Post zygotic hybridization isolation mechanisms

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Abstract

The study of the patterns of reproductive isolation in relation to species divergence is critical for the understanding of the process of speciation.Comparative analyses of this kind were previously conducted in Drosophila, Lepidoptera, and frogs, ducks, and birds‟ .In general. Information analyzed from the literatures, hybrid inviability in relation to species divergence in pigeons and doves. Four main patterns arose from this analysis as in the other groups studied, F1 hybrid inviability gradually increases as species diverge, the time needed to reach total inviability being higher in birds than in the other groups; as expected, the presence of geographic overlap does not influence the evolution of postzygotic isolation; the percentage of unhatched eggs does not differ between hybrids of the first generation and the backcrosses, but it increases in the second hybrid generation; and pigeons and doves follow Haldane‟s rule, as found in the other groups studied so far. The similarity between the results of previous different studies contributes to the growing evidence suggesting that the patterns of the evolution of postzygotic isolation, and the process of speciation in general, are shared among animal groups.The hypothesis that reinforcement accounts for behavioral isolation in sympatry assumes that hybridization and postzygotic isolation are present. Here, genomic and morphological data used to demonstrate that hybridization is ongoing between orange throat and rainbow darters and used hybrids collected from nature to measure postzygotic barriers across two hybrid generations.

Key words: - Haldane‟s rule, Hybridization, inviability, postzygotic isolation, sterility,

Introductions

Post-zygotic isolating barriers may act at the stage of the F1 hybrids or beyond(Sapir *et al.*, 2015). There are many ways in which hybridization could be costly 560 and here it is estimated only subset of these possibilities (F1 hybrid inviability and sterility), and only in lab conditions (Servedio and Noor 2003). Past research with a different pair of species (*Jaera albifrons and J. ischiosetosa*, which are more divergent than our focal species *J. albifrons* and *J. praehirsuta,* (Ribardière 2017) has found that post-zygotic barrier effects act after the first generation (back- crosses or F2 hybrids)(Ribardi *et al*., 2018).

The study has revealed that pollinator constancy and preference and poor hybrid seed viability are the most important reproductive isolating mechanisms. Reproductive isolation is practically complete by both pre- and post-zygotic barriers. Average pre-zygotic isolation is greater than post-zygotic isolation, in accordance with the trend observed in flowering plants in which reproductive isolation is principally caused by pre-zygotic mechanism (Carrió &

Güemes, 2014). Between *A. valentinum* and *A. controversum*, average post-zygotic isolation (0.819) has high and lower than pre-zygotic isolation (0.976)(Carrió & Güemes, 2014).

Reproductive isolation caused by differences in seed viability is a major isolation barrier because all interspecific crosses in *A. valentinum* gave rise to inviable seeds. By contrast, hybrid seeds from interspecific *A. controversum* crosses are highly viable with similar mass, germination percentage and speed compared to the intraspecific *A. controversum* offspring. (Carrió & Güemes, 2014). Hybrid sterility is the most common form of postzygotic reproductive isolation in plants. The best-known example is perhaps the hybrid sterility between indica and japonica

subspecies of Asian cultivated rice (*Oryza sativa L.*).Is the most common form of postzygotic

reproductive isolation. Such hybrid sterility hinders the transferring of useful genes between the two subspecies, and is a major obstacle for utilization of the strong heterosis exhibited in the hybrids(Ouyang *et al.*, 2010).Major progress has been reported recently in rice in identifying and cloning hybrid sterility genes at two loci regulating female and male fertility, respectively. Genetic analyses and molecular characterization of these genes, together with the results from other model organisms especially Drosophila, have advanced the understanding of the processes underlying reproductive isolation and speciation(Ouyang *et al.*, 2010).These findings also have significant implications for crop genetic improvement, by providing the feasibility and strategies for overcoming intersubspecific hybrid sterility thus allowing the development of intersubspecific hybrids. Addresses (Ouyang *et al* .,2010). These findings have shed light on the process of molecular evolution in reproductive isolation, and also have significant implications in crop genetic improvement (Ouyang *et al.*,2010).

Genes causing hybrid sterility:-

There has been major progress in the identification and characterization of genes contributing to hybrid sterility. A big surprise revealed by analyzing the hybrid sterility genes is that they fall into very different functional categories (Ouyang *et al.*, 2010).Second, the primary functions of the genes involved in hybrid sterility or postzygotic reproductive isolation may or may not be in reproduction. These features suggest complexity for studying hybrid sterility genes (Ouyang *et al.*, 2010).

Evolutionary significance of the triallelic systems at the hybrid sterility loci

Speciation is a gradual process and represents the emergence of barriers to gene flow between populations .In the early stages of speciation, extensive exchange of alleles is still possible, while the gene flow essentially ceases when the speciation process is completed, and the genomes of the nascent species will diverge independently.A very interesting outcome of such evolution is that there is a neutral allele at the hybrid sterility locus, which does not cause sterility when present in a heterozygous genetic background with either of the incompatible alleles (Ouyang *etal.*, 2010).

Implications of the triallelic systems for crop genetic improvement

The hybrid sterility and wide-compatibility system also has significant implications in crop genetic improvement. Rice is a main staple crop providing food for a large segment of the world population. The genetic differentiation between indica and japonica leads to strong hybrid vigor in F1 hybrids, utilization of the intersubspecific heterosis has been regarded as a promising strategy for increasing rice productivity. Large efforts have been invested in the last several decades in breeding for indica–japonica hybrids. However, such efforts have been hindered by hybrid sterility that frequently occurs in inter first, ecological differences between populations can affect postzygotic isolation; namely, ecological divergence can result in hybrids exhibiting low fitness (Ouyang *et al.*, 2010).

At least three strategies have been identified for overcoming the hybrid sterility in indica–japonica crosses. First, the neutral alleles (WCGs) can be introgressed from the WCVs into the parents whose hybrids exhibit strong yield heterosis. Thus, crossing of the parents would produce highly heterotic hybrids with normal fertility(Ouyang *et al.*, 2010). Crossing of such

„indica-compatible japonica lines‟ with targeted indica lines would produce desired hybrids(Ouyang *et al.*, 2010). The third is to produce artificial neutral alleles by suppressing expression of the genes causing hybrid sterility with RNAi or microRNA technology, if such gene silencing does not affect the plant growth or development. However, the effectiveness of these strategies may be affected by the fact that hybrid sterility in a cross frequently involves multiple loci, most of which have not been characterized(Ouyang *et al.*, 2010).

Gametic mortality:-

Here, the sperms fail to fertilize the eggs leading to gamete mortality e.g. Volpe observed in toad species of *Bufo fowleri* and *B. valliceps* that a male with non-functional gonads but with normal sex behaviour induces the female to lay eggs in water but the eggs perish, when they„re not fertilized. The same phenomenon is also encountered in sea urchins (Lillie). In abalones (large gastropods), the sperm carries a lysin protein that dissolves a hole in the egg‟s vitelline envelope but only if egg and sperm are of same species(Tanushree , 2017).

Zygote mortality:-

In nature, it’s observed that if an organism is able to elude all the earlier isolating mechanisms

and somehow able to form a hybrid, the zygote so formed shows irregular embryogeny which can cease at any stage of development. Since there is no perfect matching of two chromosomes,

zygote fails to be formed or the sperm nucleus is totally eliminated from the spindle. e.g. eggs of fishes can be artificially inseminated by sperms of many different species, but development is abnormal. However (Tanushree , 2017).

Hybrid invariability/inferiority:-

Some hybrids not only survive but exhibit luxuriance e.g. mule (a cross between horse and ass), but they are like the proverbial needle in a haystack. Normally the hybrids in nature don‟t survive or form unisexual progenies (hybrids of one sex especially male die). e.g. embryos produced by crosses between female fowler‟s toad and male Gulf coast toad develop normally into adult, but adults are all males and sterile. Natural hybrids are also found to be weak and the weakness is probably due to physiological disturbance or ecological differences. Zygote produces F1 hybrid of reduced viability i. Hybrid inviability/inferiority(Tanushree , 2017).

Hybrid viable:-

Hybrid Sterility: - The hybrids arising from certain interspecific crosses are either partially or completely sterile. This might be because of failure of pairing of chromosomes at meiosis, or abnormalities like formation of fused spindle or failure of cell division in the spermatocytes or disharmonious interaction of genes. Mule is the classical example of vigorous but completely sterile hybrid. The sterility is due to disturbances in sex cell formation and failureof gene complements of distinct species to function harmoniously.(Tanushree,2017).Reproductive isolation caused by differences in seed viability was a major isolation barrier because all interspecific crosses in A. valentinum gave rise to inviable seeds(Carrió & Güemes, 2014).

Hybrid breakdown:-

Some interspecific hybrids are partially or completely fertile in one or both sexes. If so, it still doesn‟t necessarily follow that gene exchange between populations of such species can take place without any problem. Hybrid breakdown may occur in second or backcross generations. Its cause is formation of genotypes of low fitness, owing to recombination of gene complements of parental species. F1 hybrid females from *Drosophila pseudobscura* and *D. persimilis* crosses are vigorous and deposit as many eggs as non-hybrid females. Yet, when these females are backcrossed to males of either parental species, individuals of both sexes in offspring‟s are weak and many of them are sterile(Tanushree , 2017).Many of the literature identified seven genes that

have been shown to underlie pre-pollination postzygotic barriers. Five of these genes are

responsible for variation in floral pigmentation, one for differences in flowering time and one for a shift in mating system from outcrossing to selfing(Rieseberg & Blackman, 2010).

Many cultures of wild plant species, in contrast to animals, are found to be polymorphic at genes controlling interspecies incompatibility. This fact facilitates genetic analysis of incompatibility and broadens perspectives in studying the structure, functions, and molecular evolution of the genes controlling postzygotic reproductive isolation, in view of the possible leading role of these genes in adaptive speciation(Voilokov & Tikhenko, 2009). Internal postzygotic mechanisms cause death, weakness, or sterility of the first-generation hybrids, as well as breakdown of hybrids of F 2, F 3, and subsequent generations, which is expressed as segregation of a large proportion of unviable, weak, or sterile progeny. Mechanisms(Voilokov & Tikhenko, 2009). As considered some of them mainly mechanisms of postzygotic lethality and weakness, with special reference to genetic analysis of interspecific incompatibility in plants(Voilokov & Tikhenko, 2009).

Discussions:-

According to the dominance theory, the number of incompatibilities that cause postzygotic

Isolation increases as the square of time since divergence (Aires, 2003).

Interspecific crosses between *A. thaliana* as the seed parent and *A. arenosa* as the pollen parent failed when *A. thaliana* was in its natural diploid state, but doubling the maternal contribution produced viable seed. The last can account only for the failure of a stage at which imprinting operates, which in the case of flowering plants is mainly if not exclusively endosperm development. Several predictions can be formulated. There are many reasons for post zygotic hybridization isolation mechanisms like zygote mortality, gamete mortality, hybrid sterility, hybrid inviability, hybirid breakdown .If parental imprinting is involved in interspecific seed failure, we would expect the relative ploidy of the parents to affect the outcome and also that reciprocal crosses would produce complementary phenotypes in interspecific endosperm. Conversely, the allelic incongruity and genome shock hypotheses are not necessarily ploidy dependent, and these phenomena would not be expected to cause reciprocal endosperm phenotypes (Arabidopsis *et al.*, 2015). Identifying a history of hybridization still leaves the question of how hybridization affects the evolutionary(Goulet *et al.*, 2017).
In particular, an increase in postzygotic isolation with time of divergence is predicted by the dominance theory, which postulates that postzygotic isolation arises as a by-product of independent evolution between diverging lineages, due to the accumulation of recessive incompatibilities (Aires, 2003). Incompatible alleles are connected by a dashed red line and an X.

A, Chromosomal rearrangements such as inversions present in parent taxa may be differentially 5 fixed in hybrid populations conferring partial incompatibility with both parent lineages. B, Similarly, recombinational speciation may involve the differential fixation of genic incompatibilities(Goulet,,*et al.*, 2017).

F1, hybrid sterility and “hybrid breakdown” of F2 and later generations in rice *(Oryza sativa L.)* are common and genetically complicated. Hybrid sterility appeared to be due to recombination within a number of putative differentiated “supergenes” in the rice genome, which may reflect cryptic structural rearrangements. The cytoplasmic genome had a large effect on fertility of both male and female gametes in the F, hybrids. Genetic analysis of post reproductive isolation barriers between 0. *sativa* ssp. indica and ssp. japonica may shed light on the process of speciation in plants, and provide important information for rice improvement(Li, *et al.*, 1997).

Concluding remarks and future directions

Global food security requires the development of new and effective agricultural technologies to increase grain production. Hybrid breeding in maize and rice as well as in other crops has made a significant contribution to the increase of crop yield. The identification of more male-sterility genes and understanding of gene function in different crops is the highest priority for hybrid crop breeding(Kim & Zhang, 2018).

Research should take into consideration the importance of developing strategies to propagate the male-sterile lines generated because female parent propagation is, for many crops, the limiting factor for the production of hybrids on a large scale(Perezprat, *et al.*, 2002).

It would be possible to provide a full elucidation on the origin of the genes for hybrid sterility and the evolutionary processes for the establishment of the subspecies and species. In turn, such knowledge would facilitate the formulation and development of strategies for rice improvement, which may also have implications for the improvement of other crop species(Ouyang *et al.*, 2010). Although it is still remain largely ignorant about the frequency of these processes, it is evident that both the genetic architecture of postzygotic the demographic and ecological conditions for speciation with gene flow existin nature (Ortiz *et al.*, 2009).

It is found that parental imprinting most likely is the dominant mechanism for the postzygotic hybridization barrier between *A. thaliana* and *A. arenosa*. The cross can be rescued by doubling the ploidy of the seed parent, resulting in an endosperm with balanced maternal and paternal contributions. Additionally, it has been shown that it is possible to revert to the nonviable state by hypomethylation of the seed parent, effectively raising a hybridization barrier. The ability to introduce a hybridization barrier may prove useful in the containment of genetically modified crops: genomic strength could be modified to ensure that they would be unable to produce viable seeds by hybridization with wild relatives. It is suggested that it would be possible to breach a hybridization barrier by changing the genomic strength, allowing normally isolated species to interbreed (Arabidopsis *et al.*, 2015).

Identification and molecular analysis of the hybrid sterility genes have refocused attention to the genetic basis of reproductive isolation. Although the present understanding is still rudimental and tentative, several conclusions can be drawn from the existing results. First, essentially neutral evolutionary changes within populations can produce deleterious interactions which cause sterility in hybrids between the populations. Second, genes involved in hybrid sterility may change their primary functions or genomic locations during divergent evolution. And third, the factors that cause hybrid sterility are ordinary genes which have diverse functions without preference of special functional classes. Neutral alleles (WCGs) may arise as loss-of-function mutants at these loci that may provide bridges for gene flow between differentiating populations serving as a cohesive force at the species level alleles (Ouyang *et al.*, 2010).

However, there have been no reports of the isolation of genes involved in postzygotic reproductive barriers in plants; therefore, it is unclear whether these tendencies are also present in plants. The high-resolution and physical maps in this study will be useful to isolate the gene involved in reproductive barriers and speciation, and will also help in understanding the molecular mechanism of such barriers(Miura, *et al.,* 2008). As plant evolutionary biologists, we should not be surprised by the growing realization that hybridization occurs across the tree of life. Botanists have been studying the existence and evolutionary consequences of hybridization since the birth of taxonomy, through the modern synthesis, and into the genomic era(Goulet et al., 2017).

The most surprising conclusion from this review is that identities of genes underlying both prezygotic and postzygotic RI are often predictable in a broad sense from the phenotype of the reproductive barrier. Regulatory changes (both cis and trans) dominate the evolution of pre- pollination RI in plants, whereas a mix of regulatory mutations and changes in protein coding genes underlie intrinsic postzygotic barriers. Also, loss- of-function mutations and copy number variation frequently contribute to RI. Although direct evidence of positive selection on speciation genes is surprisingly scarce in plants, analyses of gene family evolution, along with theoretical considerations, imply an important role for diversifying selection and genetic conflict in the evolution of RI. Unlike in animals, however, most candidate speciation genes in plants exhibit intraspecific polymorphism, consistent with an important role for stochastic forces and/or balancing selection in development of RI in plants(Rieseberg & Blackman, 2010).

Postzygotic reproductive isolation, based on negative interactions of genes, is a key aspect of divergent speciation in plants and animals. The effect of the interaction manifests as a drastic reduction in fitness of hybrids of the first of subsequent generations, which is expressed as hybrid lethality, weakness or sterility. Both simple genetic control of genetic incompatibility, which includes interallelic negative comple mentation or epistatic interactions of a limited number of genes, and more complex control, based on epistatic interactions of many genes, have been described in plants(Voilokov & Tikhenko, 2009). Reproductive isolation caused by differences in seed viability was a major isolation barrier because all interspecific crosses in *A. valentinum* gave rise to inviable seeds. By contrast, hybrid seeds from inter- specific *A. controversum* crosses were highly viable with similar mass, germination percentage and speed compared to the intraspecific *A. controversum* off-spring (All, 2019).

Reference

Aires, B. (2003). Hybridization and postzygotic isolation patterns in pigeons and doves. *Evolution*, *57*(6), 1411–1418.

All, U. T. C. (2019). The Genetics of Floral Divergence and Postzygotic Barriers between Outcrossing and Selfing Populations of Arenaria uniflora (Caryophyllaceae) Author (s): Lila Fishman and Donald A . Stratton Published by : Society for the Study of Evolution Stable URL : https://www.jstor.org/stable/3449321 Society for the Study of Evolution is collaborating with JSTOR to digitize , preserve and extend access to Evolution THE GENETICS OF FLORAL DIVERGENCE AND POSTZYGOTIC BARRIERS, *58*(2), 296–307.

Carrió, E., & Güemes, J. (2014). The effectiveness of pre- and post-zygotic barriers in avoiding hybridization between two snapdragons (Antirrhinum L .: Plantaginaceae), 159–172.

Goulet, B. E., Roda, F., & Hopkins, R. (2017). Hybridization in Plants : Old Ideas , New Techniques [OPEN], *173*(January), 65–78. https://doi.org/10.1104/pp.16.01340

Kim, Y., & Zhang, D. (2018). Molecular Control of Male Fertility for Crop Hybrid Breeding. *Trends in Plant Science*, *23*(1), 53–65. https://doi.org/10.1016/j.tplants.2017.10.001

Li, Z., Pinson, S. R. M., Patemon, A. H., Parks, W. D., & Stanselt, J. W. (1997). Genetics of Hybrid Sterility and Hybrid Breakdown i n an Intersubspecific Rice (, (1974).

Mechanisms, I. (2017). Isolation and Isolating Mechanisms Dr Tanushree Saxena. *Isolation and Isolating Mechanisms*, *110036*.

Miura, K., Yamamoto, E., Morinaka, Y., Takashi, T., & Kitano, H. (2008). The hybrid breakdown 1 (t) locus induces interspecific hybrid breakdown between rice Oryza sativa 9 cv . Koshihikari and its wild relative O . nivara, *105*, 99–105.

Ortiz-barrientos, D., Grealy, A., & Nosil, P. (2009). The Genetics and Ecology of Reinforcement Implications for the Evolution of Prezygotic Isolation in Sympatry and Beyond, *182*, 156–182. https://doi.org/10.1111/j.1749-6632.2009.04919.x

Ouyang, Y., Liu, Y., & Zhang, Q. (2010). Hybrid sterility in plant : stories from rice. *Current*

Opinion in Plant Biology, *13*(2), 186–192. https://doi.org/10.1016/j.pbi.2010.01.002

Perez-prat, E., Campagne, M. M. V. L., Perez-prat, E., & Lookeren, M. M. Van. (2002). Hybrid seed production and the challenge of propagating male- sterile plants, *7*(5), 199–203.

Ribardi, A., Pabion, E., Daguin-thi, C., Broquet, T., Universit, S., Biologique, S., … Biologique, S. (2018). Sexual isolation with and without ecological isolation between sympatric isopods. *Sexual Isolation Is Often Coupled with Other Barriers, and Sexual Isolation Mechanisms Can Be Intrins*.

Rieseberg, L. H., & Blackman, B. K. (2010). Speciation genes in plants. *Annals of Botany*, *106*(3), 439–455. https://doi.org/10.1093/aob/mcq126

Sapir, Y., Dieckmann, U., & Program, E. (2015). Interim Report Post-zygotic reproductive isolation among populations of Iris atropurpurea : The effect of spatial distance among crosses and the role of inbreeding and outbreeding depression in determining niche width Yuval Sapir, (February).

Species, A., Bushell, C., Spielman, M., & Scott, R. J. (2015). The Basis of Natural and Artificial Postzygotic Hybridization Barriers in The Basis of Natural and Artificial Postzygotic Hybridization Barriers inArabidopsis Species, (October). https://doi.org/10.1105/tpc.010496

Voilokov, A. V., & Tikhenko, N. D. (2009). Genetics of postzygotic reproductive isolation in plants. Russian Journal of Genetics,45(6),637–650. https://doi.org/10.1134/S1022795409060027