Chapter 4

The Application Models of Chromosomal Techniques in Agriculture

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Özet

Özellikle ıslah çalışmaları başta olmak üzere tarımda kromozomal teknikler, biyolojinin sitogenetik alanındaki gelişmelerine paralel olarak ilerlemektedir. Bu teknikler, özellikle ekonomik açıdan önemli bitkilerde, bitki genomlarından elde edilen genetik bilgi kullanılarak, bitki geliştirme çalışmalarında (örneğin; daha dayanıklı, daha verimli, besin değeri daha yüksek vb.) kullanılmaktadır. Kısaca kromozomal teknikler tercih edilen gelişmiş özellikler içeren tarımsal ürünlerin elde edilmesinde önemlidir. Tarımda kromozomal tekniklerin kullanım alanları ve bunların detaylı incelenmesi bu bölümün temelini oluşturacaktır. Bunlar sitogenetik, hibridizasyon ve poliploidi, kromozom mühendisliği, kromozoma özgü ıslah programları, fonksiyonel genomik, genetik haritalama, genom dizileme, polimeraz zincir reaksiyonu (PCR), düzenli aralıklı kısa palindromik tekrar kümeleri (CRISPR-CAS9) teknolojisi ve işaretleyici destekli seleksiyon (MAS) olarak sıralanabilir. Klasik sitogenetik yöntemler tarımsal ürünlerin geliştirilmesinde kullanılan en eski stratejilerdir. Hibridizasyon, poliploidi, kromozom mühendisliği ve kromozoma özgü ıslah programları bu stratejilerin devamı niteliğindeyken, moleküler sitogenetik ise en uç noktasını oluşturur. Bu bölümde, kromozomal tekniklerin tarımdaki uygulama modelleri en eskiden en yeniye doğru değerlendirilmiştir. Bunlardan ilki olan sitogenetik kromozomların sayı, şekil ve yapılarıyla ilgilenen genetiğin alt dallarından biridir. Hibridizasyon, birbirini tamamlayan iki tek sarmallı molekülün birleşerek çift sarmallı bir molekül oluşturması sürecidir; poliploidi ise somatik hücrelerde iki veya daha fazla kromozom setinin bulunmasıdır. Kromozoma özgü ıslah programları istenen özelliklere sahip tarımsal ürünler elde etmek kullanılan için yapay seçilim yöntemleridir. Moleküler sitogenetik, moleküler biyoloji ve sitogenetik tekniklerinin birleşmesiyle oluşan klasik sitogenetik yöntemlerin daha gelişmiş modelidir.

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1. Overview of Chromosomal Techniques

1.1. Cytogenetics

The cytogenetics, is a sub-branch of genetics that deals with the number, shape and structure of chromosomes. Although cytogenetics first emerged as a discipline in the early 1900s, the first cytogenetic applications in agriculture were Barbara McClintock's (1902-1992) studies on maize (McClintock and Creighton, 1931). Since then, the cytogenetics were used in crop domestication and development studies (e.g., more resistant, more productive, more nutritionally valuable etc.) using genetic information from plant genomes, particularly in economically important plants.

The cytogenetic techniques developed rapidly, particularly after Belling introduced the crushing method (Belling, 1921). The classical cytogenetics includes the function and movement of chromosomes during cell division, determination of chromosome structure and number (basic and diploid number), and karyotype analysis (Singh, 2018). The most appropriate situation to determine these chromosomal parameters is to observe the chromosomes in the metaphase stage of cell division (Figure 1). For this purpose, the plant seeds were germinated between moist Whatman papers in Petri dishes. Then, the root tips were pretreated in hydroxyquinoline, α-mono-bromonaphthalene, or colchicine; fixed with fixative solution (ethanol:acetic acid); stored in ethanol (70%); hydrolyzed with 1N HCl; stained with carmine, orcein, or fuchsin; and squashed for preparation and observation. At least 10 metaphase plates with well-distributed, uncontracted chromosomes, distinct chromosome morphology, and chromosomes lying in a plane are evaluated for observation. After imaging, the chromosomal measurements are performed using a karyotype computer software program. After the total chromosome lengths, long arm lengths, short arm lengths, and chromosome arm ratios are determined; the karyotype formulae, relative lengths, centromeric index values, and symmetry/asymmetry index values are calculated. The chromosomal types are determined based on chromosome arm ratios and centromere location according to the criteria proposed by Levan et al. (1964). The ideograms are drawn in order of chromosome type from largest to smallest (Figure 2).

The molecular cytogenetics is a more advanced model of classical cytogenetic methods combining molecular biology and cytogenetics techniques. Thus, it is a discipline that expands the scope of classical cytogenetic techniques consisting of routine chromosome analysis and increases the value of their intended use in agriculture. Molecular

cytogenetic applications of agricultural products began in the early 1970s with the advanced characterization of somatic chromosomes by C-banding and fluorescence in situ hybridization (FISH) techniques (Gill and Kimber, 1974) and progressed with DNA sequencing and mapping studies. The concepts related to classical and molecular cytogenetics are briefly mentioned in this section, as they will be covered in detail in other topics.

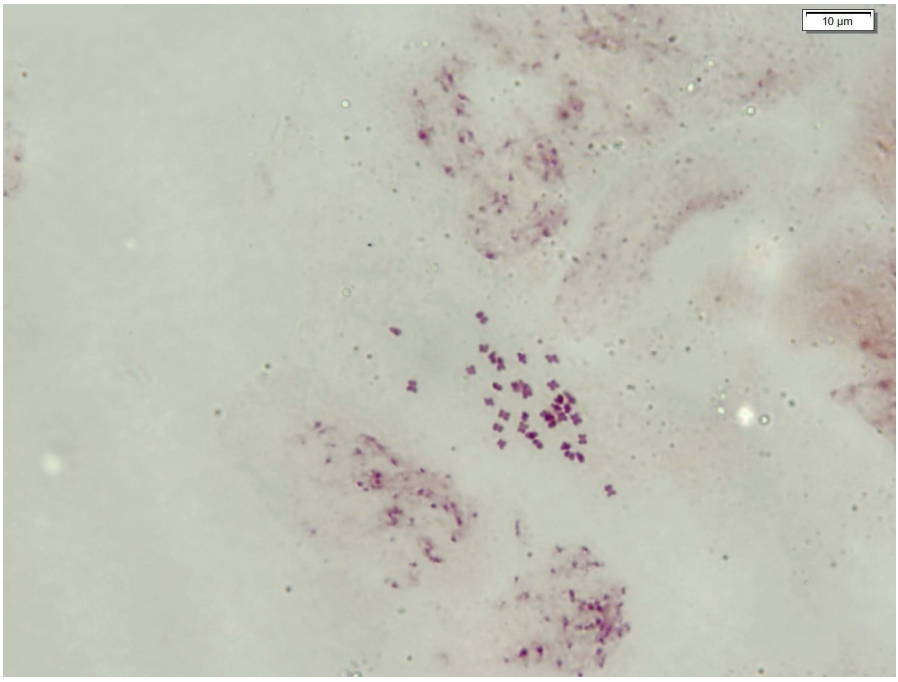

Figure 1. The metaphase plate used to observe chromosomes. It is important that metaphase areas have well-distributed, unshrunken chromosomes, distinct chromosome morphology, and chromosomes lying in one plane.

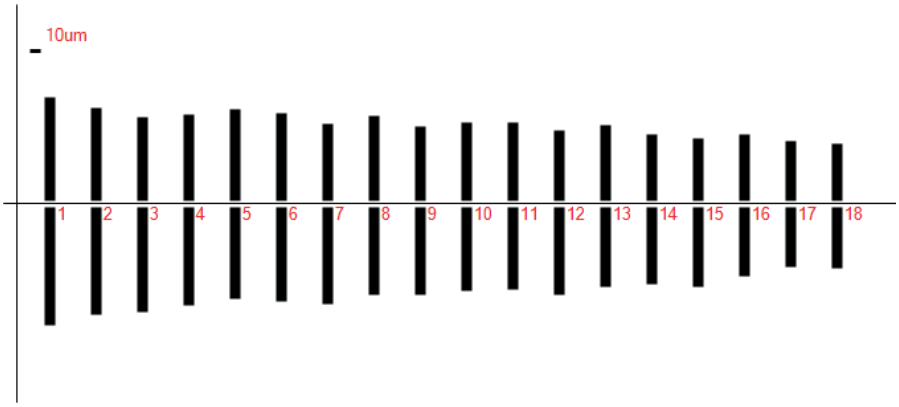

Figure 2. An example ideogram with diploid (2n = 36) chromosomes. The chromosomes are arranged from largest to smallest based on centromere position.

1.2. Hybridization and Polyploidy

The hybridization is a process in which two complementary single-stranded molecules combine to form a double-stranded, while polyploidy is the presence of more than two sets of chromosomes in somatic cells. In agriculture, hybridization enables the emergence of new genotypes and hybrids by crossing two genetically different plants. The artificial hybridization that a controlled crossover or artificial selection model, is one of the most important mechanisms in plant breeding. Important consequences of this mechanism are self- or cross-pollinated plant development and heterosis (hybrid vigour). The hybrid vigour is the display of superior or higher characteristics (biomass, growth rate etc.) in hybrid offspring compared to their parents (Chen, 2010).

Organisms may have one (monoploid, n) or two sets (diploid, $2n$) of chromosomes, but they may also have more than two sets (polyploid) of chromosomes. This mechanism, called general polyploidy, also has special definitions such as triploidy ($3n$), tetraploidy ($4n$), and pentaploidy ($5n$) (Figure 3). If the extra genome resulting from polyploidy comes from the same species, it is called autopolyploidy; if it comes from different species, it is called allopolyploidy (Eroğlu, 2022). The allopolyploidy is a mechanism that leads to the fixation of hybrid vigour. Some agricultural crops are grown as hybrids (*Oryza sativa*, *Zea mays*, *Brassica juncea* etc.), while others (*Gossypium hirsutum*, *Triticum aestivum*, *Arabidopsis suecica* etc.) are grown as allopolyploids (Chen, 2010).

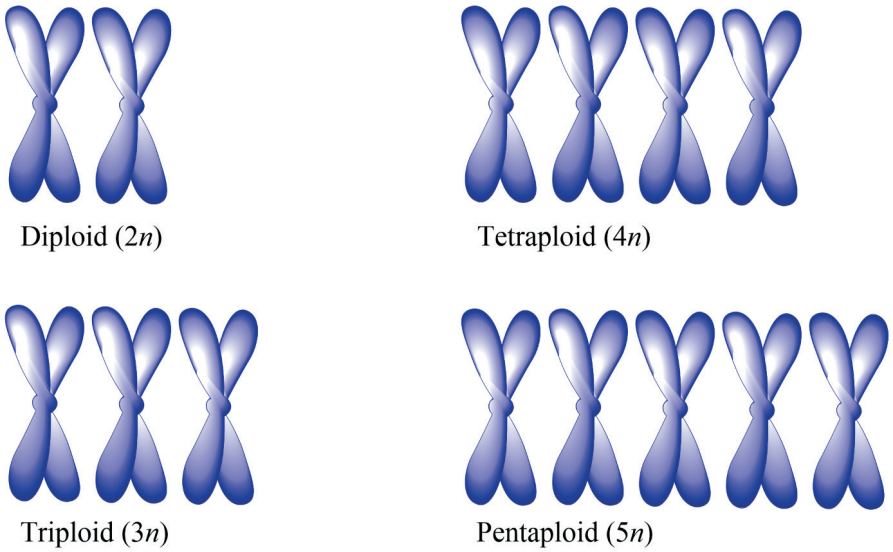

Figure 3. The general view of diploid (2n), triploid (3n), tetraploid (4n), and pentaploid (5n) chromosome sets. Here, autopolyploidy is present for polyploidy is expressed on only one homologous chromosome pair.

The polyploids can arise naturally or artificially. The natural polyploids arose spontaneously due to various factors and progressed towards speciation over a long period of time (Wood et al., 2009).

1.3. Chromosome Engineering

Increasing population growth and limited resources have made it necessary to achieve high efficiency in agriculture. (Gerland et al., 2014). The study of manipulating chromosomes to develop crops resistant to diseases, pests, or environmental stresses forms the basis of chromosome engineering. The chromosome manipulation can be achieved through mechanisms such as CRISPR/Cas, which allows for the specific introduction of mutations to a specific chromosome region, or directly through genotoxic agents (Pacher and Puchta, 2017). The chromosome engineering in agriculture was first used in wheat (*Triticum aestivum*) chromosomes using X-ray irradiation to insert foreign chromosome fragments (*Aegilops umbellulata*) into them (Sears, 1956). Although X-ray irradiation is still preferred in breeding studies, many modern chromosome engineering techniques have been developed and used today. The modern chromosome engineering techniques, starting with methods based on specific DNA sequences using endonucleases, include the engineering of plant mini-chromosomes, the

engineering of plant centromeres, the insertion of genes of interest into engineered chromosomes, centromere engineering to produce haploid inducers, the redirection of meiotic recombination, the breaking of genetic linkages through chromosomal translocations, engineered apomixis, and aspects of meiotic recombination (Puchta and Houben, 2024).

The mini-chromosomes have been generated by telomere-mediated chromosomal excision in *Arabidopsis thaliana*, maize, barley, rice, wheat, and rapeseed (Puchta and Houben, 2024). Creating centromeres from scratch in agriculture is a highly useful chromosome engineering technique, but direct transformation of centromere sequences is not feasible in plants. Therefore, in most plants, it resorts to epigenetic marking of the centromere with CENH3 (histone H3 variant) (Liu et al., 2023).

1.4. Chromosome-Specific Breeding Programs

The chromosome-specific breeding programs are artificial selection methods used to obtain agricultural products with desired traits. Advances in molecular genetics have enabled plant breeders to select desired genes throughout the genome in agriculture and develop targeted agronomic traits. The chromosome-specific breeding programs have been proposed to control allelic variation in genes associated with agriculturally desirable traits (Peleman and van der Voort, 2003). The chromosome-specific breeding programs, or "breeding by design," have evolved into their current form after going through various stages. The techniques began with "selection breeding," then progressed to "hybridization breeding," "marker-assisted breeding," and "breeding by design" (Zhang, 2021). While the selection breeding only allows the selection of agricultural plants that show spontaneous variation and the selected agricultural products are the result of years of experience-based selection by agricultural producers (Zeven, 1998), the chromosome-specific breeding programs allow the selection of desired genes from the entire genome in three stages. The first stage involves mapping all agronomically important loci; the second stage involves examining allelic variation at mapped loci; and the third stage involves performing chromosome-specific breeding with the desired alleles (Peleman and van der Voort, 2003).

The chromosome-specific breeding programs have been used in the improvement of many agricultural crops such as rice (*Oryza sativa*, *Oryza glaberrima*, *Oryza nivara*, *Oryza rufipogon*, *Oryza barthii*, *Oryza meridionalis*, and *Oryza glumaepatula*), wheat (*Triticum aestivum*), cotton (*Gossypium*

hirsutum, *Gossypium tomentosum*, and *Gossypium barbadense*), maize (*Zea mays*), and *Aegilops tauschii* (Zhang, 2021).

1.5. Functional Genomics

Many genes are known that affect the characteristics such as durability, resistance, yield, quality etc. of agricultural products, and focusing on these genes is very important for breeding studies. The functional genomics applications, which investigate the connections between genes and their effects, reveal valuable data about genes that control vital characters such as durability, resistance, yield, and quality (Li et al., 2025). The functional genomics makes significant contributions to the development of agricultural products together with different disciplines (especially computer technology). The functional genomics applications are technologies that investigate critical genes and their quantitative loci (**QTL**, quantitative trait loci) that show rapid adaptation and response to changing environmental conditions. Thus, the development of agricultural products that are more durable, more resilient, and higher yield and nutritional value (Yang, 2025).

The genome studies of agricultural products are generally divided into three genomic models: structural, quantitative and functional genomics. The integration of these models in the form of structural-quantitative, quantitative-functional, and structural-functional makes it more convenient to determine the desired properties (Yang, 2025). There are many agricultural examples of applications of functional genomics (Table 1).

Table 1. Functional genomics applications in agriculture. Agricultural products are listed alphabetically.

Agricultural product	Characteristic	References
Carrot (*Daucus carota*)	Fertility Abiotic stress	Duran and Ipek, 2022 Hao et al., 2020
Cotton (*Gossypium* sp)	Fiber yield and quality Drought tolerance	Naoumkina and Kim, 2023 Sharif et al., 2024
Maize (*Zea mays*)	Cold tolerance Heat stress Salt stress Drought	Farooqi et al., 2022 Waqas et al., 2021
Peanut (*Arachis hypogaea*)	Biological stress Pathogen resistance	Cai et al. 2023
Rice (*Oryza sativa*)	Disease resistance Heat tolerance	Yang et al., 2024
Soybean (*Glycine max*)	Biological stress resistance Oil yield Potein content	Du et al., 2023 Liu et al., 2023
Wheat (*Triticum aestivum*)	Yield Disease resistance Drought tolerance Nutritional quality	Boehm Jr and Cai, 2024 Roychowdhury et al., 2024

1.6. Genetic Mapping

Genetic mapping, which determines the linear connection of chromosomes as relative distance, uses recombination and genetic markers for these processes. The genetic mapping is a technique that facilitates advanced genomic studies in the improvement of agricultural products. Linkage maps allow calculation of the relative distance between two genes based on the crossover rate or recombination frequency. These maps are very important in agriculture as they provide an introduction to fields such as comparative genomics, candidate gene detection, quantitative trait loci (QTL) mapping, detection of trait-marker relationships, and marker-assisted selection. In genetic markers, it is essential to establish both quantitative trait loci mapping and high-quality linkage maps. The genetic markers closely associated with a gene or locus that expresses a desired trait are widely used in the breeding of agricultural products. The mapping product population, selection of appropriate genetic markers, genotyping and polymorphism screening of the population, and construction of linkage maps are the basic requirements for genetic mapping (Begna and Yesuf, 2021).

While a high-resolution map yields markers with the same order as the physical map, there is no linear relationship between the number of base

pairs (**kb**) and the distance (**cM**, centimorgan) in terms of measurement. The relative distances in linkage maps reveal different distance profiles in agricultural products. For example, 1 cM distance corresponds to a length of 30 to 550 kb in *Arabidopsis thaliana*, 258.5 kb in rice, and 118 to 22.000 kb in wheat (Schmidt et al., 1995; The Rice Genome Sequencing Project, 2005).

1.7. Genome Sequencing

Genome sequencing is crucial for identifying genes that express desired traits in agricultural crops. The genomes of many plants, especially agricultural foods, have been sequenced (Table 2). Because breeding improved varieties requires a thorough understanding of the crop genome and this is possible with information from the genome, transcriptome, proteome, and epigenetics (Thottathil et al., 2016).

Table 2. The genome sequences of the important agricultural products (alphabetically).

Agricultural product	Genome size (mb)	References
Bean (*Phaseolus vulgaris*)	587	Schmutz et al., 2014
Cabbage (*Brassica oleracea*)	630	Liu et al., 2014
Maize (*Zea mays*)	2.300	Schnable et al., 2009
Pigeon pie (*Cajanus cajan*)	833	Varshney et al., 2011
Rapeseed (*Brassica napus*)	1.130	Chalhoub et al., 2014
Rice (*Oryza sativa*)	430	Yu et al., 2002
Soybean (*Glycine max*)	1.115	Schmutz et al., 2010
Sugar beet (*Beta vulgaris*)	758	Dohm et al., 2014
Tobacco (*Nicotiana tabacum*)	4.500	Sierro et al., 2014
Wheat (*Triticum aestivum*)	17.000	Brenchley et al., 2012

1.8. Polymerase Chain Reaction (PCR)

Polymerase Chain Reaction (PCR) is a technique that facilitates the detection and analysis of trait with reliable, rapid, and accurate results to the feature of interest by amplifying a specific sequence. This technique is widely used in agriculture for purposes such as quality and yield control, agricultural product authenticity, pathogen detection and resistance, resistance, and genetically modified organism (**GMO**) analysis (Chavan, 2002).

Many different PCR models for different purposes in agricultural studies, such as conventional PCR, real-time PCR (RT-PCR), nested PCR, colony PCR, asymmetric PCR, thermal asymmetric interlaced PCR (TAIL-PCR),

reverse transcription PCR, multiplex PCR, assembly PCR, nanoparticle assisted PCR (Nano-PCR), single specific primer PCR (SSP-PCR), allele specific PCR, methylation specific PCR, inverse PCR, linear after the exponential PCR (LATE-PCR), degenerate PCR, and hot start PCR. is used (Chavan, 2002).

1.9. Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR-CAS9)

Genome editing systems, which modify the genome in a desired, predictable, rapid, and precise manner, are widely used methods in agriculture. Four families of directed nucleases such as CRISPR-associated protein (CRISPR-Cas), homing endonucleases (HEs), transcription activator like effector nucleases (TALENs), and zinc finger nucleases (ZFNs) are involved in genome editing. According to the site-directed nuclease, CRISPR/Cas, which works with the complementarity of the guide RNA to a specific sequence, is a simpler cheaper, faster and more efficient system (Cong et al., 2013).

The working mechanism of the CRISPR/Cas9 system in agriculture consists of the following steps:

(1) Selection of genes to be regulated and determination of gene-specific spacers.

(2) Prepare ribonucleoprotein or transformation carrier.

(3) Deliver foreign proteins or nucleotides into the agricultural product cells.

(4) Identify edited lines in T0 generation with next generation sequencing.

(5) Select null agricultural products by the gene edited in T1 and confirm them with next generation sequencing in T2 generation.

(6) Obtaining the lines edited homozygous and evaluation of expression of the gene.

(7) Using null lines at new agricultural breeding variety (Liu et al., 2021).

In agriculture, studies are being carried out to improve traits such as grain size, length and width, slender grain shape, fruit size, shape and colour, seed colour, root colour, leaf colour, flower longevity and colour, long shelf life, low or high amylose content, fragrant, super sweet and waxy product, high β-carotene content, low Cd accumulations, high oleic acid proportion,

low phytic acid content, high lycopene content, low phytic acid content, high oil production, low gluten content, and low tartaric acid content using the CRISPR/Cas system. Thus, this improves the agricultural product's physical appearance and texture quality, increases palatability, and enriches its nutritional elements (Liu et al., 2021).

1.10. Marker-Assisted Selection (MAS)

Marker-assisted selection (MAS) is the selection of agriculturally important traits using DNA markers. The markers can significantly increase durability, productivity, nutritional value, sensitivity, etc. The marker approach involves selecting and transferring loci expressing desired traits. The development of molecular maps and genetic markers has facilitated the applicability of marker-assisted selection. Because the success of marker-assisted selection depends on many factors, such as the distance between genes underlying the gene maps, the number of related genes, and genetic markers. Trait improvement has been achieved in many agricultural products by the applications such as marker-assisted evaluation of breeding material, marker-assisted backcrossing, marker-assisted pyramiding, early generation marker-assisted selection, and combined marker-assisted (Collard and Mackill, 2008).

For marker-assisted selection to achieve full success in achieving desired agronomic traits, it is necessary to utilize its advantages over traditional methods. The applications such as preliminary studies and computer simulations can facilitate this success (minimize costs and maximize genetic gain) (Kuchel et al., 2005).

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