed into successful new crop species.
- Extensive breeding work is essential to improve the traits of allopolyploids, a process which is resource-intensive and time-consuming.

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