

Genetic polymorphisms in *Drosophila*

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In a population evolving by gradual change, the amount of genetic variation is important because the rate of evolution is absolutely limited by the degree of genetic variability. Various forces of evolution such as natural selection, random genetic drift and migration operate on genetic variability which provides the raw material for evolution. Thus the rate of evolution is absolutely limited by the amount of genetic variability already existing in the population. The basic parameters of evolutionary genetics are: (a) the amount of genetic variation measures the evolutionary potential of a population at a given time, and (b) the amount of genetic differentiation between populations reflects the operation of evolutionary processes since the divergence of populations from the common original population. Extensive work has been done on a variety of organisms to estimate the degree of genetic variability in natural populations at the level of chromosome, allozyme and DNA. The results of these studies have shown that there exists a considerable degree of genetic variability although there are interspecies-specific and intraspecies-specific variations in the degree of genetic polymorphism. *Drosophila*, a dipteran insect commonly known as fruit fly, occupies a unique status among the species which have been used for this kind of research. It was used for the first time in 1905 by Carpenter for experimental studies and in 1909 by Morgan for genetic studies. Since then it has served as a good biological model for different types of studies such as genetics, behaviour, evolution and development. The present review summarizes briefly the work done on genetic polymorphism with particular reference to chromosome, allozyme and DNA polymorphism in *Drosophila*, with a brief discussion on balanced polymorphism, genetic coadaptation, linkage disequilibrium and genetic hitch-hiking, which are of considerable evolutionary significance.

Keywords: Allozyme, DNA polymorphism, *Drosophila*, inversion.

EVOLUTION is the continuing process of change, especially with reference to natural selection. Darwin¹ proposed his theory of natural selection to explain the mechanisms of evolution. As explained in his book¹ Darwin's theory of natural selection has two components: Descent with modification – all species living and those extinct have descended from one or a few original forms

of preexisting species, and (ii) natural selection as causal agent of evolutionary change operating on variations. As a result of the struggle for existence, variability and inheritance, the successive generations tend to become better adapted to their environment. These adaptations are preserved and accumulated in the individuals of the species and ultimately lead to the origin of new species from the old ones.

The most serious drawback of Darwin's theory stemmed from his lack of knowledge about heredity. He could not explain the nature and causes of variations which are important for evolution and it was the demerit of Darwinism. The Missing link in Darwin's argument was provided by Mendelian genetics. Mendel's paper published in 1866 formulated the fundamental principles of a theory of heredity that accounts for biological inheritance through particulate inheritance (now called genes), one from each parent, which do not mix or blend but segregate in the formation of sex cell or gamete. The rediscovery in 1900 of Mendel's laws led to the emphasis on the role of heredity in evolution. The genes are the functional units of biological activity. However, the genes are not the principal units of evolutionary change. Researches during the last 70–80 years have shown that evolutionary forces do not act upon individual genes or individuals, but upon groups of individuals known as a population. A population consists of pooled genes of all individuals within the group. Natural selection acts upon this gene pool. Thus the population forms the stage on which elemental forces of evolution operate and during this process the individual genes may be eliminated or reproduced and certain genotypic combinations may be favoured over others. Thus evolution is any change in the genetic composition of a population. In 1908, Hardy (Great Britain) and Weinberg (Germany) made a fundamental discovery about the nature of gene pool of a population. They suggested that frequency of particular genes and resulting genotypes will remain constant generation after generation. This is called Hardy–Weinberg equilibrium (genetic equilibrium). The frequency of genotypes will be in the proportion of $p^2 : 2pq : q^2$. This is known as Hardy–Weinberg law or binomial square law ($p + q = 1$, $(p + q)^2 = p^2 + 2pq + q^2 = 1$), when there are two alleles of a genetic locus, *A* and *a* with frequencies *p* and *q* respectively. The Hardy–Weinberg equilibrium is maintained under certain conditions: random mating (panmixia), absence of mutation, natural selection, random genetic drift and migration. Evolution occurs only when this equilibrium is

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modified. The forces which modify this equilibrium are known as elemental forces of evolution: mutation, natural selection, genetic drift and migration. The restoration of Darwin's theory of natural selection as the primary guiding factor in evolution began with the birth of population genetics in 1920s based upon the work of Chetverikov, Fisher, Haldane and Wright.

Dobzhansky's work with *Drosophila* provided new evidence which supported Darwin's theory that natural selection acting on genetic variations in populations, is a driving force in evolution. Dobzhansky's book² published in 1937 advanced a comprehensive account of the evolutionary process in genetic terms, laced with experimental evidences supporting the theoretical arguments. During that time, experimental biologists and naturalists embraced the new understanding of the evolutionary process as one of the genetic changes in populations. The modern synthetic theory of evolution as a generally accepted way of approaching the problems of evolutionary mechanisms was born in 1937 with the publication of Dobzhansky's book² which integrated genetics and evolution. Because of this reason, Dobzhansky is considered as the foremost architect of synthetic theory of evolution, although the term was used for the first time by Huxley³ in 1942. Genetic variability in the populations is most important because it provides raw materials on which various forces of evolution operate and populations accumulate genetic variations. The amount of genetic variability present in the population at a given time reflects its evolutionary potential. Thus the rate of evolution is absolutely limited by the degree of its genetic variability. A large body of information concerning population genetics has been accumulated as a result of work done on a variety of organisms. Earlier work has mainly told us about concealed genetic variability due to deleterious mutations and structural chromosomal variations. However, due to the development of new techniques in molecular biology, application of molecular methods to evolutionary studies has already illuminated many aspects of evolutionary history. Genetic polymorphisms have been studied extensively in a variety of organisms. Of the millions of species that inhabit the Earth, biological researchers tend to concentrate on relatively few organisms that subsequently become model systems⁴. Many organisms have been studied, but some have become popular models: house mouse, yeast, *Escherichia coli*, corn, *Drosophila*, zebrafish, *Caenorhabditis elegans* and *Arabidopsis*. Among all these models, *Drosophila* has received maximum attention and has become the most popular biological model. At global level, more than 1500 species of *Drosophila* are known and in India more than 100 species have been reported which include both new species and new records⁵. Thus there is rich species diversity in the genus *Drosophila*. The most commonly used species for different kinds of studies is *Drosophila melanogaster*. However, in India the most extensively studied species from evolutionary

point of view is *Drosophila ananassae*. This is a cosmopolitan and domestic species having common occurrence in India and endowed with several unusual genetic features⁶⁻¹¹. Genetic polymorphisms have been extensively studied in a large number of species of *Drosophila* at the levels of chromosome, allozyme and DNA. The present review briefly summarizes the work done on different species of *Drosophila* with particular reference to inversion, allozyme and DNA polymorphism with a brief discussion on balanced polymorphism, genetic coadaptation, linkage disequilibrium and genetic hitch-hiking, which are of considerable evolutionary significance related to genetic polymorphism.

Inversion polymorphism

Sturtevant¹² detected inversions for the first time in *D. melanogaster* through the suppression of crossing over in inversion heterozygotes. Since then, extensive work has been done on chromosomal polymorphism in numerous species of *Drosophila* throughout the world. The findings have demonstrated that chromosomal polymorphism due to paracentric inversions is common in the genus *Drosophila*¹³⁻¹⁹. It has also been demonstrated that inversion polymorphism in *Drosophila* is subject to selection and is an adaptive trait. Inversion polymorphism in *Drosophila* is one of the best studied systems in population genetics. Chromosome inversions can be used as genetic markers or alleles and are used to study species population genetic parameters. Further, *Drosophila* inversions have become a cornerstone example in experimental work⁴. The degree and pattern of inversion polymorphism vary in different species. Frequency of inversion may vary in different populations of the same species. The most convincing evidence for selective control of inversion frequencies comes from observations in natural populations of different species of *Drosophila*. It shows geographic, seasonal, altitudinal and latitudinal variations. In certain cases, north-south clines in inversion frequencies have also been reported¹⁶. Dobzhansky and co-workers²⁰⁻²² found a good correspondence between the mean number of heterozygous inversions per individual and an index expressing environmental heterogeneity in natural populations of *D. willistoni*. Populations at the centre of geographic distribution have high degree of inversion polymorphism than the marginal populations. Based on these findings, it has been suggested by Dobzhansky and others that inversion polymorphism in *Drosophila* is a device to cope with the diversity of environments, which is referred to as ecological niche hypothesis. Carson²³⁻²⁵ found similar results in *D. robusta*. He measured the amount of chromosomal variability by an index of free recombination (IFR – how much of euchromatin is free to undergo recombination). Polymorphism is lower in marginal populations (high IFR) than in the central ones (low IFR). Carson suggested that the amount of recombination is an essential adaptive

factor and that the low level of polymorphism in marginal populations where homoselection (selection favouring homozygotes) predominates, gives a high potential for free recombination from which adaptive novelties can be synthesized. In geographically central populations, there is high level of inversion polymorphism where heteroselection (selection favouring heterozygotes) predominates. Thus marginal populations have more adaptability, whereas the central ones have more adaptedness. The concentration of inversions is higher in urban populations than rural ones, which has been found in *D. funebris*²⁶, *D. ananassae*²⁷ and *D. melanogaster*²⁸. This has been explained by suggesting that the high degree of urbanization probably leads to an increase in the number of ecological niches and consequently the high degree of inversion polymorphism. The species of *Drosophila* which have been subjected to the study of inversion polymorphism and inversions have been detected include *D. melanogaster*, *D. ananassae*, *D. pseudoobscura*, *D. persimilis*, *D. robusta*, *D. pavani*, *D. nasuta*, *D. subobscura*, *D. flavopilosa*, *D. silvestris*, *D. guaramunu*, *D. rubida*, *D. paulistorum*, *D. willistoni* and *D. bipectinata*^{4,16,17,19}.

Inversion polymorphism has also been studied in certain species of *Drosophila* found in India. *D. nasuta* shows considerable degree of inversion polymorphism and there is existence of geographic differentiation and altitudinal clines with respect to inversion polymorphism in Indian natural populations^{29,30}. *D. bipectinata* shows relatively less number of inversions (only 13 paracentric inversions) in its natural populations³¹. Only three inversions have been found to persist in laboratory stocks due to heterozygote superiority³²⁻³⁴. Inversions occur at low frequency in natural populations and there is no evidence for geographic differentiation in natural populations, which lends support for rigid inversion polymorphism in *D. bipectinata*³⁵. More than 300 paracentric inversions have been reported in *D. melanogaster*³⁶. In Indian populations of *D. melanogaster*, 40 paracentric inversions have been detected³⁷⁻³⁹. Inversions do not persist in laboratory stocks^{40,41}. However, there are geographic differentiations of inversion polymorphism in Indian natural populations and north-south clines in inversion frequencies^{38,39}. *D. ananassae*, is characterized by several unusual genetic features⁶⁻⁸. It shows high degree of chromosomal polymorphism⁹. In total, there are 78 paracentric inversions, 21 pericentric inversions and 48 translocations⁴². However, only three paracentric inversions (AL in 2L, DE in 3L and ET in 3R) which are called as cosmopolitan inversions, have wide geographic distribution^{43,44}. These three inversions often persist in laboratory populations due to heterotic buffering associated with these inversions^{45,46} and their frequencies may change due to random genetic drift⁴⁷. Extensive data on inversion frequencies in Indian natural populations of *D. ananassae* have shown that there are geographic differentiations in natural populations at the level of inversion polymorphism and cosmopolitan inver-

sions occur in high frequency in South India, including Andaman and Nicobar Islands^{27,48-54}. There is evidence for population sub-structuring at the level of inversion polymorphism in Indian natural populations⁴². Singh¹⁹ compared the pattern of inversion polymorphism in three species – *D. melanogaster*, *D. bipectinata* and *D. ananassae* belonging to the *melanogaster* species group and found that they vary in the degree and pattern of inversion polymorphism, although they belong to the same species group. He suggested that these species have evolved different mechanisms for adjustment to their environments. Thus there is enough evidence to show that there are a large number of *Drosophila* species which harbour genetic polymorphism at the level of chromosomes maintained by selection.

Allozyme polymorphism

Earlier work has revealed a great deal about concealed genetic variability caused due to deleterious genes and cytological variations in *Drosophila*². The pioneer work of Lewontin and Hubby⁵⁵ made conceptual breakthrough in the area of molecular population genetics by providing numerical estimates of genic variations in natural populations of *D. pseudoobscura* through the study of allozyme polymorphism. Since then, numerous cases of protein (enzyme) polymorphism controlled by different alleles of the same locus through the technique of gel electrophoresis have been reported in a large number of *Drosophila* species. Such studies provide information about genic variation, degree of polymorphism and level of heterozygosity. Enzymes differing in electrophoretic mobility as a result of allelic differences in a single gene are called as allozymes. Allozyme polymorphisms have been studied in about 50 species of *Drosophila* analysing a large number of loci and extensive data are documented, which demonstrate that a large number of loci tested are polymorphic⁵⁶⁻⁶⁵. In *D. melanogaster*, the allozyme polymorphism produced by the *Adh* locus (alcohol dehydrogenase) shows correlation between their frequencies and environmental temperatures demonstrating the role of natural selection⁶⁶. Evolutionary relationship among different species has been discussed on the basis of allelic frequency (allozyme data). The work of Ayala⁵⁶ and others provides evidence that protein polymorphism is maintained by selection. Both interspecies-specific and intraspecies-specific comparisons have been made. Although the selectionists versus neutralists controversy exists, there are certain clear evidences in favour of selection playing a role in the maintenance of allozyme polymorphism in *Drosophila*⁴.

DNA polymorphism

Application of molecular techniques to evolutionary studies has already illuminated different aspects of population

genetics. In population genetics, it is important to interpret the molecular sequences of genes and proteins and employing these sequences to derive inferences about the evolutionary history of species. Population genetics is also concerned with the processes and mechanisms by which the evolutionary changes occur. DNA polymorphism has been studied in different species of *Drosophila* employing two methods: (i) restriction fragment length polymorphism (RFLP) which detects restriction sites in DNA with the help of restriction enzymes and separating the restriction fragments using electrophoresis (Southern blot using probe DNA molecule) and (ii) DNA sequence variation may be studied using Maxam–Gilbert sequencing method or Sanger dideoxy sequencing method. If we study the nucleotide sequence of a gene, it will yield the ultimate resolution of genetic variation. If the protein bands from two individuals migrate the same way during protein electrophoresis or restriction fragments of a particular locus look similar, one cannot be sure that the alleles are identical. It is highly unlikely that the two genetic loci identical in the DNA sequence come from different ancestral genes. Thus the DNA sequence identity is particularly important for various current tests about major evolutionary forces which operate in the Mendelian populations and make use of DNA sequence data. This also may be useful for reconstructing the phylogeny. Polymorphism may be compared using DNA sequence data related to several alleles from many individuals of the same population of the same species and genetic variation can be quantified. Natural populations of many species of *Drosophila* do contain substantial genetic polymorphism detectable as allozyme polymorphism through electrophoresis. We still do not know what level of polymorphism and heterozygosity is characteristic of the entire genome. However, the absolute level of genetic variability is now amenable to investigate at the level of DNA either directly by means of DNA sequencing or indirectly by examining variation in restriction sites (RFLP). As far as genetic polymorphism at the level of nucleotides in *Drosophila* is concerned, two important studies are worth mentioning: (i) Cross and Birley⁶⁷ measured the amount of DNA polymorphism indirectly from restriction site data (RFLP) in the region of alcohol dehydrogenase gene of *D. melanogaster* in a population descended from flies trapped in a Dutch fruit market in Groningen. They used five restriction enzymes each with six base restriction sites. The region contained a total of 23 sites, and 16 of the sites were cut in all the individuals in the sample and 7 sites were found to be polymorphic in a sample of 10 chromosomes. Estimates of the proportion of polymorphic nucleotide sites in the population and heterozygosity per nucleotide sites are 0.029 and 0.010 respectively. This method has greater resolution than enzyme electrophoresis in estimating genetic variation. (ii) DNA sequence data have also been obtained for *Adh* locus in *D. melanogaster*⁶⁸. Eleven alleles were sequenced in a

2659 bp region of the *D. melanogaster* genome, including the *Adh* locus. The level of nucleotide polymorphism was estimated to be 0.0162, because 43 of 2659 sites were seen to differ. The comparison of nucleotide diversity in the *Adh* gene showed that there is a clear tendency of the exons to remain less variable than the introns. Stephan and Langley⁶⁹, and Stephan⁷⁰ analysed the restriction site variation in the centromeric region of the X chromosome in *D. ananassae* using six cutter enzymes. They found significant differences in the frequency distribution of polymorphism/haplotypes among three populations – Burma, India and Brazil, and low nucleotide variation in Brazilian population of *D. ananassae* was explained by suggesting the role of recent bottleneck of population size (founder principle). Restriction site variation in mt DNA has been compared between two sibling species of *Drosophila*: *D. melanogaster* and *D. simulans* using restriction enzymes⁷¹. The number of polymorphic sites varies between these two species; 20 in *D. melanogaster* and three in *D. simulans*, which shows that the degree of DNA polymorphism varies between two sibling species of *Drosophila*, although both are cosmopolitan in distribution. The ultimate level for the study of genetic polymorphism is that of the DNA sequence itself and the smallest unit of polymorphism is the single nucleotide polymorphism (SNP). This is said to be present at a particular nucleotide site if the DNA molecules in the population frequently differ in the identity of the nucleotide pair that occupies the site⁷². In *Drosophila*, SNPs have been studied and found to occur frequently and are useful markers for genetic mapping experiments^{73–75}.

Maintenance of molecular genetic variations

Natural selection is an important factor of evolution operating on raw materials generated by mutations and recombination. It is an important component of the modern synthetic theory of evolution. However, gene frequency may change in the evolving population due to random genetic drift which is a non-directional force of evolution and operates in small populations. Kimura⁷⁶ advanced the neutral theory of molecular evolution which states that at the level of nucleic acids and proteins, most evolutionary changes are not governed by natural selection but by random fluctuations of adaptively neutral variants (genetic variants which do not differ in their fitness). This theory assumes that the carriers of different genotypes for adaptively neutral traits do not differ in their adaptedness to the environment and their population frequencies are not affected by natural selection. The frequencies of neutral variants would change from generation to generation due to sampling accidents or random genetic drift. Most DNA and protein differences between species are attributed to random process of chance but not selection. If molecular evolution is explained by selection, the rate of evolution at the molecular level will be slow and the cost of selec-

tion will be high. Under natural selection hypothesis, a large number of mutants arising in a population may be deleterious and this will lead to the loss of many individuals in terms of genetic death and also add to the genetic load of the population. In each generation, an enormous number of genetic deaths will make the rate of evolution slow and the cost of selection high. Because of this presumably high cost of selection, Kimura and other neutralists suggested that most amino acid/nucleotide substitutions are neutral in their effects. Since selection among neutral alleles is lacking, the fixation of such alleles does not produce genetic load and depends upon the mutation rate and random genetic drift. It has been argued by the neutralists that if molecular genetic variations are maintained by natural selection, it would produce considerably greater degree of genetic load which may become intolerable for the species. Under neutral theory, it is presumed that morphological, behavioural and physiological characteristics of organisms evolve by natural selection, but evolution at molecular level occurs mainly through random processes such as genetic drift. Some workers have termed the neutral theory as non-Darwinian theory. But this is misleading because there are other non-Darwinian theories such as Lamarckism, etc. The neutral theory in fact comes within the framework of modern synthetic theory of evolution as it is primarily based on random genetic drift. However, selectionists are of the view that natural selection is the main process directing the evolution of organisms by promoting their adaptation to the environments which they inhabit. There are enough evidences in favour of this hypothesis. Ayala⁵⁶ and others strongly support the natural selection theory to explain the maintenance of molecular genetic variations in natural populations. They have also suggested that the pattern of molecular variations in different cases are inconsistent with the neutral theory of Kimura. It has been found that different populations of the same species are genetically very similar, showing identical frequencies of different alleles. Occasionally, a pair of populations may show somewhat different configuration of allelic frequencies at a locus. Similarly, comparison has been made between different species also. At certain loci, any two species are very similar but may be very different at other loci. The pattern of similarity and differentiation is not compatible with the neutral theory of molecular evolution⁵⁶. Evidence in favour of selection hypothesis is also provided from studies on DNA polymorphism. In general, nucleotide sequence analysis has demonstrated that polymorphism is significantly greater in those DNA sequences that do not determine amino acid sequences compared to DNA sequences that transcribe and translate into amino acids. Natural selection reduces the variability in amino acid coding regions because such sequences have greater effect on the phenotype than do non-coding regions⁷⁷. Active role of selection is also postulated when duplicate genes are compared that are in the process of becoming

functionally different⁷⁸. Thus selective forces influence polymorphism at the molecular level and help maintain the same under some circumstances. The role of random genetic drift and neutral mutations cannot be excluded as important factors for some or even many polymorphisms. Some genetic variants may be neutral at certain times or under certain conditions, but may have selective value when the environment changes⁷⁹.

Balanced polymorphism and heterosis

The superiority of heterozygotes over the corresponding homozygotes is known as heterosis, a term coined by Shull⁸⁰ for hybrid vigour which leads to balanced polymorphism, a term invented by Ford⁸¹ to describe the preservation of genetic polymorphism through selection. When polymorphism is balanced, due to operation of selection both alleles are maintained in the population at definite frequencies which are known as equilibrium frequencies. Under balanced polymorphism, there is no fixation/elimination of alleles. This type of polymorphism is important in evolutionary context as it permits certain degree of polymorphism to be maintained in the population, and the population may be able to adjust rapidly to changes in the environment and thus avoid extinction. Extensive data are available with *Drosophila* in which polymorphism for allelic genes and inversions has been shown to exist with equilibrium frequencies and polymorphism is balanced due to superiority of heterozygotes. The theory of balanced polymorphism has been developed by Haldane, Wright, Fisher, Dobzhansky and others. Examples of *Drosophila* species in which balanced polymorphism has been demonstrated are: *D. pseudoobscura*, *D. persimilis*, *D. robusta*, *D. ananassae*, *D. polymorpha*, etc. When the experiments were conducted in laboratory population cages, the ST and CH chromosome arrangements of the third chromosome of *D. pseudoobscura* remained at equilibrium frequencies of 70% and 30% respectively, and polymorphism was balanced due to adaptive superiority of ST/CH heterozygotes². Similar results were reported by Singh and Ray-Chaudhuri⁴⁵ in *D. ananassae* using ST and AL chromosome arrangements of the second chromosome when tested in laboratory population cages. Clinal pattern of geographic variation shows that some kind of balancing selection maintains the allozyme polymorphism (Adh) in *D. melanogaster*⁶⁶.

Genetic coadaptation

Based on his extensive work on inversion polymorphism in *D. pseudoobscura* and other species, Dobzhansky⁸² suggested the hypothesis of genetic coadaptation and is considered as the main architect of this concept. The gene pool, that is the collection of all genes in a population,

adjusts itself and this internal adjustment has been called genetic coadaptation by Dobzhansky. Although the original use of the word coadaptation in Neo-Darwinian writings was by Dobzhansky, who concluded that in each locality the chromosomes with different gene arrangements are mutually adjusted or coadapted to produce highly fit inversion heterozygotes, the term has been used in a number of different ways⁸³. Mayr⁸⁴ suggested that the total gene complexes of a population are coadapted and this coadaptive nature of gene pool provides the basis for origin of new species. Thus the harmonic coadaptation of genes within a population exists not only for genes within the inverted section, but for all genes of the genome⁸⁵.

Dobzhansky⁸² has shown that in *D. pseudoobscura*, any two gene arrangements of one chromosome coming from the same geographic locality give, as a rule, a heterotic heterozygote. However, this adaptive superiority of heterozygote is lost when chromosomes with different gene arrangements are derived from different populations. Thus the complexes in the chromosomes found in the population of one locality are mutually adjusted or coadapted through long continued natural selection due to which inversion heterozygotes possess higher Darwinian fitness. On the other hand, the genes in the chromosomes with same or with different gene arrangements vary from locality to locality and gene complexes in different localities are not mutually adjusted or coadapted as heterozygotes for such foreign gene complexes are not found in nature. Evidence for genetic coadaptation has also been provided based on the results obtained in other *Drosophila* species such as *D. willistoni*, *D. paulistorum*, *D. pavani* and *D. bipectinata*⁸⁶⁻⁸⁹. In these species, breakdown of heterosis associated with inversion polymorphism was observed in interracial hybridization experiments involving strains of different geographic origins. The coadapted supergenes can be easily disrupted as a result of recombination in interracial hybridization experiments with a consequent loss of heterosis. On the contrary, persistence of heterosis associated with cosmopolitan inversions in *D. ananassae* was observed in interracial experiments⁹⁰⁻⁹². Thus the results obtained in *D. ananassae* are not in agreement with those reported in other species of *Drosophila*. There is lack of evidence for genetic coadaptation in *D. ananassae*. Singh⁹² has suggested that heterosis associated with cosmopolitan inversions in *D. ananassae* appears to be simple luxuriance and coadaptation of chromosomes is not involved. McFarquhar and Robertson⁹³ also found lack of evidence for coadaptation in geographic populations of *D. subobscura*. In this species, neither first filial generation (F_1) heterosis nor second filial generation (F_2) breakdown was found by these investigators. Relevant information regarding genetic coadaptation in different species of *Drosophila* has also been provided from studies on linkage, epistasis and non-random associations between inversions and allozyme loci⁸⁸.

Linkage disequilibrium

While the entire gene pool is integrated by the selection of genes, which gives a good combination in most of the genotypes, chromosome inversion protects coadapted polygenic complexes against dissociation. The genotype interaction can go even a degree further. Two inversions or loci of the same chromosome tend to occur together due to epistatic gene interaction. Mutual adjustment involves the establishment of favourable linkage relation and selection of genes, which interact to maximize fitness^{88,94}. Evidence for coadaptation is thus evidence for the importance of interaction in evolution⁹⁵. Epistatic selection and balanced polymorphism tend to produce supergenes which are major features of evolution. Non-random association between genes/gene arrangements was termed as linkage disequilibrium by Lewontin and Kojima⁹⁶, since the rate of approach to randomness is reduced by linkage. However, Hedrick and co-workers⁸³ prefer to use the term gametic disequilibrium to describe this phenomenon because factors other than linkage may affect the rate of decay and it concerns non-random association within gametes as a phenomenon. The amount of linkage disequilibrium can be measured and is generally a function of the rate of recombination⁹⁷. Presence of linkage disequilibrium is usually attributed to differential selection involving epistatic interaction. Apart from selection, other factors such as tight linkage, genetic drift, migration, gene flow and genetic hitch-hiking may generate linkage disequilibrium. Nonrandom association between inversions was reported for the first time by Levitan⁹⁸ in *D. robusta*. Since then this phenomenon has been studied in a large number of species and interesting findings have been reported by numerous investigators pertaining to linked inversions⁹⁴. It has been shown that selection involving epistatic interaction, suppression of crossing over and genetic drift are the main causative factors for linkage disequilibrium between inversions, although the results vary in different species. Even within the species, the results may vary for different chromosomes⁹⁹.

There are reports showing that linkage disequilibrium may be present between alleles at allozyme loci within inversions and inversions themselves in different species of *Drosophila*¹⁰⁰⁻¹⁰². Linkage disequilibrium is often observed between closely linked SNPs using the data on allele frequencies and haplotypes⁷². In *D. melanogaster*, linkage disequilibrium was detected in natural populations for coding SNPs¹⁰³. Cross and Birley⁶⁷ also detected linkage disequilibrium between A versus C nucleotide polymorphism in the gene for alcohol dehydrogenase in a natural population of *D. melanogaster*. Linkage disequilibrium between linked inversions in *D. ananassae* occurs due to founder effect in isofemale lines¹⁰⁴. The rate of decay of associations among alleles at marker loci within a chromosome of *D. melanogaster* has been studied by Clegg *et al.*¹⁰⁵. It has been found that the rate of decay of disequilibrium is generally accelerated by selection¹⁰⁶.

Genetic hitch-hiking

Due to tight linkage or nucleotide site within loci, there is a statistical association of alleles at a neutral locus with another locus undergoing selection. Then the neutral allele may be carried along because of the selective advantage of the associated allele, which is known as genetic hitch-hiking⁹⁷. The impact of genetic hitch-hiking in evolutionary context and linkage disequilibrium have been considered by numerous researchers. Selection of this type results in the reduction of genetic variations for a region surrounding each selected target. It has been shown in *Drosophila* that the levels of genetic variation are lower in regions of reduced local recombination rate and this could be partly due to hitch-hiking^{107,108}.

Conclusion

Drosophila is characterized by rich species diversity and is often used for various kinds of studies pertaining to genetics, evolution, behaviour, development, molecular biology, ecology, etc. It is interesting to mention that there are more than 500 species of *Drosophila* inhabiting the Hawaiian Islands, which have been extensively used for studies in the field of evolutionary biology and interesting information has been obtained with particular reference to the role of founder principle in speciation¹⁰⁹. Genetic polymorphisms with particular reference to inversion polymorphism, allozyme polymorphism and DNA polymorphism have been extensively studied in a large number of species. The data generated so far in this regard provide ample evidence for the presence of substantial level of genetic polymorphism in *Drosophila* species, although the degree of polymorphism may show interspecies-specific and intraspecies-specific variations. The role of different evolutionary forces has also been demonstrated in the maintenance of these polymorphisms. Further, interesting results have been reported pertaining to the species found in India, e.g. *D. ananassae*, a cosmopolitan and domestic species characterized by numerous unusual genetic features^{8,9}. It is hoped that research in this line will be continued in future and more data will be generated to understand the mechanism of evolution as genetic polymorphisms are useful in the study of genetic relationship among subpopulations of a species. From the evolutionary point of view, genetic polymorphisms may be useful to draw inferences about evolutionary history and the evolutionary processes⁷².

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