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POPULATION GENETICS OF *Drosophila ananassae*: CHROMOSOMAL ASSOCIATION STUDIES IN INDIAN POPULATIONS

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Forty-five natural populations of *Drosophila ananassae* and laboratory stocks made from these flies were analysed for chromosome inversions. Quantitative data on the frequencies of these inversions were utilized to test intra- and interchromosomal interactions in *D.ananassae*. In most of the natural as well as laboratory populations no significant deviation from randomness of intra- and interchromosomal associations (2L-3L, 2L-3R, 3L-3R) was found hence, providing evidence for random associations. However, in some instances, significant deviation from randomness was found in both natural and laboratory populations, which could be due to excess of certain combinations, deficiency of others and

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complete absence of some combinations. Possible role of genetic drift could be implicated due to tight-linkage between linked gene arrangements. This strengthens the previous suggestion that there is lack of genetic coadaptation in *D. ananassae*

Key words: Drosophila ananassae, inversions, intra- and interchromosomal associations, epistatic selection, random genetic drift

INTRODUCTION

Chromosomal polymorphism mainly due to paracentric inversions is very common in the genus *Drosophila* and constitutes an adaptive character (DA CUNHA, 1960, DOBZHANSKY, 1970, SPERLICH and PFRIEM, 1986). It is often maintained due to higher Darwinian fitness of inversion heterozygote, which is the main factor for the maintenance of balanced chromosomal polymorphism.

Chromosomal associations are basically intra-and interchromosomal types, which may be non-randomly (linkage disequilibrium) or randomly associated, and has been reported in many species of *Drosophila*, which are characterized by considerable degree of inversion polymorphism. However, the factors, which cause non-random associations between inversions, vary and show different scenario in different species regarding their maintenance (see review by SINGH, 2008). Linkage disequilibrium studies can shed considerable light on the basic problems of population genetics. The occurrence of linkage disequilibrium can be explained by epistatic selection, random drift and gene flow between populations differing in gene arrangement frequencies at more than one locus. When the last two explanations and historical and mechanical reasons in the case of association between alleles and inversions are excluded, selection is the only remaining possibility. This is the main reason for the interest in such studies after the pioneering work of PRAKASH and LEWONTIN (1968, 1971).

Inversion polymorphism found in different species of *Drosophila* offers a good material for testing epistatic interactions. The phenomenons of epistatic interactions between linked inversions are well documented (BRNCIC, 1961, BANERJEE and SINGH, 1996, see review by SINGH, 2008). On the basis of non-random association of linked inversions in *D. robusta*, LEVITAN (1958b) has shown that linkage disequilibrium between 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 proved by LEVITAN (1958a,b, 1961, 1973, 1978) and PRAKASH (1967) that linked inversions in *D. robusta* are associated non-randomly due to selection favoring linkages between interacting genes that are not part of allelic blocks. Recently, meiotic drive causing linkage disequilibrium has also been suggested (DYER *et al*. 2007).

The phenomenon of interchromosomal interactions, however, has been given less attention. PRAKASH (1967) was first to present evidence for interchromosomal interactions in *D. robusta*. SPERLICH and FEUERBACH-MRAVLAG

(1974) also reported data on interchromosomal associations in *D. subobscura*, as various unlinked inversions were associated randomly. Similar studies have also been conducted in *D. melanogaster* (DAS and SINGH, 1990, SINGH and DAS, 1991b) and *D. bipectinata* (BANERJEE and SINGH, 1995).

Drosophila ananassae is a cosmopolitan and domestic species. It harbors a large number of inversions in its natural populations (SINGH, 1998, SINGH and SINGH, 2007a). Out of these, only three, namely, alpha (AL) in 2L, delta (DE) in 3L and eta (ET) in 3R are cosmopolitan in distribution (SINGH, 1998). Two linked inversions namely delta (3L) and eta (3R) of the third chromosome show non-random association in laboratory stocks (SINGH, 1983, 1984, SINGH and SINGH, 1988, 1990, 1991, SINGH and SINGH, 2004). However, the same two inversions are associated randomly in natural populations (SINGH, 1984). Similarly, for unlinked inversions no evidence for interchromosomal interaction has been found in *D. ananassae* in both natural populations and laboratory stocks (SINGH, 1982, 1983, SINGH and SINGH, 1989, SINGH and SINGH, 2004).

Present communication reports extensive data on intrachromosomal (3L-3R) and interchromosomal (2L-3L & 2L-3R) associations in natural populations collected from across the different eco-geographic regions of the country as well as laboratory populations established from naturally impregnated females of *D. ananassae*.

MATERIALS AND METHODS

D.ananassae flies were collected from forty-five eco-geographic localities in India (SINGH and SINGH, 2007b). Naturally impregnated females from each collection were kept individually in a fresh food vial and F_1 larvae were squashed by lactoaceto-orcein method to detect chromosome inversions. The quantitative data is based on the identification of the karyotypes of only one F_1 larva from each wild female. Data on frequencies of three cosmopolitan inversions have been reported elsewhere (SINGH and SINGH, 2007b).

For each natural population laboratory stock was established from females collected from nature and was maintained on simple culture medium under normal laboratory conditions by transferring about fifty flies (males and females in equal number) to fresh food bottles in each generation. After several generations (minimum ten), chromosomal analyses of these populations were made to obtain quantitative data on frequencies of three cosmopolitan inversions, which have been described elsewhere (SINGH and SINGH, 2008). Quantitative data on the frequencies of different karyotype combinations have been analyzed to obtain the numbers of various intra- and interchromosomal associations in natural populations and laboratory stocks of *D. ananassae*.

RESULTS

Due to the occurrence of AL inversion in 2L, DE inversion in 3L and ET inversion in 3R, nine combinations between 2L-3L, 2L-3R and 3L-3R karyotypes

could be ascertained. Under the assumption of random combination of karyotypes, their expected numbers have been calculated from the marginal totals of R X C contingency table. The significant deviation from expectation would indicate non-random association between inversions.

Although, the frequencies of different 2L and 3L associations vary in different natural populations, the deviation from randomness is insignificant in most of the populations (data not shown) except, AD ($p < 0.01$), PU ($p < 0.05$), VD ($p < 0.05$), BL ($p < 0.01$) and ER ($p < 0.05$) (Table 1, only data showing significant deviation from randomness has been given here and in subsequent tables). In all the populations there is an excess of certain combinations and deficiency of other combinations. Also, there is complete absence of some combinations as in (AD). For 2L and 3R karyotypic combinations in natural populations, only four populations namely, GU ($p < 0.05$), SH ($p < 0.001$), GY ($p < 0.01$) and BL ($p < 0.05$) show significant deviation from expectation (see Table 2), reason being the same. In SH and GY, there is absence of certain combinations. Similarly, for 3L and 3R chromosomal associations only two populations DH ($p<0.05$) and BL ($p<0.05$) show non-random association (Table 3). In both cases coupling linkages are present in overwhelming number. This could be due to tight linkage between linked gene arrangements. Only, BL population out of total forty-five populations show significant deviations from randomness in all the three types of chromosomal associations.

Table 1. Observed and expected numbers of different combinations between 2L and 3L karyotypes in natural populations of D. ananassae

Populations		Karyotype combinations									
	2L	ST/ST	ST/ST	ST/ST	ST/AL	ST/AL	ST/AL	AL/AL	AL/AL	AL/AL	
	3L	ST/ST	ST/DE	DE/DE	ST/ST	ST/DE	DE/DE	ST/ST	ST/DE	DE/DE	χ^2
AD	Obs.	0	0	0	1	1	2	15	2	0	10.58**
	Exp.				3.04	0.57	0.38	12.95	2.42	1.61	d = 2
PU	Obs.	0	0	1	0	2	1	10	1	1	12.58*
	Exp.	0.62	0.18	0.18	1.80	0.56	0.56	7.50	2.25	2.25	d = 4
VD	Obs.	5	0	1	2	3	0	3	5	7	10.90*
	Exp.	2.30	1.84	1.84	1.92	1.53	1.53	5.76	4.61	4.61	d = 4
BL	Obs.	0	1	3	6	9	0	2	13	2	18.28**
	Exp.	0.88	2.50	0.55	3.33	9.58	2.08	3.77	10.86	2.36	d = 4
ER	Obs.	0	0	3	8	6	3	6	11	21	12.12*
	Exp.	0.72	0.87	1.39	4.10	4.90	7.91	9.10	11.10	17.60	d = 4

* $p < 0.05$; ** $p < 0.01$

Table 2. Observed and expected numbers of different combinations between 2L and 3R karyotypes in natural populations of D.ananassae

Populations		Karyotype combinations									
	2L	ST/ST	ST/ST	ST/ST	ST/AL	ST/AL	ST/AL	AL/AL	AL/AL	AL/AL	
	3R	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	χ^2
GU	Obs.	0	0	1	4	5	4	37	42	8	11.54*
	Exp.	0.40	0.46	0.12	5.27	6.04	1.67	35.31	40.48	11.19	d = 4
SH	Obs.	0	0	0	0	0	2	22	15	2	19.44***
	Exp.				1.07	0.73	0.19	20.92	14.26	3.80	d = 2
GY	Obs.	0	0	0	0	6	0	45	25	3	10.05**
	Exp.				3.41	2.35	0.22	41.58	28.64	2.71	d = 2
BL	Obs.	2	0	2	8	6	1	11	6	0	12.65*
	Exp.	2.33	1.33	0.33	8.75	5.0	1.25	9.91	5.66	1.41	d = 4

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 3. Observed and expected numbers of different combinations between 3L and 3R karyotypes in natural populations of D.ananassae

Populations		Karyotype combinations									
	3L	ST/ST	ST/ST	ST/ST	ST/DE	ST/DE	ST/DE	DE/DE	DE/DE	DE/DE	
	3R	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	χ^2
DH	Obs.	23	2	0	17	0	0	3	0	1	12.40*
	Exp.	23.36	1.08		15.89	0.73	0.36	3.73	0.17	0.11	d =4
BL	Obs.	4	4	0	14	8	1	3	0	2	10.27*
	Exp.	4.66	2.66	0.66	13.41	7.66	1.91	2.91	1.66	0.41	d = 4

* $p < 0.05$

In case of laboratory populations with respect to 2L-3L karyotype combinations only four populations namely, HD ($p < 0.01$), AB ($p < 0.001$), BP ($p < 0.05$) and BL ($p < 0.01$) show significant deviation from expectation (see Table 4), while in rest of the populations deviation from expectation is not significant. Similarly, for 2L-3R, combinations only five populations namely, AB ($p < 0.001$), JR ($p < 0.05$), SI ($p < 0.05$), ER ($p < 0.01$) and KR ($p < 0.01$), show significant deviation from expectation, reason being the same. In (JR) there is absence of some combinations. For 3L-3R combinations, eleven populations are showing significant deviations from expectations. These populations are JU ($p < 0.001$), PN ($p < 0.001$), IM ($p < 0.001$), HW ($p < 0.01$), SD ($p < 0.001$), DW ($p < 0.001$), VP ($p < 0.01$), VD ($p < 0.01$), PJ ($p < 0.001$), ML ($p < 0.05$), ER ($p < 0.001$). Excess of certain combinations and low number of other combinations (less than 5) could have a role. In (SD) there is absence of certain combinations. In most of the cases, the reason

being excess of coupling homozygotes, except IM and JU where repulsion combinations are more.

Table 4. Observed and expected numbers of different associations between 2L and 3L karyotypes in laboratory populations of D.ananassae

Populations		Karyotype combinations									
	2L	ST/ST	ST/ST	ST/ST	ST/AL	ST/AL	ST/AL	AL/AL	AL/AL	AL/AL	
	3L	ST/ST	ST/DE	DE/DE	ST/ST	ST/DE	DE/DE	ST/ST	ST/DE	DE/DE	χ^2
HD	Obs.	16	6	1	12	24	2	29	9	1	16.57**
	Exp.	13.11	8.97	0.92	21.66	14.82	1.52	22.23	15.21	1.56	d = 4
AB	Obs.	17	14	0	9	2	0	56	2	0 2	3.79***
	Exp.	25.42	5.58		9.02	1.98		47.56	10.44		d = 2
BP	Obs.	12	6	0	45	4	0	23	9	1	9.89*
	Exp.	14.40	3.42	0.18	39.20	9.31	0.49	26.40	6.27	0.33	d = 4
BL	Obs.	9	20	16	18	17	4	4	11	1	14.88**
	Exp.	18.45	21.60	9.45	15.99	18.12	8.19	6.56	7.68	3.36	d = 4

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 5. Observed and expected numbers of different associations between 2L and 3R karyotypes in laboratory populations of D.ananassae

Populations		Karyotype combinations									
	2L	ST/ST	ST/ST	ST/ST	ST/AL	ST/AL	ST/AL	AL/AL	AL/AL	AL/AL	
	3R	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	χ^2
AB	Obs.	25	6	0	6	5	0	20	28	10	20.15***
	Exp.	15.81	12.09	3.10	5.61	4.29	1.10	29.58	22.62	5.80	d = 4
JR	Obs.	3	0	0	6	3	0	82	6	0	7.31*
	Exp.	2.73	0.27		8.19	0.81		80.08	7.92		d = 2
SI	Obs.	25	1	0	34	5	0	24	8	3	10.98*
	Exp.	21.58	3.64	0.78	32.37	5.46	1.17	29.05	4.90	1.05	d = 4
ER	Obs.	0	1	2	21	17	6	34	18	1	18.14**
	Exp.	1.65	1.08	0.27	24.20	15.84	3.96	29.15	19.08	4.77	d = 4
KR	Obs.	4	11	4	17	20	14	19	11	0	15.82**
	Exp.	7.60	7.98	3.42	20.04	21.42	9.18	12.0	12.60	5.40	d = 4

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 6. Observed and expected numbers of different associations between 3L and 3R karyotypes in laboratory populations of D.ananassae

Populations		Karyotype combinations									
	3L	ST/ST	ST/ST	ST/ST	ST/DE	ST/DE	ST/DE	DE/DE	DE/DE	DE/DE	
	3R	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	ST/ST	ST/ET	ET/ET	χ^2
JU	Obs.	17	20	9	15	31	0	8	0	0	25.51***
	Exp.	18.40	23.46	4.14	18.40	23.46	4.14	3.20	4.08	0.72	d = 4
PN	Obs.	37	29	10	4	12	1	0	1	6	31.42***
	Exp.	31.16	31.92	12.92	6.97	7.14	2.89	2.87	2.94	1.19	d = 4
IM	Obs.	8	9	2	27	33	0	20	0	1	24.81***
	Exp.	10.45	7.98	0.57	33.0	25.20	1.80	11.55	8.82	0.63	d = 4
HW	Obs.	26	18	4	13	20	0	17	2	0	13.97**
	Exp.	26.88	19.20	1.92	18.48	13.20	1.32	10.84	7.60	0.76	d = 4
SD	Obs.	39	14	0	38	0	0	9	0	0	14.43***
	Exp.	45.58	7.42		32.68	5.32		7.74	1.26		d = 2
DW	Obs.	17	0	1	32	23	0	16	4	7	29.12***
	Exp.	11.70	4.86	1.44	35.75	14.85	4.40	17.55	7.29	2.16	d = 4
VP	Obs.	36	33	15	0	11	4	0	0	1	14.38**
	Exp.	30.24	36.96	16.80	5.40	6.60	3.0	0.36	0.44	0.20	d = 4
VD	Obs.	18	26	8	2	32	12	1	0	1	16.41**
	Exp.	10.92	30.16	10.92	9.66	26.68	9.66	0.42	1.16	0.42	d = 4
PJ	Obs.	19	3	1	27	32	1	6	6	5	26.29***
	Exp.	11.96	9.43	1.61	31.20	24.60	4.20	8.84	6.97	1.19	d = 4
ML	Obs.	37	33	18	2	9	0	1	0	0	9.75*
	Exp.	35.20	36.96	15.84	4.40	4.62	1.98	0.40	0.42	0.18	d = 4
ER	Obs.	51	17	3	3	18	4	1	1	2	35.31***
	Exp.	39.05	25.56	6.39	13.75	9.0	2.25	2.20	1.44	0.36	d = 4

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Most importantly, none of the laboratory populations show the evidence of chromosomal interactions for all the three karyotype combinations (2L-3L, 2L-3R and 3L-3R). Thus, the results from these populations show that both linked and

unlinked inversions are associated randomly in most of the natural as well as laboratory populations of *D. ananassae*.

DISCUSSION

Present data on intra- and interchromosomal associations in *D. ananassae* clearly demonstrate that both linked and unlinked inversions occur in random association in most of the natural as well as laboratory populations of *D. ananassae*. Among natural populations with respect to interchromosomal associations, only in some populations out of total forty-five populations, deviation from randomness is statistically significant, but it does not indicate the presence of chromosomal interactions, as certain combinations were either absent or occur in very low frequency (less than 5). This shows that none of the combinations between the second and third chromosome karyotypes is favored by natural selection owing to its epistatic interaction (SINGH, 1982). Similar is the case in laboratory populations with respect to interchromosomal associations, which is well supported by earlier studies in *D. ananassae* (SINGH, 1982, 1983, SINGH and SINGH, 1989, SINGH and SINGH, 2004) and other species (SPERLICH and FEUERBACH-MRAVLAG, 1974, SINGH and DAS, 1991a, b). Two main causes, viz. absence of crossing-over between the arrangements and natural selection acting differentially for certain arrangements (as certain chromosomal associations may be adaptive in a given set of environment) could account for non-random association. Since complete suppression of crossing-over probably never occurs as long as there is non-inverted area between the arrangements, natural selection is probably the main factor in maintaining the non-random association. Natural selection may also aid in the maintenance of non-random association by influencing the recombination rates. It has been shown that the magnitude of linkage disequilibrium depends on the fitness of genotypes involved and also on the rate of recombination between them (PARSONS, 1973). Since, mechanical factors related to the twisting of the inversions during synapses probably interfere with pairing and so reduce crossing-over, it therefore affects the magnitude of linkage disequilibrium (LEVITAN, 1958a). There may be interpopulation variation regarding the cause of linkage disequilibrium as the genetic factors may vary in different populations of the same species (LOUKAS *et al*. 1974, SINGH and DAS, 1991a).

In natural populations with respect to intrachromosomal association, coupling linkages are found to be in excess. The frequencies of coupling combinations are in excess of numbers than expected if the arrangements on the two arms of the same chromosome are independent (BANERJEE and SINGH, 1996). The excess of coupling linkages may also result from epistatic gene interaction (SINGH, 1974, 1983). Earlier studies (SINGH, 1974, 1983, 1984, SINGH and SINGH, 1988, 1990, 1991) in *D. ananassae* with respect to intrachromosomal associations show that two linked inversions are randomly associated in natural and mass culture laboratory populations as contrasted to isofemale lines. This suggests that random drift is the cause of non-random association (linkage disequilibrium) in isofemale lines. The tight linkage between the two inversions as evidenced by the results of

recombination studies reported earlier supports the notion that linkage disequilibrium is caused by drift (SINGH and SINGH, 1990). This reinforces the tight linkage theory between linked inversions in *D. ananassae*. In *D. pavani*, non-random association in natural and laboratory populations were found to be due to excess of coupling and deficiency of repulsion combinations (BRNCIC, 1961).

Non-random association of independent inversions of the same chromosome have been found in *D. robusta* (LEVITAN, 1958a, 1961, 1973, PRAKASH, 1967), *D. guaramunu* (LEVITAN and SALZANO, 1959), *D. pavani* (BRNCIC, 1961), *D. euronotus* (STALKER, 1964), *D.subobscura* (SPERLICH and FEUERBACH-MRAVLAG, 1974), *D. melanogaster* (KNIBB *et al.* 1981, SINGH and DAS, 1991b, DAS and SINGH, 1990), *D. bipectinata* (SINGH and DAS, 1991a, BANERJEE and SINGH, 1995,1996) and others (see review by SINGH, 2008). Most studies in these species support the hypothesis of LEVITAN (1958a), that the natural selection involving epistatic interaction between linked gene arrangements is the main factor for maintaining linkage disequilibrium between inversions. SPERLICH and FEUERBACH-MRAVLAG (1974) have interesting finding in *D. subobscura* whereby, within the same species two chromosomes behave differently with respect to linkage disequilibrium. Almost complete linkage disequilibrium between inversions of an autosome and X chromosome of *D. subobscura* has been observed. Whereas, the linkage disequilibrium between inversions of an autosome was found to be due to complete suppression of crossing-over in the region between them, the linkage disequilibrium between inversions of sex chromosome was due to epistatic interaction. It may be that the two cases demonstrate two different stages of gene interaction in evolution. Sex chromosome arrangements may represent a very early stage whereas autosomal arrangements may be considered as the end-point of the development.

It is believed that linkage disequilibrium is most easily produced under a 2-allele system and its occurrence becomes more difficult as the number of allele present in the populations increases (YAMAZAKI *et al.* 1984). Since, most polymorphic loci are of multiple allele system, it is highly likely that non-occurrence of linkage disequilibrium between inversions in natural populations may be due to highly developed chromosomal inversion system (SINGH et al. 1975). Natural selection may favor one or the other association and we may find certain combinations more frequent than expected by chance. Since, the larvae were taken directly from culture bottles any significant deviation from expectation would indicate differential viability of various chromosomal associations between inversions.

Non-random association could also be generated when tight linkage is combined with epistatic selection or genetic drift or population subdivision. So, linkage disequilibrium patterns observed in natural populations are result of complex interplay between biological factors, such as recombination, mutation and population demography and evolutionary history (KOJIMA and LEWONTIN, 1970). The structure and effective size of the populations as well as selection regime (co-selection of loci, selective sweeps) are important determinant for regional linkage disequilibrium patterns (MUELLER, 2004).

Most of the results obtained from these species of Drosophila support the hypothesis of LEVITAN (1958a), that the natural selection involving epistatic interaction between linked gene arrangements is the main factor for maintaining linkage disequilibrium between inversions. In *D. pavani* (BRNCIC, 1961), the main factor in the origin and maintenance of non-random association of gene sequences is related to selective pressure. The existence of random equilibrium of various alternative combinations of linked gene sequences or the persistence of only some of them (presence of both inversions in the same homologous chromosomes, for instance) confer different adaptive values to the populations. In each region, natural selection will favor the fittest condition. The fact that non-random associations occur almost invariably in the stocks maintained for a long time in the laboratory further emphasizes the primary selective nature of the phenomenon, i.e. older a culture greater the association of inversions in the same chromosome. This relation has been observed even in the stocks originated from natural population in which inversions were randomly distributed. The role of drift could also be attributed to the tight linkage between inversions but since stocks were maintained by using large number of flies, so the role of drift is unlikely (SINGH, 1983). Linkage disequilibrium may of course come about for reasons other than epistatic selection, these could be (i) random drift due to small population size (HILL, 1976), (ii) Population mixing (with different allele frequencies) or migration (OHTA, 1982), and (iii) genetic hitchhiking (HEDRICK *et al.* 1978). The possible role of these factors must be taken into account before attributing linkage disequilibrium to epistatic selection.

It could be said that in both natural populations and laboratory stocks there is deviation from randomness in some of the cases. However, there is apparent difference between the two. In the former the chi square test for goodness of fit between observed and expected was significant in some cases indicating interpopulation variation with respect to association of inversions. In the laboratory stocks on the other hand the difference between observed and expected values are greater and significant which could be due to the number of generations, the populations have been kept in the laboratory (LEVITAN, *et al.* 1954). From the results obtained in different species of *Drosophila*, it is clear that the main factor for causing non-random association between inversions is natural selection although the tight linkage between inversions may also cause non-random association in some cases (SINGH and DAS, 1991a).

It could therefore be concluded that in most of the natural as well as laboratory populations no significant deviation from randomness of intra- and interchromosomal associations (2L-3L, 2L-3R, 3L-3R) was found hence, providing evidence for random associations. However, in some populations, significant deviation from randomness was found in both natural and laboratory populations, which could be due to excess of certain combinations, deficiency of others and complete absence of some combinations. Possible role of genetic drift could be implicated due to tight-linkage between linked gene arrangements. Most importantly, there is lack of genetic coadaptation in geographic populations of *D. ananassae* (SINGH, 1972, 1985).

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POPULACIONA GENETIKA *Drosophila ananassae* : ISPITIVANJA INDIJSKIH POPULACIJA

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I z v o d

Vršena su ispitivanja inverzija hromozoma kod četrdeset pet prirodnih populacija *Drosophila ananassae* i populacija formiranih u laboratoriji iz tih populacija. Kvantativni podaci o učestalosti tih inverzija su korišćeni za testiranje intra – i interhromozomalnih interakcija kod *D.ananassae.* Kod većine kako prirodnih tako I laboratorijskih populacija nisu nađene značajne devijacije u poređenju sa slučajnim intra I interhromozomalnim asocijacijama (2L-3L, 2L-3R, 3L-3R) što ukazuje na random asocijacije.

U nekim slučajevima utvrđene značajne devijacije u odnosu na slučajne kako u prirodnim tako I u laboratorijskim populacijama mogu da budu objašnjene kao ekscesi nekih kombinacija, delimično ili potpuno odsustvo nekih kombinacija. Jedno od objašnjenja može da bude uloga genetičkog drifta zbog bliske ukopčanosti structure vezanih gena. Ovi rezultati su u saglasnosti sa ranijiom sugestijom o odsustvu genetičke koadaptacije kod *D. ananassae.*

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