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Mini review

A look at polyploidy and plant breeding

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Abstract

Polyploidization is a process that generates genetic variability and therefore one of the engines of biological evolution. Since polyploidization produces important changes in the phenotype, mainly an increase in the size of the organs (i.e.: flowers and fruits), it is also a very important and powerful tool for plant improvement. Despite its intense use in breeding programs for various species, very little is known so far about the nature of this phenomenon. This work presents a brief review of the results obtained by the use of this tool in plant breeding and also raises some reflections on its mechanism of action.

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Introduction

Biodiversity provides the base and sustenance of ecosystems and, from a human point of view, it is considered the basis of agriculture, the source of all recent crops and livestock species domestic since the beginning of human civilization [1]. Indeed, from the beginning of its history, humanity resorted to the Vegetable Kingdom in order to obtain feed, flavors, and medicine.

Genetic variability is one of the pillars of neo-Darwinism and it is responsible for the existing biodiversity.

The polyploidization phenomenon also named the whole duplication genome and its consequences on the plant genome are one of the main sources of this variability.

Discussion

According to Levin [2], polyploidy can greatly alter the genetic, biochemistry, cytology, physiology and behavior of organisms. In plants, these modifications can range from evident phenotypic changes to not-so-noticeable changes at the molecular level. Among noticeable phenotypic changes, it is expectable to observe increases in organ size (and biomass), intensification of colors, changes in the architecture of the plant, and slowing down of growth. Others are observed at tissue and cytological levels, such as stomata and pollen grains sizes, and larger trichomes. At the molecular level, polyploidization has given plants great adaptive capacity due to the development and expansion of important gene families responsible for the process of plant speciation, diversification, and evolutionary innovation [3].

Phenotypically, the most immediate and noticeable effect of polyploidy in plants is the increase in cell size. The volume of tetraploid cells generally increases by 1.5 times relative to that of their diploid progenitors [4]. Because of this, various authors suggest that metabolism and growth are retarded in polyploid cells due to alterations in the geometric relationships between the nucleus and the rest of the cell [2]. Likewise, at the cellular level, the duration of mitosis is another parameter closely correlated with the amount of nuclear DNA. In this sense, the reduction of the number of cell divisions during development is a characteristic of polyploidy. Certain physical parameters of the plant, including mitotic cycle time, duration of mitosis, chromosome size, and nuclear and cellular volumes, are determined by the amount of DNA per nucleus regardless of the DNA information content. The contribution of DNA content, together with the increase in cell size, is perhaps the most consistent effect of polyploidization [5].

As a consequence of the increase in cell size, the original phenotype is modified, resulting in increases in the width/length ratio and size of both leaves and flowers, as well as increases in the thickness and color of the leaves. These characteristics are frequently the target of induced polyploidization in horticultural and ornamental species [6].

Another important effect associated with polyploidization is the increase in the production of secondary metabolites, which has been observed in various aromatic and medicinal species [7]. Other features observed are greater drought tolerance, resistance to pests, and longer flowering times [8].

The importance of these changes lies in the fact that they could allow polyploids to access new ecological niches [9] or, from a human benefit point of view, increase the aptitude of the original genotype as a crop.

As it was mentioned above, polyploidization is one of the mechanisms that can lead to adaptations to different selection pressures produced by the environment. It is not a coincidence that humanity has emulated nature using technological procedures that allow the obtaining of artificial polyploids as a source of genetic variability, in order to increase quality and productivity, as well as the adaptability of crops to prevailing climate change, to overcome barriers of sexual incompatibility due to imbalance of chromosomes between species and to obtain triploid hybrids without seeds [10].

The stability of polyploids in angiosperms implies that this state of the genome has an adaptive meaning and that it is positively selected [9]. In this sense, the main advantages that polyploidy individuals have with respect to the original parents are genome buffering, the increasing of allelic diversity and heterozygosity, generating novel phenotypic variations, especially in allopolyploids (Udall and Wendel 2006). Some of these traits, such as larger organ sizes (leaves, flowers, etc.), higher biomass, tolerance to drought, resistance to pests, diverse flowering time, and other modifications could allow polyploids to occupy new ecological niches [9]. For breeders, these characteristic polyploid traits are very attractive; these genotypes are more likely to be selected for agronomic uses [8]. Polyploidization is recognized as one of the most important and frequent tools used in plant breeding.

Both natural and artificial polyploids are used for the improvement of many of our most important crops, for example, among the allopolyploids can be found wheat (*Triticum aestivum*), tobacco (*Nicotiana tabacum*), peanut (*Arachis hypogaea*), cotton (*Gossypium hirsutum*) (Udall and Wendel, 2006), and *Brassica* genus (Osborn, 2004). Among the crops improved by autopolyploid appear banana, watermelon, and apple (triploids), potato and alfalfa (tetraploids), oat and chrysanthemum (hexaploids), and dahlia, strawberry and pansies (octoploid) [6,10,11].

Likewise, ancestors of cultivars such as maize, soybean, and cabbage, apparently experienced the polyploidization process (paleopolyploids), although genomic rearrangements have concealed the evidence [8]. It is possible that each plant species has undergone polyploidy cycles throughout its evolution, although we can only recognize recent events [12]. In fact, based on its complete genome analysis [13], even the small genome of the model organism *Arabidopsis thaliana* seems to have been subjected to polyploidization during its evolution. In the last decades, new and improved cultivars of economically important species have been developed by inducing artificial or synthetic polyploids using mutagenic agents (autoploid) [6,7,10].

Eng and Ho [10] make a thorough review of crops improved by polyploidization. These authors cite 30 species that include horticultural, fruit, ornamental, and forest. A few specific examples of different species are cited below. In horticulture crops, Muthoni, et al. [14] studied the importance of the level of ploidy in the production of *Solanum tuberosum*. Tanaka [15] determined that some of the artificial tetraploids developed from *Solanum melongena* recovered their fertility and showed greater resistance to insects and drought. In ornamental crops, *Rosa rugosa* [16], *Mecardonia tenella* [17], *Dianthus caryophyllus* [18], *Gerbera jamesonii* [19], *Glandularia* (hybrid) [20], *Calendula officinalis* [21], among others, showed an increase of flower and/or leaves size; in the case of *Petunia axillaris* [22] increasing plant compactness were reported. In fruit crops, it was reported increasing fruit size and quality in *Actidinia chinenesis* [23] and *Fortunella crassifolia* [24], plant compactness in *Eriobotrya japonica* [25] and reduced fertility in *Punica grabatarum* [26]. Concerning aromatics and medicinal plants, an increase in secondary metabolites production was reported in *Artemesia annua*, *Catharanthus roseus*, *Centella asiatica*, and *Lippia integrifolia* by Lin, et al. [27]; Xing, et al. [28], Kaensaksiri, et al. [29] and Iannicelli, et al. [30], respectively.

Among the major crops, rice – a diploid species – represents a very interesting challenge for its improvement through polyploidization. In the last years and in order to a better understanding of the "polyploid effects" on plant genome, a great advance was made increasing the seed setting rate of polyploid rice lines (Chen, et al. 2021).

Actual wheat is an allopolyploid obtained after millennia of natural and artificial hybridization. *T. turgidum* (durum wheat) originated 500,000 years ago from the hybridization of *Triticum urartu* (diploid) and a diploid extinct species related to *Aegilops speltoides*. Ten thousand years ago, the crossing between *T. durum* (tetraploid) x *Aegilops tauschii* (diploid), originated the artificial hybrid *T. aestivum* (hexaploid) with the common name of bread wheat [31].

Wheat is a clear example of how the ploidy level affects the phenotype and, from an industrial point of view, the properties and uses of each genotype.

The domestication of wheat is the possible cause of the origin of our civilization, after all, both species changed dramatically their way of life. One might wonder who domesticated whom?

As it was previously indicated, polyploidy induces phenotypic changes that are of interest to breeders, but the impact of polyploidy on agricultural production through grafting must also be highlighted. In a recent review work, Ruiz, et al. [32] analyzed the advantages of using polyploid rootstocks and scions. These authors reported that, in general, grafting improves agronomic traits by combining well-adapted rootstocks and improved scions. And in particular, polyploidy induces large changes in anatomical traits in the rootstock as well as in the scion, which also may contribute to stress adaptation.

These authors conclude that although our knowledge of the "polyploid effect" on genome expression regulatory mechanisms needs to be deepened, the evidence indicates that the production of new triploids and tetraploids genotypes is relatively simple and the use of these new poliployd varieties, both on stems and grafts, could significantly benefit to the crops grown using this technique.

According to FAO / IAEA [33], in 2020 there were 3,364 registered mutants, of which 47 were polyploids obtained via colchicine. The condition of polyploidy profited for plant breeding in several species. In this work, we have cited just a few examples. Likewise, it is necessary to keep in mind that it is not possible to know in advance the immediate practical utility of a polyploid, nor even establish rules for their obtaining. However, there are some issues that would facilitate the obtaining of a useful artificial polyploid. The following aspects should be considered when the development of artificial polyploids is required.

1. Species with low chromosomal numbers.
2. Allogamous species.
3. Species whose agronomic value is the use of their vegetative parts (for example, leaves) or their reproductive parts (flowers).
4. Species that easily reproduce vegetatively.
5. Species in which spontaneous autoploids already exist.

Conclusion

Finally, one of the conclusions reached throughout *in vitro* polyploidization assays carried out by our group, is that polyploidization is not a linear phenomenon. Even if the polyploid individuals were obtained under strict experimental design in a very controlled way, the autopolyploid obtained were not identical to each other and not did seem to be the strict “sum of two genomes”. On the contrary, each one of the recovered autotetraploid individuals showed their distinctive traits being significantly different in some cases from the rest, either in color intensity, organ size, or production of secondary metabolites. Moreover, these traits did not always show to be "twice" concerning the original.

This fact indicates that each polyploid individual recovered from a trial should be considered an *independent polyploidization event* until it is analyzed and the existence of similarities will be demonstrated.

What is the cause of this phenomenon? Is it from physicochemical or biological nature? Does it only depend on the affected cell that initiates the new polyploid lineage or does the surrounding microenvironment also have to be considered?

Besides, since the autopolyploids were developed under *in vitro* conditions, the *tissue culture effect* must be considered.

Although our knowledge about polyploidization and its evolutionary consequences has increased in recent years, the adaptability of plants and the "fluidity" of their genome still have many questions to answer.

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