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Experiences in developing and propagating polyploidy crop plants

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ABSTRACT

The main objective of the study was to assess polyploidy use experience in crop improvement and to generate information for crop breeders for future endeavor**.** Due to the rapid development of sequencing technologies, there is increased evidence to support that polyploidization plays an important role in the diversification of plant species, evolution of genes, and the domestication of crops. The occurrence of many independent polyploidization events in plants was found to be tightly associated with the timing of extreme climate events or natural disasters on earth, leading to mass extinction while possibly facilitating increased polyploidization. Moreover, polyploidization was found to significantly impact species diversification, with subsequent effects on crop domestication and the development of traits with agronomic importance.

Keywords: Polyploidization, Autopolyploidy, Allopolyploidy, speciation, crop domestication.

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Introduction

Polyploidy (genome doubling), discovered in 1907, is an important driver of eukaryotic evolution, evident in many animals, fungi, and plants (Grant 1981; Hovav et al., 2008; Wood et al., 2009). Almost all eukaryotes have had a history of ancient polyploidization events followed by diploidization and then repeated polyploidization (Birchler and Veitia 2010; Salmon and Ainouche 2010). Polyploid plants have been generated from evolutionary processes, crop domestication, and/or artificial synthesis via chemical or physical mutations. Studies of polyploid plants across various genomic scales have occurred relatively more recently, particularly after the whole-genome sequence of arabidopsis became available and it was discovered that this species has experienced at least two whole-genome duplication events (Blanc et al., 2003). Since then, sequencing of more and more plant genomes has revealed evidence of multiple whole genome duplication events (Jaillon *et al*., 2007; Tuskan *et a*l., 2006).

To date, polyploidy plants have been used in various aspects of genomics research including evolutionary genomics, functional genomics, and comparative genomics (yang *et al*., 2010).

Sexually reproducing organisms normally have two sets of chromosomes (2N). During normal sexual reproduction, each parent donates half its chromosomes (N) to the offspring. Having received one set of chromosomes from each parent, the offspring contains two sets of chromosomes (2N), and is called "diploid." When the offspring matures and can reproduce, the process of sexual reproduction continues.

However, sometimes something goes awry during the process of sexual reproduction, and the offspring receives all of the chromosomes from both parents. Rather than being "diploid" (e.g. 2N, or two sets of chromosomes) it has four sets of chromosomes --4N, or "tetraploid." Various mistakes that can occur during the biological processes of sexual reproduction can lead to offspring with abnormal numbers of chromosomes (e.g. 3N, 4N, or even more). In general**,** when offspring end up having more chromosomes than normal, this is called polyploidy.

In animals, these abnormalities are usually lethal. But plant breeders have known for centuries that hybrid crosses between different plant species can sometimes (though certainly not always) result in new varieties (1).

1.1. Terminology

Euploids:- Organisms with multiples of the basic chromosome set (n,2n,3n,…)

Aneuploids:- Have a chromosome number that differs from the normal number for the species by a small number of chromosomes (2n-1, 2n+1…)

Autopolyploidy:-Autopolyploids are polyploids with multiple chromosome sets derived from a single species. Autopolyploids can arise from a spontaneous, naturally occurring genome doubling, like the potato. Others might form following fusion of 2n gametes (unreduced gametes). Bananas and apples can be found as autotriploids. Autopolyploid plants typically display polysomic inheritance, and therefore have low fertility, but may be propagated clonally.

Allopolyploidy:-Allopolyploids are polyploids with chromosomes derived from different species. Precisely it is the result of multiplying the chromosome number in an F1 hybrid. *Triticale* is an example of an allopolyploid, having six chromosome sets, allohexaploid, four from wheat (*Triticum turgidum*) and two from rye (*Secale cereale*). *Amphidiploids* are a type of allopolyploids (they are allotetraploid, containing the diploid chromosome sets of both parents. Some of the best examples of allopolyploids come from the Brassicas, and the Triangle of U describes the relationships between the three common diploid Brassicas (*B. oleracea, B. rapa,* and *B. nigra*) and three allotetraploids (*B. napus, B. juncea,* and *B. carinata*) derived from hybridization among the diploids(2).

2. Literature review

2.1. Ploidy level

Polyploidy has been an important factor in angiosperm evolution, underlying episodes of adaptive radiation in many plant families (Soltis & Soltis, 1999) and in the angiosperms as a whole (Soltis *et al*., 2009 and references therein). It is estimated that 15% of speciation events in the angiosperms involve polyploidization (Wood *et al*., 2009). A number of traits associated with polyploidy, such as larger seed size, increased disease resistance, and decreased allocation to reproduction are advantageous in domesticates (Lewis, 1980; Levin, 1983). Some crops, like wheat, have been derived from wild ancestors through a process of allopolyploidization, conferring desirable characteristics of both ancestors on the new species. Other crops have been domesticated or improved via autopolyploidization (e.g. potato). Autopolyploids typically have larger cells and organs than their diploid progenitors as a result of doubling of the DNA content, while allopolyploids are variable in this regard (Ozkan *et al*., 2003). The alteration of plant traits may also confer a fitness advantage in certain habitats, allowing species to adapt to marginal environments beyond the natural range of their diploid ancestor (Ramsey, 2011). This could enable domesticates to adapt to disturbed agricultural environments that are not suitable for the wild ancestor. Furthermore, polyploidization provides a mechanism for sympatric speciation, by providing reproductive isolation of the new species from the co-occurring diploid form (Soltis *et al*., 2007). This may allow the rapid divergence and fixation of traits that are of interest for cultivation by limiting gene flow between wild and cultivated forms. Despite the importance of increased ploidy in the domestication syndrome of such major crops as wheat and potato, little is known about the frequency and importance of ploidy changes in domestication syndromes across a broader sample of crops. Of the crops with known ploidy (n = 199), our dataset includes 64% diploid crops and 17% polyploid crops, while 19% of the crops have both diploid and polyploid varieties. This last proportion is slightly larger, although comparable, to the number of angiosperm species that include multiple ploidy levels (12–13%; Wood *et al*., 2009). We examined how many polyploidy angiosperm crops underwent polyploidization during the process of domestication and identified 37 crops (19%). Therefore the frequency of these ploidy changes is similar and only slightly higher than the frequency observed in speciation events among angiosperms, which is 15% (Wood *et al*., 2009), suggesting that ploidy changes do not distinguish evolution under domestication.

Of these, 51% were the result of autopolyploidy and 24% were the result of allopolyploidy, while 10% may have arisen from a combination of both and the remainder were of unknown origin or the result of ploidy reduction. Perennial crops were the most common category of domesticates with ploidy changes as a domestication trait (78%). Of these, 90% were mainly propagated vegetatively under cultivation, and therefore would not have suffered decreased reproductive output in the event of genome duplication (Ramsey & Schemske, 2002). This is further supported by the observation that, of the crops with domestication syndrome involving a ploidy change, nearly half (43%) also exhibited a change in reproductive strategy from outcrossing or self-fertilizing to vegetatively propagate. This is a trend previously noted for fruit trees (Zohary & Hopf, 2000).

The proportion of crops with a domestication syndrome involving both a ploidy change and a reproductive strategy change was significantly higher than the null expectation. A remaining 38% of crops with a ploidy change in their domestication syndrome were already propagated vegetatively in their wild form. Human intervention facilitating the propagation of crops with increased ploidy is also supported by the simultaneous increase of ploidy changes and reproductive strategy changes in domesticated crops. This coincides with a wave of domestication of perennials. The out crossing crops in our dataset exhibit a lower frequency of changes in ploidy as a domestication syndrome trait compared with self-fertilizing and vegetatively propagated crops. Furthermore, in the dataset as a whole, only 19% of crops with either a self-fertilizing or an out crossing reproductive strategy had a change in ploidy occurring under domestication that was not associated with a transition to vegetative propagation (bread wheat, noni, oat, okra, rapeseed, soy, and sump weed). Model cases of changed ploidy in sexually reproducing crops, such as wheat, are therefore exceptional, as vegetatively propagated crops domesticated either for edible vegetative tissue or for fruit, not seed crops, are most strongly associated with ploidy changes.

2.2. Reproductive strategies

Our dataset included a relatively even distribution of out crossing, self-fertilizing and vegetatively propagated crops. Similar proportions were also found in a review of 124 crops by Simmonds (1976, 1979). There is considerable variation in reproductive strategies for a number of crops: of the total 203 crops, both self-fertilizing and out crossing strategies characterized 25 crops, both self-fertilizing and vegetative propagation strategies characterized 32 crops, and both out crossing and vegetative propagation strategies characterized 66 crops.

A number of crops exhibit a change in reproductive strategy between their wild and domesticated forms, either from out crossing to self-fertilizing or from sexual reproduction to vegetative propagation. This is considered an important feature of crop domestication because, similar to a change in ploidy level, it is a mechanism for establishing reproductive isolation, allowing farmers to maintain desired phenotypes. It also allows for the production of desirable fruits with few or no seeds (Gepts, 2004). Both of these types of change in the reproductive strategy used under cultivation are frequently documented in this dataset. These changes occurred in 27% of the crops reviewed. Shifts from out crossing to a self-fertilizing system are considered a relatively common domestication syndrome trait for fruit and seed crops (Gross & Olsen, 2010; Roumet *et al*., 2012). Overall, however, our data do not support this theory as common: results of analyses showed a negative association between self-fertilizing crops and changes in reproductive strategy. Furthermore, this transition characterized fewer than 20% of the self-fertilizing crops, indicating that most were already self-fertile in their wild state. This likely contributed to making them favorable candidates for domestication.

2.3. Synthetic polyploidy crop plants

H.R. Warmke also experimented with breeding programs during the war years. Polyploidy Cannabis plants were produced by treatment with the alkaloid colchicine. Colchicine interferes with normal mitosis, the process in which cells are replicated. During replication, the normal doubling of chromosomes occurs, but colchicine prevents normal separation of the chromosomes into two cells. The cell then is left twice (or more then) the normal chromosome count.

Warmke's experiments concluded that polyploidy contained higher concentrations of the "active ingredient." However, the procedure for measuring that ingredient was much the same is described for grafting, with probably similar shortcomings.

Polyploid Cannabis has been found to be larger, with larger leaves and flowers. Recent experience has shown that polyploids are not necessarily higher in potency. Usually they are about equal to diploid siblings.

Colchicine is a highly poisonous substance. The simplest and safest way to induce polyploids is to soak seeds in a solution of colchicine derived from bulbs of winter or autumn crocus (Colchicum). Mash the bulbs and add an equal part of water. Strain through filter paper (or paper towels). Soak seeds in the solution and plant when they start to germinate. Cultivate as usual.

Only some of the seeds will become polyploidy. Polyploidy sprouts generally have thicker stems, and the leaves are often unusually shaped, with uneven-sized blades. Leaves also may contain more than the usual number of blades. As the plant grows, leaves should return to normal form, but continue to be larger and with more blades.

If no polyploids sprout, use less water in preparing the solution. Colchicine is also a prescribed drug for treatment of gout and is taken in pill form. These usually contain .6 mg per tablet. Use 10 tablets per ounce of water, and soak the seeds as described above.

Colchicine is also sold by mail-order firms which advertise in magazines such as Head or High Times. Because colchicine is a poison, it should be handled carefully. It is not known if plants from seeds treated with colchicine will contain a harmful amount of colchicine when plants are grown. Harm is unlikely, because the uptake by the seed is so small, and because the colchicine would be further diluted during growth, as well as diminished by smoking. But we cannot guarantee that you can safely smoke colchicine-treated plants (3).

In some situations, polyploid crops are preferred because they are sterile. For example, many seedless fruit varieties are seedless as a result of polyploidy. Such crops are propagated using asexual techniques, such as grafting.
Polyploidy in crop plants is most commonly induced by treating seeds with the chemical colchicine.

Examples

- Triploid crops: apple, banana, citrus, ginger, watermelon
- Tetraploid crops: apple, durum or macaroni wheat, cotton, potato, canola/rapeseed, leek, tobacco, peanut, kinnow, Pelargonium
- Hexaploid crops: chrysanthemum, bread wheat, triticale, oat, kiwifruit
- Octaploid crops: strawberry, dahlia, pansies, sugar cane, oca (*Oxalis tuberosa*)
- Dodecaploid crops: some sugar cane hybrid (4).

In plant breeding, the induction of polyploids is a common technique to overcome the sterility of a hybrid species. Triticale is the hybrid of wheat *(Triticum turgidum)* and rye *(Secale cereale)*. It combines sought-after characteristics of the parents, but the initial hybrids are sterile. After polyploidization, the hybrid becomes fertile and can thus be further propagated to become triticale.

Polyploid plants in general are more robust and sturdy than diploids. In the breeding of crops, those plants that are stronger and tougher are selected. Thus, many crops have unintentionally been bred to a higher level of ploidy:

- Triploid crops: banana, apple, ginger
- Tetraploid crops: durum or macaroni wheat, maize, cotton, potato, cabbage, leek, tobacco, peanut, kinnow, Pelargonium
- Hexaploid crops: chrysanthemum, bread wheat, triticale, oat
- Octaploid crops: strawberry, dahlia, pansies, sugar cane

Some crops are found in a variety of ploidy. Apples, tulips and lilies are commonly found as both diploid and as triploid. Daylilies *(Hemerocallis)* cultivars are available as either diploid or tetraploid. Kinnows can be tetraploid, diploid, or triploid.

In the case of bananas, while the original bananas contained rather large seeds, triploid (and thus seedless) cultivars have been selected for human consumption. Cultivated bananas are sterile (parthenocarpic), meaning that they do not produce viable seeds. Lacking seeds, another form of propagation is required. These are propagated asexually from offshoots of the plant (5).

2.4. Classification and assessment of polyploids

Polyploid plants can be classified based on three different parameters: genomic origin, formation approach, and time after polyploid formation. Polyploid origin can be divided into autopolyploids, which are derived from a whole-genome duplication event of the same ancestral chromosome set, and allopolyploids, which are derived from a hybridization event of alternate parental genomes followed by genome duplication (Pignatta *et al.*, 2010). Multiple pathways, as illustrated could lead to the formation of autopolyploids or allopolyploids. Chromosome doubling in polyploidy formation involves two major mechanisms: somatic doubling and unreduced gamete (i.e., 2n gamete) formation (Bretagnolle and Thompson 1995; Carputo *et al*. 2003; Stuessy et al., 2004). Based on the time after polyploidy formation, polyploids can be classified as ancient, young, and newly-formed polyploids. The ‘‘ancient’’ vs.‘‘young’’ term is not rigidly defined in any absolute temporal basis, but are only relative to each comparison (Bennett, 2004). Polyploids can also be divided into natural and synthetic polyploids. Natural polyploids result from spontaneous genome-doubling, whereas synthetic polyploids are result of induced genome-doubling with or without prior genome hybridization. Based on the sets of homologous chromosomes post-doubling, polyploids can be classified as triploid, tetraploid, hexaploid, octoploid etc. However, this classification becomes challenging as many species with whole-genome sequences available indicate that they experienced multiple rounds of genome doubling, meaning that they are ancient poplyploids (Bowers *et al*., 2003).

Ploidy level in plants is often estimated by measuring the C-value (amount of DNA in the unreplicated gametic nucleus) using flow cytometry (Clarindo *et al*., 2008; Dart *et al*., 2004; Eaton *et al*. 2004; Grundt *et al*., 2005; Halverson *et al*., 2008; Harbaugh 2008).

2.5. Polyploidy and plant improvement

Considering the profound importance of polyploidy in plant evolution, it is understandable that there was considerable interest in developing induced polyploids when mitotic inhibitors were first discovered in the 1930s. However, despite the fact that polyploids have been developed for many major crops, these plants are almost always found to be inferior to their diploid progenitors. Somatic doubling does not introduce any new genetic material, but rather produces additional copies of existing chromosomes. This extra DNA must be replicated with each cell division. Enlarged cell size is often associated with polyploids, which can result in anatomical imbalances. Other deleterious effects can include erratic bearing, brittle wood, and watery fruit. High-level polyploids (e.g., octaploids) can be stunted and malformed, possibly resulting from the extreme genetic redundancy and somatic instability that leads to chimeral tissue. Despite the drawbacks of induced autopolyploids, these plants may be valuable if they are in turn used in a breeding program to enhance the degree of heterozygosity and further selected for desirable traits. In most cases it appears that inducing autopolyploids will do little for plant improvement unless substantial heterozygosity can be incorporated. Historically, work with polyploids has not progressed much beyond somatic doubling-resulting in considerable genetic redundancy. Based on our knowledge of natural systems and evolution, it appears much greater advances can be made by working towards enhanced heterozygosity, including the development of allopolyploids.

Polyploidy can result in a wide range of effects on plants, but the specific effects will vary dramatically based on the species in question, the degree of heterozygosity, the ploidy level, and the mechanisms that relate to gene silencing, gene interactions, gene dose effects, and regulation of specific traits and processes (Ranney,2007).

2.5.1 Opportunities

i. Overcoming Barriers to Hybridization: In some cases, desirable crosses are difficult to obtain due to differences in ploidy levels between prospective parents. Such interploid barriers appear to arise from abnormal endosperm formation. In species where there is an interploid block, seeds will often only develop normally if there is a 2 maternal : 1 paternal ratio in the genomic makeup of the endosperm, which would be the normal case for two diploid parents. Seeds that don’t meet this criterion are often underdeveloped or abort. In some cases this ratio is not exact, but the greater the disparity, the lower the viability of the seeds. In cases where interploid blocks exist, barriers to hybridization may be overcome by manipulating the ploidy levels to match prior to hybridization (Ranney, 2007).

ii. Developing Sterile Cultivars: The introduction and movement of invasive species can be a significant threat to certain ecosystems. Development of sterile forms of important nursery crops is an ideal approach for addressing this problem. In doing so, plants can be grown and used for landscaping while minimizing the possibility that these plants could sexually reproduce and become invasive. There are a number of methods available for developing sterile plants. However, one of the most rapid and cost-effective approaches for inducing sterility in a plant is by creating polyploids. In most cases these plants function normally with the exception of reproduction, specifically meiosis. In some cases doubling the chromosomes of an individual plant (autotetrapoid) will result in sterility due to multiple homologous chromosomes and complications during meiosis. Despite these complications, autotetraploids of some species can produce fertile seeds. In this case, tetraploids can then be hybridized with diploids to create sterile triploids. Triploids have an additional reproductive barrier in that the 3 sets of chromosomes cannot be divided evenly during meiosis yielding unequal segregation of the chromosomes (aneuploids). Even in the unusual case when a triploid plant can produce a seed (apples are an example), it happens infrequently and seedlings are usually abnormal.

Development of triploids of some species can be complicated due to the presence of an interploid block that prevents the normal development of triploid embryos. However, embryo culture is an additional technique that can be employed to overcome this problem and produce sterile triploid plants. An alternative approach for creating triploid plants is regeneration of plants from endosperm found in seeds. Although the embryo in most angiosperm seeds is diploid, the adjoining endosperm (nutritive tissue) originates from the fusion of three haploid nuclei (one from the male gametophyte and two from the female) resulting in triploid tissue. This tissue can be excised from developing seeds and cultured in vitro (tissue culture) to eventually give rise to regenerated embryos and plantlets. This approach has been successful for a range of plants including citrus, kiwifruit,loquat, passionflower, acacia, rice, and pawpaw(Ranney,2007).

iii. Restoring Fertility in Wide Hybrids. It is not unusual for hybrids between distant taxa (different species or genera) to be sterile. This often occurs due to failure of the chromosomes to pair correctly during meiosis — referred to as chromosomal sterility. By doubling the chromosomes of a wide hybrid, each chromosome has an exact duplicate and chromosomal homology and fertility can be restored. This technique has been used successfully to restore fertility in Rhododendron 'Fragrans Affinity' and 5Chitalpa tashkentensis. However, in some cases this approach has been unsuccessful in restoring fertility, as was the case with tetraploid hybrids of Alstroemeria aurea 5 A. caryophyllaea(Ranney,2007).

iv. Enhancing Pest Resistance and Stress Tolerance. The influence of polyploidy on adaptability and resistance to biotic and abiotic stresses has been widely studied in crop plants. In some cases polyploids have demonstrated greater resistance to pests and pathogens, greater nutrient uptake efficiency, better drought resistance, and superior cold tolerance. However, polyploidy often results in reduced resistance to these same stresses as well. It should not be assumed that polyploids are necessarily more stress tolerant.

There are a number of strategies for inducing polyploids as a means of enhancing adaptability. Increasing the chromosome number and related gene dose can sometimes enhance the expression and concentration of certain secondary metabolites and defense chemicals. However, this is not always the case and little is generally known about the relationship between gene dose, gene silencing, and expression of secondary metabolites. A more promising approach would be to create allopolyploids between plants with diverse endogenous secondary metabolites. A unique and valuable characteristic of allopolyploids is that the secondary metabolites from the parental species are typically additive. That is to say that allopolyploids often produce all the enzymes and metabolites (including defense chemicals) of both parents. This could be particularly effectively for combining the pest resistant characteristics of two species, and potentially contributing to a much broader, more horizontal form of pest resistance. A similar approach may have utility for enhancing tolerance to certain environmental stresses.

v. Enlargement and Enhanced Vigor: Although enlarged cell size found in some polyploids can have undesirable effects, it can sometimes also be beneficial. In some plants, polyploidy results in significant enlargement. Fruit from tetraploid apples can be twice as large as diploid fruit, though they tend to be watery and misshapen. For apples, triploids have proven to be a happy medium that combines larger fruit while retaining good quality and are often grown for commercial production. This type of enlargement can be particularly desirable for ornamental flowers. Flower petals can also be thicker and flowers can be longer lasting in polyploid plants (Ranney, 2007).

3. *Perspective and conclusion*

Polyploid plants have been studied for decades and, more recently, been the focus of genomics research. Genomic changes after polyploid formation comprise a long, dynamic process that can be divided into three stages: (1) initial responses after genome doubling, (2) short-/mid-outcome, And(3) long-term outcome. Genomic studies in these three stages require an investigation of alternate types of polyploidy plants, as illustrated in Fig. 3. Genomics research using ancient polyploids, such as Arabidopsis with ancient tetraploid background (Thomas *et al*., 2006) and grapevine with ancient hexaploid origin (Jaillon *et al*., 2007), can provide insights into the long-term outcome of polyploidy evolution. To understand the short-term evolutionary consequences in polyploidy, young polyploid lines generated from crop breeding, such as Populus (Tuskan et al. 2006) and wheat (Gao *et al*., 2007), may be appropriate plant materials. A new trend in genomics research has been to create synthetic polyploid plants in model species, such as cotton (Flagel and Wendel, 2010), Arabidopsis (Beaulieu et al., 2009), and Brassica (Schranz and Osborn, 2000).Using the newly-created polyploid plants, the researchers can investigate the initial genomic changes after polyploidy formation. For genetic improvement in crop species, clonally-propagated polyploid plants may convey superior traits in commercial settings. In these cases, it may be desirable to maintain the genomic status of the selected polyploid clones or slow down the diploidization process. Genetic engineering is moving from the gene level to the whole chromosome level, with an artificial chromosome introduced for improvement in pathways or complex traits (Ananiev *et al*., 2009; Goyal *et al*., 2009). It will be increasingly important to understand the genomic consequences of ‘‘invasion’’ by a whole artificial chromosome. Studying evolutionary dynamics in newly-synthesized polyploids could increase our understanding of molecular mechanisms leading to stabilized allopolyploid plants, as demonstrated by a recent study on wheat allohexaploids (Mestiri *et al*., 2010). Previous studies using various polyploidy plants have revealed a complex pattern of evolutionary dynamics and contributed to our knowledge about the relationship between genomic composition and gene function. The ongoing advances in DNA sequencing technology offer unprecedented opportunities for monitoring genomic and transcriptomic changes in polyploid plants. More polyploid plants will likely be used for fundamental genomics research, consequently increasing our understanding of plant genomics as a whole. The increased knowledge on polyploid formation, maintenance, and post-duplication divergence at both whole-genome and sub genome levels will not only help plant biologists understand how plants have evolved and diversified, but also assist plant breeders in designing new strategies for crop improvement.

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