REVIEW ARTICLE

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Dobzhansky's concept of genetic coadaptation: *Drosophila ananassae* is an exception to this concept

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Abstract. Dobzhansky was the first to show that the inversion polymorphism in *Drosophila pseudoobscura* is subject to natural selection and is a device to cope with the diversity of environments. His extensive work on *D. pseudoobscura* has revealed interesting phenomena of population genetics. In continuation of his work on this species, he constructed a number of homozygous lines for different gene arrangements in the third chromosome, and while employing these lines in intrapopulation and interpopulation crosses, he quantified the fitness of inversion homokaryotypes and heterokaryotypes. Interestingly, his results showed that heterokaryotypes formed by chromosomes originating from the same geographic area exhibited superiority over the corresponding homokaryotypes. However, superiority of heterokaryotypes was lost in the crosses when chromosomes were derived from different localities. Based on these results, Dobzhansky suggested the concept of genetic coadaptation. According to this concept, 'in each locality, the chromosomes with different gene arrangements are mutually adjusted or coadapted to yield highly fit inversion heterozygotes through long continued natural selection. However, this adaptive superiority of inversion heterozygotes breaks down in interracial hybridization experiments when two gene arrangements are derived from different localities'. This concept has received experimental evidence in its favour on the basis of work done in other species of *Drosophila*, such as *D. willistoni*, *D. paulistorum*, *D. pavani* and *D. bipectinata*. In all these species, interracial hybridization led to the loss of superiority of inversion heterozygotes. Further, it has been suggested that coadapted polygenic complexes contained in the chromosomes are disrupted as a result of recombination in interstrain crosses. This concept was also tested in *D. ananassae*, a cosmopolitan and domestic species commonly found in India, while employing three cosmopolitan inversions exhibiting heterotic buffering. In interstrain crosses involving monomorphic and polymorphic strains due to three cosmopolitan inversions, the persistence of heterosis was observed, which does not support the above-mentioned hypothesis of Dobzhansky. Thus, evidence for coadaptation is lacking in natural populations of *D. ananassae*, which is considered as an exception to the Dobzhansky's concept of genetic coadaptation. Thus, heterotic buffering associated with the three cosmopolitan inversions in *D. ananassae* is not populational heterosis; rather, it appears to be simple luxuriance.

Keywords. genetic coadaptation; *Drosophila* species; inversion polymorphism; Dobzhansky's concept; *Drosophila ananassae*.

Introduction

Drosophila is considered as the best biological model and has been extensively used in a variety of studies in different areas such as genetics, behaviour, evolution, ecology, molecular biology etc. (Singh 2010). Dobzhansky, considered as the main architect of synthetic theory of evolution, provided genetical basis of evolution. Based on his work on inversion polymorphism in *Drosophila pseudoobscura*, he was the first to demonstrate that inversion polymorphism is an adaptive trait (Dobzhansky 1947). Genes do not act independently, rather they tend to organize themselves in functional gene complexes or supergenes

(Darlington and Mather 1949), which confer an adaptive advantage to the recipient genotype. In general, the relative selective values can properly assigned to genetic systems as a whole, and thus evolution depends on the fitting together of a harmonious system of gene effects (Wright 1964). Epistatic selection and balanced polymorphism tend to produce supergenes, and thus constitute a major feature of evolution. On the basis of Dobzhansky extensive work on *D. pseudoobscura*, he suggested the concept of genetic coadaptation and has been called as the main architect of this concept. The pioneering study conducted by Wright and Dobzhansky (1946) on experimental populations of *D. pseudoobscura* maintained in

population cages containing different gene arrangements of the third chromosome revealed that inversion polymorphism is balanced and maintained due to adaptive superiority of inversion heterozygotes over the corresponding homozygotes. Since then, a number of studies conducted on various species have confirmed that inversion polymorphism is maintained by balancing selection in *Drosophila*. Any two gene arrangements originating from the same natural population exhibit heterosis in *D. pseudoobscura* (Dobzhansky 1951). However, the superiority of inversion heterozygotes in interracial hybridization experiments is lost in *D. pseudoobscura* (Dobzhansky 1950, 1957). According to Dobzhansky (1950), the Darwinian fitness of inversion heterozygotes is not always determined by the gene arrangements in the chromosome which it carries, but it must be determined in part by the genes in these chromosomes. These findings in *D. pseudoobscura* have been explained by Dobzhansky (1949, 1950, 1951) by suggesting the genetic coadaptation hypothesis. According to Dobzhansky's concept, the chromosomes with different gene arrangements carry different complexes of genes (polygenes). These polygenic complexes in the chromosomes found in one locality have been mutually adjusted or coadapted through long continued natural selection, so that inversion heterozygotes possess higher adaptive value. These polygenic complexes in chromosomes with the same or different gene arrangements may vary from locality to locality. There is no coadaptation by natural selection between the polygenic complexes in different localities, as inversion heterozygotes for such foreign gene complexes are not found in nature. The superiority of heterozygotes is thus an outcome of a long historic process of adaptation to the environment. Interestingly, the development of heterosis was demonstrated by Dobzhansky and Levene (1951) in inversion heterozygotes in experimental populations for a pair of inversion sequences derived from different populations which initially did not exhibit heterosis (for further reference see Singh 1991).

The genetic coadaptation hypothesis of Dobzhansky, who has been considered as Darwin of the 20th century (Marinkovic 2006; Singh 2012), has been supported by experimental results pertaining to interracial hybridizations involving chromosomally monomorphic and polymorphic strains in various species of *Drosophila*, such as *D. willistoni*, *D. paulistorum*, *D. pavani* and *D. bipectinata* (Dobzhansky and Pavlovasky 1958; Brncic 1961a; Singh and Banerjee 1995).

Dobzhansky and Pavlovasky (1958) studied inversion polymorphism in natural populations of *D. willistoni* and *D. paulistorum*, and established laboratory populations from the flies collected from nature. Interracial hybridization was made and hybrid lines as well as parental lines were maintained for several generations in the laboratory. Both these species are characterized by a high degree of chromosomal polymorphism and the frequency of inversion heterozygotes remains high in natural and laboratory populations. Thus, heterosis is associated with inversions in these species. In the parental populations, the frequency of heterozygotes remained high. However, the superiority of inversion heterozygotes was lost in hybrid populations of mixed geographic origin in both the species, as indicated by very low frequency of inversion heterozygotes in interracial hybridization experiments. Based on these results, Dobzhansky and Pavlovasky (1958) suggested that interracial hybridization leads to break-down of coadapted polygenic complexes in *D. willistoni* and *D. paulistorum*. Thus, heterosis associated with inversions is not a necessary consequence of being heterozygous for chromosomes with a given pair of gene arrangements, but it is determined by the polygenic complexes which these chromosomes contain. These authors further suggested that in a given Mendelian population, the gene contents contained in the chromosome are mutually adjusted or coadapted to yield high-adaptive value in inversion heterozygotes as a result of the action of natural selection. Through the suppression of recombination between chromosomes, inversions play an adaptive role in protecting the integrity of coadapted polygenic complexes carried by these chromosomes (Dobzhansky and Pavlovasky 1958).

The coadaptation hypothesis has also been tested in *D. pavani* by Brncic (1961a), who studied inversion polymorphism in natural and laboratory populations and found that inversion heterozygotes exhibit heterosis as the frequencies of inversion heterozygotes remained above 50% in most of the populations studied. However, the pattern of inversion polymorphism in this species remains rigid, as there were no seasonal and geographic variations in inversion frequencies in natural populations of *D. pavani* (Brncic 1961a, b). Brncic (1961a) also tested genetic coadaptation hypothesis by making interracial hybridization, employing chromosomally polymorphic strains of *D. pavani* derived from distant localities in Chile. Interestingly, he found that the frequencies of heterozygotes for certain inversions in hybrid populations decreased below the level of parental populations. This clearly demonstrated that interracial hybridization leads to the break-down of heterosis in *D. pavani* which extends evidence in favour of Dobzhansky's coadaptation hypothesis. Thus, the higher adaptive fitness of inversion heterozygotes, which carry chromosomes with different gene arrangements is determined by polygenic complexes contained in inverted sections in *D. pavani*. Natural selection acts in such a way to adjust the gene complexes present in each Mendelian population. It has been suggested that coadapted supergenes can be easily disrupted as a result of crossing over in interracial hybridization experiments with a consequent loss of heterosis.

Inversion polymorphism has been studied in laboratory and natural populations of *D. bipectinata* (Bock 1971; Singh and Das 1991; Das and Singh 1992; Banerjee and Singh 1996). A number of paracentric inversions have been detected. However, only three inversions often

persist in laboratory stocks, due to superiority of inversion heterozygotes and inversions in different arms of the same chromosome, showing linkage disequilibrium due to epistatic interaction (Singh and Das 1991; Das and Singh 1992). Since certain inversions persist in the laboratory stocks due to heterotic buffering, it provided an opportunity to test the genetic coadaptation in *D. bipectinata*. While using the three inversions (In(D)2 L, In(C)2R and In(H)3 L), Singh and Banerjee (1995) tested the coadaptation hypothesis by making interracial hybridization in *D. bipectinata*. Four stocks of *D. bipectinata* originating from different geographic localities and chromosomally polymorphic due to the presence of inversions were crossed with each other. Hybrid and parental lines were maintained for 10 generations and were analysed chromosomally. It was found that all the lines remained polymorphic, but there was a decrease in the frequency of inversion heterozygotes in certain hybrid lines of mixed geographical origins. Although there was variation in the frequency of inversion heterozygotes in interracial crosses, the decline in the frequency of inversion heterozygotes clearly showed that there was a break-down of polygenic complexes, due to recombination in interracial crosses extending evidence for genetic coadaptation in geographic populations of *D. bipectinata*.

Thus, a decrease in the frequency of inversion heterozygotes in interracial hybridization experiments in the above-mentioned species clearly suggests that gene arrangements in different populations are mutually adjusted or coadapted due to action of natural selection. According to Mather (1943) and Lerner (1958), polygenes exhibit two types of balance: internal balance and relational balance. The concept of coadaptation is similar to relational balance between the polygenic complexes suggested by Mather (1943). The relational balance is responsible for high-adaptive feature of inversion heterozygotes and for the establishment of balanced polymorphism (Dobzhansky 1955). The chromosome inversions provide a mechanism for maintaining the integrity of coadapted polygenic complexes in natural populations by suppressing recombination. In interracial hybridization experiments, mutually adjusted polygenic complexes are broken down, due to recombination with a consequent loss of superiority of inversion heterozygotes. Thus, it is evident from the studies of *D. pseudoobscura*, *D. paulistorum*, *D. willistoni*, *D. pavani* and *D. bipectinata* that heterosis associated with chromosome inversions is due to previous selectional coadaptation (Singh 1991). However, based on inversion polymorphism and interracial hybridization, lack of coadaptation was suggested in *D. ananassae* by Singh (1972, 1974, 1981, 1985) and *D. nasuta* by Kumar and Gupta (1991). Based on body size, development time and survival in *D. subobscura*, McFarquhar and Robertson (1963) tested the genetic coadaptation hypothesis and found no evidence for it, as there was no break-down of heterosis in F_2. They suggested that *D. subobscura* may be a wide-open species, as there is no coadaptation of gene pool in local populations. On the other hand, extensive genetic differentiation between O chromosome gene arrangements suggests that selection can maintain coadapted gene complexes in *D. subobscura* (Santos 2009).

According to Hoffmann *et al.* (2004), recent molecular genetic studies suggest that inversion polymorphisms in *Drosophila* have been dynamic systems and the patterns of linkage disequilibrium and variation have been consistent with coadapted gene complexes. Further, they have emphasized that inversions are associated with disequilibrium among loci suggesting that they have potential to lock-up coadapted alleles. There are suggestions against the coadaptation hypothesis of Dobzhansky. Neither drift nor coadaptation between alleles (epistasis) is needed so the local adaptation mechanism may apply to a broader range of genetic and demographic situations than the coadaptation hypothesis, and by suppressing recombination between the loci a new inversion can spread (Kirkpatrick and Barton 2006). Population models suggest that chromosomal inversions may spread, suppressing recombination between alleles that independently increase fitness, without epistasis or coadaptation (Hoffmann and Rieseberg 2008). Thus, it has been emphasized that reduced recombination is a process which promotes the spread of inversions in population. However, population genomic studies on inversion polymorphism of *D. melanogaster* suggest that powerful selective pressure governs the distribution of polymorphic inversions, and inversions interact with polymorphism not only in break-point regions but also across chromosomes (Corbett-Detig and Hartl 2012).

Linkage disequilibrium and genetic coadaptation

Since inversions suppress crossing-over they protect coadapted polygenic complexes against dissociation, and the genotypic interactions become important in evolutionary perspective. Due to epistatic interactions, two independent inversions of the same chromosome tend to occur together. The mutual adjustment involves the establishment of favourable linkage relation and the selection of genes which interact to maximize fitness. Evidence for coadaptation is thus evidence for the importance of interaction in evolution (Barker 1979). Epistatic selection and balanced polymorphism tend to produce supergenes which are major features of evolution. Loss of heterosis in interracial hybridization experiments clearly lends support to the genetic coadaptation hypothesis in *Drosophila*. Further, linkage disequilibrium (nonrandom associations) between inversions and also between allozyme loci and inversions themselves which has been extensively studied in various species of *Drosophila* (Singh 2008) are also relevant to determine the extent of coadaptation as it involves gene interaction at the fitness level (Singh 1991).

Since the rate of approach to random association is reduced by linkage, nonrandom associations between genes were termed as 'linkage disequilibrium' by Lewontin and Kojima (1960). However, Hedrick *et al.* (1978) suggested that this term is misleading and should not be used, as factors other than linkage may affect the rate of decay. Even the unlinked loci on different chromosomes may show linkage disequilibrium. Hedrick *et al.* (1978) preferred the term 'gametic disequilibrium' to describe this phenomenon. Although both the terms, linkage disequilibrium and gametic disequilibrium, have been frequently used in the literature, this author has preferred linkage disequilibrium in this review because only these are cited which deal with linked loci. When linkage disequilibrium is present, there has been a tendency to attribute it to differential selection involving multilocus interaction. If significant linkage disequilibrium is present and is consistent between populations, it can be attributed to selection (Lewontin 1974). Besides selection, there are other factors such as tight linkage, random genetic drift, migration, gene flow and hitch-hiking which can generate linkage disequilibrium in the absence of selection.

Singh (2008) has reviewed the nonrandom associations (linkage disequilibrium) between linked inversions in various species of *Drosophila*. This phenomenon was reported for the first time in *D. robusta* by Levitan (1954). Since then, it has been found in a large number of species, such as *D. pavani*, *D. guaramunu*, *D. subobscura*, *D. bipectinata*, *D. rubida*, *D. silvestris* etc. (see Singh 2008). Levitan (1958) suggested that linkage disequilibrium (nonrandom associations) between linked inversions is caused by two main factors, either alone or in combination: (i) suppression of crossing-over between linked inversions and (ii) natural selection acting against certain recombinant arrangements. It has been demonstrated by Levitan (1958, 2001) that linked inversions in *D. robusta* are associated nonrandomly due to natural selection favouring linkages between interacting genes, which are not part of the allelic blocks. Although, natural selection involving epistatic interaction has been considered as an important factor maintaining linkage disequilibria, genetic drift can also cause linkage disequilibria (Hill and Robertson 1968; Ohta and Kimura 1969; Loukas *et al.* 1979; Singh and Singh 1990).

The phenomenon of linkage disequilibrium between alleles at allozyme loci within inversions and the inversions themselves has been studied in several species of *Drosophila* which extends evidence for chromosomal coadaptation. Prakash and others (Prakash and Lewontin 1968, 1971; Prakash and Merritt 1972; Prakash 1974) have shown that chromosomal inversions in *D. pseudoobscura* and *D. persimilis* differ in multilocus genotypes for allozyme loci, which has been taken as direct evidence for genetic coadaptation. Similarly, such associations of specific alleles with specific inversions have been reported in *D. robusta* (Prakash and Levitan 1973, 1974) and *D. pavani* (Nair and Brncic 1971). While examining whether genetic differentiation is due to coadaptation, Prakash and Lewontin (1968) found strong associations between allozyme loci and gene arrangements in *D. pseudoobscura* and *D. persimilis* and suggested that two loci (*Pt 10* and *amylase*) show coadaptation to a high degree. Thus, gene contents of inversion are coadapted by selection (Prakash and Lewontin 1968). Since the first report by Prakash and Lewontin (1968), this relationship between allozyme loci and inversions themselves has been demonstrated in a number of studies using various species of *Drosophila* (for references, see Singh 1991). There are suggestions (Nei and Li 1975) that such associations do not provide direct evidence for genetic coadaptation. An alternative explanation has been suggested by Ishii and Charlesworth (1977) that the associations observed are due to an absence of recombination in heterokaryotypes, so that an inversion remains associated with the allele contained in the gametes in which it originally occurred. Because of low recombination, a neutralist explanation has also been suggested. Fontdevila *et al.* (1983) and Zapata *et al.* (1986) provided evidence for genetic coadaptation in *D. subobscura* on the basis of allozyme loci and O chromosome arrangements. A number of cases of linkage disequilibrium between allozyme loci and chromosome arrangements in natural populations of *D. subobscura* have been reported (Lakovaara 1981; Cabrera *et al.* 1983). A very good example is given in *D. subobscura*, which shows the role of selective forces for the maintenance of linkage disequilibrium involving alleles at the *Hbdh* and *6Pgdh* loci with A_2 and A_{2+6} chromosome arrangements of sex chromosome (Cabrera *et al.* 1983).

There are a few recent studies on genetic coadaptation in *Drosophila*. Zivanovic *et al.* (2000) studied inversion polymorphism and genetic load of O chromosome in three natural populations of *D. subobscura* from southeastern Europe. In all the three populations, inversion polymorphism was extensive and the genetic load was also high. The lethal allelism test showed lethality is nonrandomly associated with O_{st} gene arrangement. The amount of genetic load is heavy in gene arrangements with high frequency, in comparison with the ones with a low frequency, and this has been taken as evidence for coadaptation (Zivanovic *et al.* 2000). The data pertaining to molecular markers of the third chromosome of *D. pseudoobscura* and nucleotide diversity support the model of genetic coadaptation where genes along particular gene arrangements are maintained by epistatic selection (Schaeffer *et al.* 2003). The patterns of diversity and linkage disequilibrium within the inversion in *D. melanogaster* are indicative of coadaptation (Kennington *et al.* 2006). It has been demonstrated that chromosomal rearrangements in *D. pseudoobscura* have captured sets of genes that differ in their expression levels, which suggests that gene expression is a potential target for selection of gene arrangements (Fuller *et al.* 2016). It is interesting to note that the coadapted genome for parthenogenesis has been suggested in *D. mercatorum* (Chang and Chang 2014).

Absence of genetic coadaptation in *D. ananassae*

D. ananassae is a cosmopolitan and domestic species which occupies a unique status among *Drosophila* species. Due to certain peculiarities in its cytogenetic and genetic behaviour, such as spontaneous male recombination, varied chromosomal polymorphism, high mutability, Y-4 linkage of nucleolus organizer, segregation distortion, parthenogenesis, absence of genetic coadaptation, extrachromosomal inheritance and *Om* hypermutability system (Singh 1996, 2000, 2010; Singh and Singh 2008; Singh and Yadav 2015). It belongs to the *ananassae* species complex of the *ananassae* subgroup of the *melanogaster* species group (Bock and Wheeler 1972). Further, its common occurrence in India coupled with its genetic peculiarities attracted the attention of Indian researchers (Singh 2015; Singh and Yadav 2015). *D. ananassae* has been considered as a good model species for genetic, behavioural and evolutionary studies (Singh 2010). Population dynamics of three cosmopolitan inversions has been extensively studied in Indian populations of *D. ananassae*, and it is evident from the results that there is a considerable degree of genetic divergence at the level of inversion polymorphism. In general, the populations from south India including Andaman and Nicobar Islands show more differentiation than those from the north (Singh 1998, 2015; Singh and Singh 2007). The three cosmopolitan inversions which are coextensive with the species often exhibit heterosis (Singh 1996, 1998). Singh and his students have studied certain aspects of behaviour genetics in *D. ananassae*, and their results clearly showed evidence for sexual isolation, significant variations in mating propensity of geographic strains and inversion karyotypes, diminishing effects of mutations on mating propensity, positive response of selection to high-mating and low-mating propensity and female remating, providing evidence for genetic control of sexual behaviour in *D. ananassae*. There is evidence for rare male mating advantage and polygenic control of larval pupation behaviour in *D. ananassae* (Singh and Chatterjee 1985, 1986, 1987, 1988, 1989; Singh and Pandey 1993; Singh and Singh 2001). Inversion frequencies may change due to random genetic drift in laboratory populations (Singh 1987, 1988). Ecological adaptation has also been studied in *D. ananassae* (Sisodia and Singh 2010, 2012; Sisodia *et al.* 2015) and the main findings are: (i) there are significant variations in resistance to different kinds of stress such as heat and cold shocks, starvation and desiccation in populations of *D. ananassae*, (ii) flies from lower latitudes had higher starvation resistance, heat resistance and lipid content but the pattern was reversed for desiccation resistance, (iii) there is a high degree of variation in stress resistance at the population level in *D. ananassae*, (iv) *D. ananassae* adapts different stress tolerance and life history strategies according to the quality of available diets (protein/carbohydrate) which are correlated with phenotypic adjustment at the anatomical and physiological levels, and (v) a novel factor was identified which showed that depositions of uric acid crystals in Malpighian tubules of flies have a regulatory role in tolerance to desiccation. Thus, *D. ananassae* has a number of unique features.

The author has been using *D. ananassae* as a model species for his research in the areas of population genetics, behaviour genetics and evolution (for references, see Singh 2010; Singh and Yadav 2015). He tested the genetic coadaptation hypothesis of Dobzhansky in *D. ananassae* employing three cosmopolitan inversions, which are coextensive with the species and exhibit heterosis (Singh 1972, 1974, 1981, 1985). Singh (1972) conducted interracial hybridization experiments in *D. ananassae*. While testing the genetic coadaptation hypothesis of Dobzhansky, he carried out different types of experiments by using the three cosmopolitan inversions, which are coextensive with the species. He has used the geographic strains originating from distant localities in India. Even the strains from other countries were also used. While testing this phenomenon in *D. ananassae*, Singh took care to employ monomorphic as well as polymorphic stocks of *D. ananassae*. In one study (Singh 1972), polymorphic strains were used. Parental stocks as well as hybrid lines were maintained in the lab for several generations. Cytological analysis of parental and hybrid lines was done and interesting results were obtained. All the original stocks and interstrain crosses remained polymorphic, and heterokaryotypes were superior to the corresponding homozygotes. Thus, hybridization did not lead to the loss of heterosis in *D. ananassae*, even when the stocks were taken from geographically distant localities. Singh (1972) interpreted these results by suggesting that *D. ananassae* results contradict the results of other species, and there is no coadaptation in geographic populations of *D. ananassae*. The question may be asked why the results are different from other species. The general biology of *D. ananassae* makes it a special case, as it was concluded. In *D. ananassae*, it is of special significance since Indian populations are genetically differentiated at the level of inversion polymorphism (Singh 1989, 1996, 1998; Singh and Singh 2007, 2008). According to Dobzhansky (1955), 'the relational balance established between the genes in a pair of homologous chromosomes is responsible for the adaptive superiority of inversion heterozygotes'. But the data presented in this work failed to confirm the existence of relational balance between the genes with respect to these chromosomal rearrangements, since there was no break-down of heterosis in the interracial hybridization experiments. Thus, the presence of genetic coadaptation has not been realized in such widely separated populations of *D. ananassae* (Singh 1972).

In the second type of experiments, Singh (1974) prepared homozygous lines for the standard gene arrangement in the third chromosome and for DE (3 L) and ET (3R) inversions in the third chromosome of *D. ananassae*. The stocks homozygous for delta and eta inversions were Kerala and Kamorta (Nicobar Islands). The stocks

homozygous for standard gene arrangement were Jamsoti, Lowari, Tejpur, Nagpur and Tripura. These widely separated stocks were crossed and in F_1 the females were testcrossed with parental males. In F_2, a large number of larvae were analysed chromosomally to know their karyotypic constitution. In all the crosses, there was abundance of heterozygotes than of homozygotes. Heterozygotes were statistically more frequent than homozygotes in F_2. Theoretically there should be a 1:1 ratio between heterozygotes and homozygotes, but there was significant deviation from 1:1 ratio in favour of inversion heterozygotes, which clearly demonstrated that heterozygotes formed by chromosomes of distant localities exhibit heterosis and provide evidence for the lack of coadaptation in *D. ananassae.*

In the third type of experiment, Singh (1981) conducted interracial hybridization experiments in *D. ananassae* by employing strains homozygous for the ST or AL gene arrangement in the second chromosome originating from geographically distant localities in India such as Gorakhpur, Tejpur, Jamsoti, Lowari, Nasgpur, Mughalsarai and Port Blair (Andaman Islands). In all the crosses, all the three karyotypes were observed but polymorphism persisted for many generations and heterozygotes were superior over the corresponding homozygotes. These results are also not in agreement with what has been found in other species of *Drosophila* by Dobzhansky and others.

In the fourth type of experiments, Singh (1985) conducted the experiments to estimate the relative viabilities of homozygotes and heterozygotes in F_2 generation of crosses involving homozygous strains of *D. ananassae*. The strains used were homozygous for ST or inverted gene orders in the second and third chromosomes. The strains employed in the experiments were from distant localities in India; Kuala Lumpur and Kota Kinabaru, Malaysia and Chiang Mai, Thailand. Heterosis was found in many interpopulation crosses, but it was absent in two intrapopulation crosses. These results clearly demonstrated that heterozygotes formed by chromosomes of different regions exhibit heterosis. Thus, heterozygosis for many genes and gene complexes does produce high fitness without previous selectional coadaptation (Singh 1985). In *D. melanogaster*, Carson (1961) have clearly shown that natural selection favours balanced polymorphism due to autosomal heterosis. The persistence of increased fitness of F_1 flies for a number of generations suggested that heterosis was of simple luxuriant sort and coadaptation of chromosomes was not involved. Thus luxuriance can function in the adjustment of organisms to their environments (Carson 1961). This conclusion of Carson (1961) is also supported by the experimental results of this author in *D. ananassae* (Singh 1985). Further, evidence for the absence of coadaptation in *D. ananassae* has also been provided by Yadav and Singh (2003) and Singh and Singh (2010). Five geographic populations of *D. ananassae* were sampled and laboratory populations were established. All these populations were crossed with each other and body size was measured in

F_1 and F_2. There was an increase in body size in F_1 and F_2 compared with parents. There was no break-down of heterosis in F_2 which suggested absence of coadaptation in *D. ananassae* (Yadav and Singh 2003). Intrachromosomal and interchromosomal associations occur randomly in natural and laboratory populations of *D. ananassae*, which strengthens the previous suggestion that there is a lack of genetic coadaptation in *D. ananassae* (Singh and Singh 2010).

In conclusion, *D. ananassae* is genetically a unique species and is of common occurrence in India (Singh 2000, 2010, 2015). Indian populations of this species are genetically differentiated at the level of chromosomal polymorphism (Singh 1996, 1998; Singh and Singh 2008). Chromosome inversions often persist in laboratory stocks, due to adaptive superiority of inversion heterozygotes. Since Dobzhansky (1949, 1950, 1957) suggested the concept of genetic coadaptation based on inversion polymorphism in *D. pseudoobscura*, it was tested in certain other species using inversion polymorphism such as *D. paulistorum*, *D. willistoni*, *D. pavani* and *D. bipectinata* and the results supported his concept. The same phenomenon was tested in *D. ananassae* by using three cosmopolitan inversions by this author (Singh 1972, 1974, 1981, 1985), but the results are not in agreement with what has been suggested by Dobzhansky. Thus, there is absence of genetic coadaptation in geographic populations of *D. ananassae*. Singh (1985) suggested that heterosis associated with the cosmopolitan inversions in *D. ananassae* appears to be simple luxuriance, and coadaptation of chromosomes is not involved. Results pertaining to the investigations on body size in geographic strains, F_1 and F_2 in *D. ananassae* also do not support the coadaptation hypothesis (Yadav and Singh 2003).

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