

The Biological Aspects of Hybridization and its Impact on the Genetic Diversity and Structure of Population

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Abstract

Hybridization is important process which led to many lineages evolution. Increasing genomic tool and methods in genomic analyses, make gene flow between different taxa which generate new phenotypic diversity, permit for variation of new species, and donate to speciation. Hybridization lead to phenotypic changes through the expression of hybrid vigor. On longer evolution time scales, hybridization cause limited alteration through the introgression of new alleles and transgressive segregation and, in some cases caused the formation of new isolates. The abundance and evolution studies of hybridization have interesting role in biology science. A lot of evidences concerning how and why hybridization contributes to biological diversity currently being investigated were first proposed tens and even hundreds of years ago. In this Update, we discuss how new advancements in genomic and genetic tools are revolutionizing our ability to document the occurrence of and investigate the outcomes of hybridization in plants. Moreover, the impacts of hybrids can either be positive or negative. Among the positive attributes of hybrids that have been exploited is heterosis, which results either from dominance, over-dominance or epistasis. Negative ones include sterility, arrested growth of the pollen tube, failure to nuclear reprogramming, proper placenta formation and maternal immune response and embryo abortion.

Keywords: Hybridization; Individuals; Species; Sterility

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Introduction

From unlike populations that are genetically different or through crossing two individuals, the natural or artificial process called hybridization lead to production of hybrids [1]. The previous action causes no genetic material changes in the quantity or quality and the contents of the DNA remained constant but the genes forms novel groups leading to positive attractive characters or new phenotypic individuals. Many problems including sexual incompatibility, polyembryony, and male or female sterility may appeared due to hybridization process [2]. For plant growth enhancement and plant developments, the hybridization process is used to: 1- produce a new plant species or hybrids with some wanted characters, 2- mix some important characters in definite plants and produce one plant with certain characters and finally to use the new hybrid in crop production and biological applications. Generally, hybridization mainly aimed to produce a hybrid with a new genetic material that differed from the original parents.

In normal habitats, hybridization causes certain population differences which may lead to strong reproductive barrier evolutions to create novel isolates or varieties. It is also used to produce novel crops with special characters and cause popular differences between lineages in addition to it produce new varieties. DNA analysis and sequencing of the produced crops confirm the importance of genetic introgression

and hybridization. This cause a progress in detection techniques used for studying gene flow in natural hybridization and phylogenomic analysis due to genomic information's which cause or inform about gene flow [3,4]. There is increasing respect about the widespread of hybridization which lead to a significant evolution, leading to believing that plants may affect extending to animals [5,6]. Concerning animal flora and fauna reproduction protocols, normal hybridizations process a vital role in genetic material morphology and evolution of insects and birds taxa. Mainly, hybridization appeared among two differ animal races which may change to wild types [7-11]. Concerning bird's hybridization, the analysis of genomic information gives ornithologists to discover the ecological and evolution processes of multispecies hybridization [12].

Genetic changeability among strains or species may be used professionally by breeders to obtain best plants, birds or animals [13]. In plants, preface of novel experiments concerning sexual crosses between different taxa inside or among strongly allied genera [13]. In bird, some species can hybridize with different species that are plainly noticeable in the genera, *Anas platyrhynchos* belong to Anseriformes, *Phasianus colchicus* from Galliformes, and *Larus argentatus* from Charadriiformes. Entertainingly, those outliers with large sharing rate and leading to ample opening interact together and potentially interact within species. Our query wither these species can hybridize with other more related isolates or breed with other unrelated taxa or isolates



(intergeneric hybridization) was appeared [9,14]. Plant hybridization was start from ten of years but until now it face many problems until obtaining flourishing interspecies hybridization. Therefore, the present review aimed to focusing light on different area of hybridization and its effects in modeling biological isolates and explaining the progression relations inside species.

Hybridization

Biologists give the term Hybridization many definitions and can be limited to individuals that are obtained from cross-fertilization among two unlike species. Moreover, hybridization was defined as breeding among two species of the community and the two species were differentiated according to heritable characters [15]. It also mean the genes transferee among individuals by backcrossing. Hybridization may mean the moving of genes among genetic related genera. The terms hybridization or introgression are the most used and give good elasticity in the studies, thus focusing on hybridization and introgression between species was carried out.

A center of attention on inter specific hybridization which need concerning of individual concepts. Unluckily, the word species is a scientific name which has many definitions. The range of differences based due to the ability to breed among the species [16]. Mainly, the groups of populations what can naturally interbreed called species. This term is important in of hybridization and speciation studies, thus, here we referred to biological species as groups of interbreeding populations, genetically isolated' moderately than 'reproductively isolated from different groups. The most hybrid zones give out a good fence in specific genetic changes and gene moving from one species to other species was noticed by many normal morphological methods [17].

Hybrid Speciation

Novel hybrid gave reproductive separation and only environmental position which change genetic movement and differences between parental hybrids. A novel species groups were obtained due to allopolyploids and homoploid hybrid speciation. Allopolyploid lineages are obtained through union of non-reduced gametes, doubling genome after hybridization process or through triploid association [18]. Hybrid of homoploid determine the presence of an original, reproductive isolates. Allopolyploid hybrid speciation is the commonest and possible shape of hybrid speciation [19]. A study demonstrated that about 11% of species out of 47 genera are of allopolyploid source while in animals, fungi, and plants only few homoploid cases were recorded [20-24]. Similarly, hybridization may lead to steady hybrid zones or parental species loss [25]. The obvious diversity in incidence gave method to detect polyploid against homoploid individuals. Homoploid species can differentiated from the others by demonstrating the hybrid origin [26] while homoploid species demonstrate the hybrid origin by special environmental needs [26,27]. In addition, many data recorded that genetic changes have many effects on less-diverged species or homoploid and more-diverged species or polyploid [28].

Success of hybrid species was noticed escape competition with initially much more numerous parental genotypes through ecological differentiation [25]. It has since been hypothesized that the rapid evolution of genome structure and gene expression following polyploidy can contribute to novel trait expression and ecological differentiation [19,29]. Synthetic allopolyploids have been created to verify the feasibility of this hypothesis [30]. It has been demonstrated that, in some cases, allopolyploids can survive in a broader range of

environments than their progenitors. This can be due to greater gene regulatory flexibility as a result of homolog of specific gene regulation [31,32] or alternative splicing [33] in response to environmental perturbation. However, there remains a need for more empirical evidence demonstrating ecological differentiation facilitated by allopolyploids [5,19,29].

Many agents had an important roles in species recombination which include highly normal collection of the best productive possible species with the fastest chromosome development and habitat accessibility of the new hybrid [34-36]. Hybrid new species developments appeared in sympatry with both parents and the hybrid derivative minimize the value of the progress of reproductive barriers. The design of these experimental studies could be improved by hypothetical studies that recognize critical parameters.

Chromosomal Rearrangements

In the past, much extensive evolution is recorded to considerate the hybrid genetic methods of in-viability, sterility and un-fertility. In crosses between chromosomes in divergent individuals on meiotic pairing, un-fertility is typically affecting the chromosomal rearrangements, thus individuals from heterozygous chromosomal arrangements showed few meiotic impairment and fertility loss [37]. Many recommendations showed the genetic agents that explain the non-fertility due to bad re-arrangement of chromosomes. Unluckily, difficulties appeared to determine the relations between chromosomes and genetic agents.

Two methods are used to determine the roles chromosome re-arrangement and gene on sterility in interspecific crosses. The first, found genetic mapping of quantitative trait loci (QTLs) and contained hybrid gene analysis of two species of lentil named *Lens culinaris* and *Lens ervoides* which were vary in only one translocation, used for fertility in F_2 hybrids. For this reason, Tadmor Y, et al. (1987), [38] tried to segregate F_2 population between the two species in order to draw a map according to eighteen markers of isozymes. The differences between 4 isozyme markers that are formed during meiosis lead to accurate recognition of the translocation end-points.

The pollen viability of different plants was about <65% are heterogeous whereas plants with pollen viability >85% were homozygous species. Thus, the chromosomal translocation do not cause primary post-mating reproductive barrier between the two individuals.

Moreover in recent times, some researches were applied in *Helianthus* plant and many isolates of this genus were different in some chromosomal translocations which were mainly well studied through hybrid pollen viability [39]. Quantitative estimation of the influence of chromosomal re-arrangements on pollen feasibility [40] and analyzed the segregation of forty eight genetic markers in BC_1 progeny of hybrids of *Helianthus argophyllus* and the other species named *Helianthus annuus*. It was found that *H. argophyllus* was similar to the isolate *H. annuus* [41] and genetic analyses reported a clear similarities between the two isolates but they were different in only 2 translocations [39]. Many cytogenetic results reported a great range of differences in viability of the produced pollen grains in the mapping family (27-93%) and more than 80% of this alteration are found due to three genetic intervals on linkage groups 1, 2 and 3, respectively. backcross hybrids meiosis analyses recorded that abnormalities of meiotic phases were correlated with chromosomal rearrangements which are responsible for dropping hybrid fertilities among the individuals.

Another successful advance which differentiates among



chromosomal and genetic agents was analysis of introgression patterns across the sterility barrier where the chromosome re-arrangements decrease hybrid suitability and connection of these rearrangements lead to selection against introgressed progeny. This approach was supported by introgression analysis between the two obtained hybrid of sunflower (*Helianthus annuus* and *Helianthus petiolaris* [42,43]. Genetic mapping studies allowed the identification of ten different chromosomes that have different genes arrangement in the 2 previous species. The other chromosomes are collinear and the interspecific genetic material distribution of in the introgression lines gave significantly reduction chromosome rearrangement.

Estimating Hybrid Fitness

Hybrid fitness is an important caveat in many discussions which related to the reliability or relevance of most of the fitness estimated. Lifetime fitness estimation is difficult to obtain for long-lived organisms and pooling data from heterogeneous hybrid genotypes. Seeing pooling data from several hybrid generations is easy but lead to wrong results [36]. Thus, pooling species from the same hybrid lead to defective conclusions due to changes in fitness. One of the difficulties in some studies is how to detect hybrid fitness which are restricted from F_1 or F_2 hybrids or backcrosses. Lastly, very few characters of hybrid fitness have been conducted under natural conditions [44].

Impacts of Hybridization in Plants and Animals

Heterosis (Hybrid Vigour)

Crossing of 2 species form a hybrid, with excellent growth rate, more biomass at maturity, and/or greater reproduction compared to the parents. This case is named a hybrid or heterosis that contained a phenotypic control and differ from the parents [45]. The biotic and abiotic resistance enhanced production and growth [46], thus have a positive effects on all living organisms production. Heterosis enhance genetic differences of the crossing parental taxa [47]. Hybridization further increased disruptions of the parental linkages and decreased or increased fitness than the parental taxa [48]. Differences within the hybrids caused hybrid superiority [46]. Other studies explained the demonstration of heterosis that occurs as a result of multiple genetic occurrences due to simultaneous effects of dominance, overdominance, epigenetics and epistasis and heterosis generally caused a single over-dominant gene [46]. In addition, petite snooping of RNA is associated with heterosis of F_1 hybrids, viewing more expression levels outside the parental taxa range [1]. The hybridization between two strains of *Oryza* called *Oryza sativa japonica* and *Oryza sativa indica* form F_1 hybrids with heterosis for spikelet fertility and harvest index [49]. As well, the same was noticed in two hybrids of wheat and rye which have heterotic action on the production. There is an increase in spike numbers and biomass [50]. The same case was found in *Zea mays* and *Tripsacum dactyloides* F_1 hybrids exhibited increased salinity tolerance than both their parents [51].

Some preceding studies are used to understand heterosis and there is a study describe this type which was conducted in maize [52]. It was suggested that the appearance of dominance was observed and may represent an example of pseudo-over dominance caused by the presence of several linked quantitative trait locus [53]. The data are most consistent with the model of dominance of favorable genes, but admit that epistasis could also play an important role [54]. New genetic and genomic techniques are used to characterize mechanisms of heterosis [55]. Premature study cause single, common cause of heterosis and multiple causal mechanisms contribute to heterosis [56].

The most believable genomic heterosis characters were used as genetic model systems including rice, maize, cotton, and Arabidopsis [57,58].

Recent genetic and genomic studies also have revealed that interactions between divergent epigenetic regulatory systems contribute to heterocyst in F_1 hybrids [59,60]. In Arabidopsis, Wang L, et al. (2015) [61] demonstrate that F_1 hybrids show gene expression levels outside of the parental range for defense, abiotic stress, and hormone response pathways, due in part to epigenetic regulation. In many cases, these pathways are downregulated, consistent with the idea that there are tradeoffs between growth and defense or abiotic stress response.

Genetic Sterility or Inviability

Hybrid sterility and inviability is well explained by the Dobzhansky-Muller model which states that a genetic change due to divergence in loci in a population, and a genetic change in the same loci in the second crossing population results to incompatibilities when the two genomes are hybridized resulting to post-zygotic incompatibilities and therefore, infertility and inviability is exhibited [62]. Sterility and inviability are the main post-zygotic fertilization barriers to hybridization [63]. They limit gene flow resulting to fewer evolutionary consequences. However, when hybridization results to gene flow within different species, then evolutionary consequences are manifested [64]. The main purpose of hybrid sterility is reproduction isolation to inhibit gene flow in order to maintain species identity [65]. Hybrid sterility is associated loss of grain yield, malfunction of pollen grains [66]. Infertility mean the formation of unviable weak and small grains [67]. Low fertility mean a reduced gamete formation and chromosomal re-arrangements of the hybrids [68]. Hybrid sterility increases as the divergence between the crossing parental taxa increases [69]. Precisely, decreased fertility is more pronounced when divergence between crossing parental taxa is more than 4 million years [70]. This is because of the accumulation of inter-locus incompatibilities between the diverging populations [71].

The hybrid between *Sorghum bicolor* and *Saccharum officinarum* resulted in 53% fertility, while, previous crosses showed a fertility rate of 0.13% [72]. A cross between *Avena sativa* and *Zea mays* formed hybrids that exhibited partial fertility [73]. Inviability was evidently exhibited between *Zea mays* and *Tripsacum dactyloides* hybrids whereby 80% of the F_1 hybrid seeds could not germinate. Furthermore, another study of the same cross showed the hybrids had pollen fertility ranging from 0% to 50% [74]. In certain cases, hybridization can result from absolute viability. For example, *Triticum durum* and *Aegilops umbellulata* hybrid seeds were unable to germinate [75]. In some cases diverse copy for the evolution of hybrid in viability or sterility is a number of diverging loci interact negatively in a hybrid genetic environment. The low interactions generally lead to viability or sterility [76]. They may suggest that meiotic lead to a key role in the evolution of post mating reproductive results [77] which were supported by a standard model in which one or two genes appear to have major effects on hybrid sterility or viability as found in cowpea, cotton, Melilotus, Mimulus, rice and wheat [78-83]. Thus, the comments do not rule out the possibility that many new genes may affect viability and sterility in these species as well. Really, some studies on the genetic basis of hybrid sterility and hybrid breakdown between subspecies of rice suggest that several mechanisms are involved [82]. These mechanisms include a cytoplasmic gene that causes both male and female sterility; and interactions between a pair of complementary genes that lead to greatly reduced fertility. Both of these mechanisms fit the standard model. In addition, Hermsen JGT, et al. (1963) [83] found that recombination between differentiated



supergenes represents a major source of sterility. Map comparisons suggest that these regions may contain inversion polymorphisms, and that sterility may be caused by crossing over between cryptic structural rearrangements (cytologically undetectable chromosomal aberrations) [84]. Thus, chromosomal mutations might also play an important role in the evolution of hybrid sterility in rice.

Li Z, et al. (1997), [82] also provide evidence that hybrid breakdown in rice largely fits the polygenic model and results from the uncoupling of coadapted subspecific gene complexes by recombination. In later-generation hybrids, semi sterility appears to be caused largely by incompatibility interactions between many loci, and hybrid weakness appears to result from the break-up of coadapted gene complexes that affect fitness traits such as heading age and floret number per panicle. The presence of these coadapted gene complexes in rice has long been suspected as a result of observations that intersubspecific hybrids tend to revert quickly back to one of the parental types in successive hybrid generations. The complex genetic basis of post mating reproductive isolation in rice accords well with studies of *Drosophila* that indicate that sterility and breakdown in fly hybrids involve many genes and higher-order epistatic interactions [76].

A complex genetic basis for post mating reproductive isolation in many species of plants is also suggested by introgression mapping studies. For instance, the presence of genomic intervals where introgression is reduced or absent is often reported in map-based studies of introgression between crop plants and their wild relatives [85,86]. Presumably, many of these genomic regions harbor genes that contribute to reproductive isolation. Likewise, strong segregation distortion is often observed in interspecific crosses, suggesting that many genes are negatively selected in hybrids. For example, Zamir D, et al. (1986) [87] report segregation distortion at 54% of loci from interspecific crosses of lentil, pepper and tomato, compared with only 13% in intraspecific crosses.

In animals, sterility of interspecies hybrid is counted as a barrier to the sustainable interspecies hybrid animal production. But sterility could be taken as an advantage to the future livestock production. As the male of almost all animal, bird and fish species show faster growth rate and heavier bodyweight than female and this is actually the result of sex hormone activity. The male hormone enhances to faster and higher growth rate over female hormone. Anyway, because of sterility none of the offspring would express their sexual behavior and the ultimate result might be equal growth rate and body weight gain as it is already established in fishes [88,89]. Beside this, the resulted offspring could be a hybrid vigor (that is resulted offspring will show larger body weight than the average body weight of its parents) and it is found in one case of sheep-goat interspecies hybrid [90]. Moreover, the sterile offspring will not be able to hamper the production goal through haphazard breeding.

To overcome the phenomenon of sterility in hybrids, chromosome doubling can be employed by application of colchicine, Amiprofos-methyl or pronamid treatment. Since the principle behind most infertility in plant hybrids is that chromosomes lack a pairing partner during meiosis, doubling of the parental sets of chromosomes ensures that pairing can take place within each set, allowing meiosis to proceed hence production of fertile gametes. The chromosome doubling technique results in amphidiploids as observed on *Syringa vulgaris* × *S. pinnatifolia* hybrids.

Polarity in Hybridization

Division in hybridization and development is a very widespread

phenomenon for interspecies crossing wherein successful hybridization. It is possible to form one grouping of the two species from two combinations of the same species. It may not give the same result and may cause low success and limited cases. The previous type of polarity is found in reciprocal crosses such as sheep-goat and cattle-buffalo interspecies hybridization. Mine OM, et al. (2000), [90] proved polarity in interspecies hybridization of cattle and buffalo and demonstrated by exposing buffalo oocytes to cattle spermatozoa and cattle oocytes to buffalo spermatozoa. During this experiment found that buffalo oocytes had almost half efficiency to the efficiency of cattle oocytes to accept foreign spermatozoa. The observation revealed that buffalo oocytes have less efficiency to accept foreign spermatozoa as compared to the cattle oocytes which shows flexibility to fertilization and blastocyst development with alien spermatozoa (buffalo, gaur, banteng, sheep, goat and so). Polarity is also found in interspecies hybridization of sheep and goat. When goat is bred to sheep occur, but in most cases, pregnancies are lost after few weeks without few exceptions (occasionally produce hybrid offspring). In contrast, when sheep are bred to goat pregnancy does not occur or very seldom occur followed by subsequent abortion, this could be interpreted as inherent disqualification of the particular species to overcome block against interspecies pregnancy and subsequent development [90].

Conclusion

In excess of the years, broad hybridization has provided a platform for non-transgenic approaches in crop improvement programs. Hybridization and introgression increase genetic diversity through the production of new recombinant genotypes, probably more rapidly than is possible by mutation. Enhanced levels of variability could allow organisms to more readily track environmental change, leading to increased rates of evolution. A possible outcome of these processes would be the origination of new species through a combination of preexisting characters in other taxa.

Despite the great potential it provides, it is still limited by the various disadvantages of certain hybrid dysgenesis like sterility, segregation, and distortions in sex ratios, high-frequency mutations, changes in the structure of chromosomes, non-disjunctions, and rearrangements in chromosomes as well as variations in leaves, and stems. There is a need for future improvements in the wide hybridization techniques as a potential alternative to transgenic crop improvement strategies. Our new challenge is to integrate advancements in genomic and genetic techniques with classical experimental protocols of genetic crosses, common garden field experiments, and controlled environment manipulations to better understand how and why hybridization has such important evolutionary repercussions. Also, in animal studies, scientists discovered alternatives to natural mating, manual fertilization (fertilization of oocytes by the sperm itself), and different genetic barriers. Now, the basic barrier is related to embryonic genome activation, nuclear reprogramming, and the interaction between genetic and mtDNA. Therefore, in the future, the research emphasis should be given to overcome the genetic barriers against successful interspecies hybrid animal production and enhance food security.

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