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The Unique Existence of Chromosomal Abnormalities in Polyploidy Plants

Van Hieu Pham

Abstract

Chromosomal abnormalities are a popular natural phenomenon, especially in polyploid plants, and their unique existence in plants is one of the major forces for speciation and evolution. This means that plants with existing chromosomal abnormalities developing through sexual and asexual pathways shed light on increasing biomass and adapting ecology. Regarding the former, plants with chromosomal abnormalities experience not only enlargement effects but also increased phytochemical compounds. As far as ecological perspectives are concerned, chromosomal abnormalities in plants enhance biotic and abiotic tolerance to climate change. This chapter focuses on chromosomal abnormalities in whole genome doubling, such as autopolyploid, allopolyploid, and aneuploidy plants, and discusses the effects and benefits of these abnormalities to evolution and ecological adaptation at the individual and population levels. It also discusses some advantages and disadvantages of polyploid animals in comparison with polyploid plants.

Keywords: chromosomal abnormality, polyploidy, evolution, climate change, reproduction

1. Introduction

Darwin's theory of natural selection maintains that the polymorphism that exhibits gross chromosomal alteration in plants as a way to reciprocally translocate along with changes in the segregation of pairs of chromosomes to ensure heterozygosity maintenance and limitation of the expression of lethal genes. Every day, living organisms ingest all kinds of food, taking in energy and nutrients to nourish, maintain, and develop their bodies. As such, food security is vitally important to survival. Attaining food security, however, has been a challenge. Potential solutions to food insecurity might lie in the genetic mechanisms regulating the reproductive process of plants. Different organisms reproduce in different ways, either via sexual combining of male and female gametes or asexually. Asexual reproduction generates a new plant by using parts of the parent plants. Some artificial asexual reproduction methods include grafting, layering, and micropropagation. Genetic identicalness to the progenitor plant is an outstanding feature of plants produced asexually. Reproductive chromosome abnormalities derive from mistaking meiosis and mitosis occur [1]. For instance, observing meiotic processes revealed evidence that the trio of genes *SMG7*, *SDS*, and *MS5* interrelated with both other chromatin organizing factors and proteins functioning DNA repair-related, involved in *MSH6*

and *DAYSLEEPER*. The convergent tasks detected (other meiotic pathways, chromosome arrangement or remodeling, ABA cues and ion transport) offer insights into the challenges of polyploidization. Investigation of the meiosis of autotetraploid potato *Solanum tuberosum* revealed a variety of challenges in correct segregation and recombination of multiple homologous chromosomes that constrain meiotic chromosomal configuration [2].

With advances in genetic engineering and continual elucidation of genes governing the reproductive pathway, humanity is on the verge of being able to control the expression and regulation of these genes [1, 3]. Key genes related to flowering, such as *CO*, *CRY2*, *FT*, *FPF1*, *FD*, *GAI*, and *ELA1*, have already been studied [3]. Scientists and breeders worldwide use biotechnology to study reproductive processes in laboratories and field trials. Sustainable agricultural development is required to increase crop diversity, stabilize yield, and increase resilience via the accelerated development of several crops containing desired traits that have the capacity to adapt to and mitigate consequences from climate change [4, 5].

In terms of biodiversity, speciation, and evolution, there are thousands of existing plant species that can adapt to various topographies and climates. This means that plant species not only increase the abundance of genetics but also enhance the ability to adapt to boost genome evolution in harsh environments [1, 6]. The best examples are those that involve autopolyploids, allopolyploids, and aneuploidy. There are more than 4000 potato varieties, including more than 180 wild potato relatives [7]. More specifically, potato, one of the most multifaceted genetic modes with a variety of ploidy levels, such as 76%, recognizes diploids, 3% triploids, 12% tetraploids, 2% pentaploids, and 7% hexaploids, among which the highest yield is tetraploid due to a further level of genetic heterogeneity [8–10]. Based on practical empirical proof, two clusters of cultivated potato have been categorized: the Andigenum group located in the high Andes of northern and central South America that exhibit a wide range of ploidy levels, and the Chilotanum group from the lowlands of southern Chile, which are tetraploids [11].

Plant karyotypes at individual, species, and genera levels exhibit an abnormal number of chromosomes. A typical example is Chayote (*Saccharum edule* (Jacq.) Sw.) with variable chromosome numbers of 12, 13, and 14 resulting from cytological analysis [12], as shown in **Table 1**.

This chapter focuses on chromosomal abnormalities in whole genome doubling, such as autopolyploid, allopolyploid, and aneuploidy plants, and then discusses the effects and benefits of these abnormalities to evolution and ecological adaptation at the individual and population levels. It also discusses some advantages and disadvantages of polyploid animals in comparison with polyploid plants.

Species	n	2n	Source
<i>Saccharum edule</i>	11, 12, 13, 14	22, 24, 26, 28	[13–17]
<i>Curcuma parviflora</i> Wall.	14, 14, 16	28, 30, 32	[18]
<i>Curcuma zedoaria</i> Rosc.	21	63, 64	[19–23]
<i>Curcuma longa</i> L.	21	62, 63, 64	[19–22, 24]
<i>Paspalum aff. arundinellum</i> Mez	10	50, 51	[25]
<i>Jacobaea vulgaris</i>	20	30, 31	[26]
<i>Brassica rapa</i> L. ssp. <i>pekinensis</i>	10	20, 24	[27]

Table 1.
Summary of plant species with chromosomal abnormalities.

2. Chromosomal abnormalities affect giant effects and alternative natural secondary metabolites

That chromosomal abnormality outranks other plants in terms of parts of plant size and biochemical compounds characteristically states that gene regulation plays an important role. Regarding the upregulation of genes, cell division and cell expansion are related to genes such as ARGOS, ANT (*AITEGUMENTA*), *CYCD3;1*, *Growth Regulating Factor 1 (AtGRF1)* and *EXPASIN 10 (AtEXPA10)* [27–29], *EXPB3*, and *TCP* [30]. Alongside these genes, lipid transport genes such as *wbc11–2* and *cer5–2* are a way to make large autotetraploid plants [31–33]. Moreover, proteins involved in cell proliferation, glutathione metabolic pathways, and cellulose, chlorophyll, pectin, and lignin synthesis play a role in enlarging plant size [34, 35]. Cytosine methylation in the whole genome also contributes to changes in organ size in polyploid plants, which can effectively improve potential and complex agro-nomic traits in many crops [36, 37]. Cell size in polyploid plants plays an important role in changing phenotypes [38]. Enlarged organ size due to chromosomal abnormalities usually leads to increased yield and production of cultivated plants [39]. Studying autotetraploid *Vicia cracca* L. revealed that seed size and germination of tetraploids are more dominant than diploid seeds [40]. Although chromosomal abnormalities lead to large plants, autotetraploid birch plants (*Betula platyphylla*) and apple plants (*Malus domestica*) have a dwarf phenotype caused by reduced growth regulation signals [41, 42].

Similarly, chromosomal abnormalities also alter secondary metabolites, especially phytochemical compounds, in several plant species [43]. For example, natural components observed in tetrasomic tetraploid opium poppy (*Papaver somniferum* L.) enhanced morphine content by 25–50% by changing the expression of several genes regulating the alkaloid biosynthesis pathway [44]. Another example is cytosine methylation occurring genome-wide, enhancing phytochemicals in autotetraploid cymbopogons [36]. The autotetraploid *Arabidopsis thaliana* Col-0 alters metabolites and genes regulating tricarboxylic acid cycle (TCA) and gamma-Aminobutyric acid (GABA) compared with diploids [45]. Lycopene significantly increased autotriploid watermelons because of a regulation of phytohormones on metabolic pathways and upregulation of genes controlling biosynthetic lycopene [46]. Interestingly, polyploidization is a promising approach for gaining significant value, especially with medicinal plants, by producing secondary metabolites [43]. For example, upregulating genes contributing to the biosynthesis pathway of podophyllotoxin (PTOX) in autotetraploid *Linum album* enhanced the content of PTOX [47]. Vitamin A enrichment in triploid banana has been initiated by inducing tetraploids from several types of diploids and then creating hybrids [48]. Many total flavonoids and gastrodin are produced in autotetraploid *Anoectochilus formosanus* Hayata [49]. The tetraploid type of *Physalis angutala* Linn. from Rajasthan alters palmitic acid, linoleic acid, and linolenic acid [50]. In the last decade, many plant studies have given objects based on the outstanding benefits of chromosomal abnormalities. Those breeders have been observing chromosomal abnormalities as a way to gain elite plant cultivars because an increase in plant organ size is derived from some of the most significant consequences of chromosomal abnormalities [51, 52].

The chromosomal abnormality of the level of ploidy variation is useful for breeding both within and among autopolyploid and allopolyploid plant species [25]. Another view is that chromosomal abnormalities contribute to plants' ability to withstand detrimental environmental conditions. As far as the first idea is concerned, a chromosomal abnormality is not appropriate for sexual reproduction in aneuploidy due to chromosomal abnormalities in gametes. Another utilization

of polyploidy is that grafted crops can use artificial polyploidy as parts of rootstock and scion with potential agronomic traits in the context of climate variability [53].

3. Chromosomal abnormalities enhance abiotic and biotic stress tolerance

Chromosomal abnormalities in plants enhance both biotic and abiotic stress tolerance. For example, many studies have proven that several pathways respond to salinity stress. Chromosomally abnormal flora use several processes to adapt to high salt concentration conditions, including accumulating Na⁺ extrusion in roots, increasing Na⁺ transport to leaves, regulating osmotics, enhancing gene expression related to antioxidants, mitigating reactive oxygen species (ROS), photosynthesizing cues, changing SNP markers related to salt stress, upregulating aquaporin genes, phytohormone transduction cues, protein processing, regulating transcription factors, upregulating ATP synthase to enhance ion transport and changing protons, and using miRNAs [54–63]. Chromosomally abnormal plants can also adapt to water insufficiency through miRNA mechanisms and target genes controlling transcriptional regulation, hormone metabolism, and plant defense. An increase in abscisic acid (ABA) content in response to drought stress in several polyploid plants such as *Paulownia fortunei*, *P. australis*, *P. tomentosa*, and *Lycium ruthenicum* has been observed [64–69]. Antioxidant defense systems were activated to sufficiently support heat tolerance in *Dioscorea* and *Arabidopsis* [70, 71]. Plants with chromosomal abnormalities might tolerate cold stress by growing antioxidants and epigenetics [72, 73]. Changing root anatomical characteristics supports autotetraploids to adapt to high concentrations of boron in soil and enhance Cu transport genes. Activation of antioxidation defense and positive regulation of ABA-responsive gene expression are ways to survive in environments containing high concentrations of copper [74, 75]. Enhancing the expression of target genes that regulate proline biosynthesis to support autopolyploid birch plants (*B. platyphylla*) in NaHCO₃ stress tolerance has been investigated [76]. In addition, biotic resistance was demonstrated in autotetraploid *Malus × domestica* and *Solanum chacoense*. More specifically, significantly increasing the *Rvi6* resistance gene locus was observed as a way to assist autopolyploids in enhancing *Venturia* resistance [77]. Similarly, autotetraploid potato has the capacity of common scab resistance by crossing 2n gametes from the diploid *S. chacoense* [78].

4. Chromosomal abnormalities help plants adapt to ecological invasion and climate variability

Chromosomal abnormalities are one of the major adaptation ecologies and climate changes, such as fixing on growth, potential morphological traits and ecological invasion, pollinators, and the factors supporting pollination in nature [79]. After appearance of chromosomal abnormality in some rare cases, the increasing cell size leads to alteration of physiological manners with their environmental condition, augmenting multiple novel alleles and changing regulatory pathways to create new potentially beneficial phenotypic variations. For instance, studying the transcriptome in aneuploidy maize revealed qualitative changes in gene expression in comparison to wild-type plants [80]. The number of expanding ecological spaces to polyploid plants has been recorded in various studies [81]. Polyploid *A. thaliana* is a plant with adaptive potential caused by the increased resources of transposable

element (TE) insertions at higher ploidy levels and enhanced gene expression related to reproduction [82, 83]. Several studies have proven that chromosomal abnormalities adapt to ecological invasion and climate variation. For example, biological invasions in *Brassicaceae* proved to be evolutionary processes to adapt and widespread in central Europe [84]. Another example is that of the native range of distribution of *Lythrum salicaria*. Several cytotypes with 2 \times , 3 \times , 4 \times , and 6 \times variations are found in regions of the Middle East, while only tetraploids are located in North America. In addition, the invasive spread of North American populations lacks differences in ploidy level [85]. Studying potato germplasm demonstrated markers related to unique geographic identity associated with traits of abiotic stress tolerance [86]. One of the priorities in genotype development is to gain stress tolerance and beneficial nutritional aspects as a way to reduce the effects of climate change [87, 88]. The view is that polyploidization contributes to better adaptation to the environment in terms of suitability for growth and other benefits of cell size. Breeders and human beings can benefit immensely from more ecological adaptation after chromosomal abnormality since it improves potential traits being exploited for breeding experiments.

For the most part, polyploidy is probably less popular in the animal kingdom than in the plant kingdom. More specifically, polyploids have been observed in amphibia (African clawed frog, *Xenopus* spp.), and different species of fishes exist [89]. This is because the polyploid animal species can overcome meiosis and exhibit parthenogenesis in which an egg cell can develop into an individual without fertilization. In addition, polyploid animal kingdoms are similar to polyploid plant kingdoms. They both have beneficial and detrimental effects and are the reason for meiotic imbalance. The greatest advantage of polyploid animals is that polyploid offspring are shielded from the deleterious effects of recessive mutations. However, chromosomal abnormalities may lead to congenital diseases and pregnancy loss in animals, especially in humans. Regarding meiotic imbalance, spindle irregularities might occur in polyploids, resulting in chaotic segregation of chromatids and aneuploid cells. An abnormal number of chromosomes in aneuploid cells might result in three or more sets of chromosomes produced in meiosis being different from diploid cells. This can explain why polyploid animals could form multiple arrangements of homologous chromosomes in metaphase I, resulting in abnormal or random segregation to produce aneuploid gametes or to form imbalanced gametes [89, 90].

5. Conclusion

It is unquestionable whether chromosomal abnormalities derived from sex or asexual reproduction are essential for the successful existence of organisms on this planet. With climate variability becoming more alarming than ever, chromosomal abnormality has been occurring naturally as a way to address the issue of food security by expanding breeding opportunities to develop seedless triploid plants, increase ornamental features, increase environmental tolerance, enhance biomass, and more. Chromosomal abnormalities are also vital to human beings mainly because their exploration can open opportunities for securing food security. For example, breeders who are experienced in hybrid development are more likely to find desired agronomic traits. More importantly, several breeders today require at least a desired trait of novel crops before considering using them for production. Chromosomal abnormalities are essential for success in adapting ecology and play a vital role in evolution due to generating variation in a natural population.

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