

UDC 575: 596.77
Original scientific paper

**THE STUDY OF CHROMOSOMAL INVERSION POLYMORPHISM OF
Drosophila subobscura OVER YEARS IN TWO DIFFERENT HABITATS
FROM MOUNTAIN GOČ**

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(2007): *The study of chromosomal inversion polymorphism of Drosophila
subobscura over years in two different habitats from mountain Goč.*–
Genetika, Vol. 39, No. 2, 155 - 167.

We analysed changes in the genetic structure of two ecologically
distinct populations of *Drosophila subobscura* by assessing inversion
polymorphism parameters for over years.

The frequencies of gene arrangements on all five chromosomes
show variability in each population. Several chromosomal arrangements
appeared for the first time in both populations. Significant difference in

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the overall distribution of gene arrangements between first and last year of study (1998/2006) in *beach* wood population of *D.subobscura* is found for chromosome A (a sex chromosome) and autosomes J and E, while in *oak* wood population the overall frequency of gene arrangements differ for autosomes J, E and O. The present significant changes of the particular gene arrangements are specific for each population and result in significant differences in comparisons at the level of individual chromosomes between years of study. Although overall heterozygosity remained unchanged over the years in *beech* habitat, it is significantly reduced in *oak* population in the fourth year.

The obtained results indicate that population structure may significantly depend on short-term and long-term microclimatic changes in habitats. Based on the results to date, monitoring of microevolutionary changes using *D.ubobscura* and its relatives seems a promising way to study the effects of global changes.

Key words: *Drosophila subobscura*, inversion polymorphism, population genetic structure, microclimatic change

INTRODUCTION

Drosophila subobscura is a typical Palearctic species which is recently, in the late 1970s, accidentally introduced into the New World, colonizing it rapidly afterwards. The haploid mitotic chromosome set of this species consists of five acrocentric and one dot chromosomes. A very rich inversion polymorphism exists in all of the acrocentric chromosomes. More than 60 different inversions forming more than 90 different chromosomal gene arrangements have been described in natural populations analyzed so far (for a review see: KRIMBAS 1992, 1993). Some of these arrangements are rare and/or restricted to limited areas, but at least two or more of them at each chromosome are widespread through the entire Palearctic area of this species and their frequencies exhibit clinal variations which are correlated with latitude (PREVOSTI, 1966, 1974). The choice of standard arrangements goes back to the chromosomal map published by MAINX et al. (1953), who used the only available laboratory strain of *D.subobscura* from Küsnacht in Switzerland, which proved to be homokaryotypic for all chromosomes. The map was later improved by KUNZE-MÜHL and MÜLLER (1958), and is commonly used until now.

Studies of inversion polymorphism in natural and laboratory populations of *D.subobscura* (summarized by KRIMBAS 1993, presented also in SOLÉ et al., 2002, BALAŇYÀ et al. 2004; SAVKOVIC et al. 2004, KALAJDŽIĆ et al., 2006) show that variability of inversion polymorphism largely depends on a variety and dynamics of different environmental i.e. ecological factors. It is generally accepted that in *D.subobscura*, high level of inversion polymorphism is quite stable, but it

still varies depending on the environment and is therefore classified as a "semi rigid" or "semi flexible" (SPERLICH and FEUERBACH, 1966).

MENOZZI and KRIMBAS (1992), analyzed frequencies of 44 gene arrangements from 108 natural populations in relation to several climatic variables and concluded, from principal component analysis, that, although historical processes cannot be ruled out, selection by climatic variables seems to have shaped the overall pattern of geographic frequency distribution of the various gene arrangements. Association between the changes of some climatic factors and gene arrangement frequencies in *D. subobscura* is confirmed in studies of spatial and temporal variability of this kind of polymorphism (for a review see: KRIMBAS 1992, 1993, ŽIVANOVIĆ et al., 1995; ORENGO and PREVOSTI, 1996; SOLÉ et al., 2002; ANDELKOVIĆ et al, 2003; BALAŃYÀ et. al., 2004).

Global climatic changes have a significant impact on living organisms and Balkan peninsula is characterised by extensive ecological diversity. From that aspect, studies of temporal variability of inversion polymorphism of *D. subobscura* represent convenient and attractive population genetic model system. The aim of the present study was to compare inversion polymorphism during four years of study in two *D. subobscura* populations with different ecological characteristics of habitat.

MATERIALS AND METHODS

D. subobscura flies were collected at mountain Goč, situated between 43° 33' - 43° 35' N and 18° 15' - 18° 40' E in central Serbia. The local populations were from two forest communities (topographically about 7 km apart), at about 800 m above sea level: *Abieto-fagetum* and *Fraxineto-quercetum*, hereafter referred to as *beech* and *oak* wood, respectively. Local differences in topography and soil composition, as well as distribution of dominant trees within *beech* and *oak* woods modify microclimates considerably (GAJIĆ, 1984). In other words, the forest communities represent two ecologically different habitats.

Both populations were sampled simultaneously at the end of June, in years 1998, 2003, 2005 and 2006. Sampling was done at the same locations in the same manner every year. Flies were attracted by fermented fruit traps and swapped with a net in the late afternoon peak of activity, between 18:00 and 20:30.

Analysis of inversion polymorphism was carried out with the wild captured *D. subobscura* males. The males were individually crossed with virgin females from Küsnacht laboratory stock, which is homozygous for Standard gene arrangement at all five large chromosomes. Salivary glands from third-instar larvae were squashed and chromosomes stained with aceto-orcein solution. Eight larvae were analyzed from the progeny of each the crosses performed. For the cytological analysis of gene arrangements, the chromosome map of KUNZE-MÜHL and MÜLLER (1958) was used. The designation of gene arrangements followed that of KUNZE-MÜHL and SPERLICH (1955).

The G-test (SOKAL and ROHLF, 1995) was used to determine the homogeneity of gene arrangement frequencies on all five chromosomes between

populations and years. Z-statistics (ZAR, 1999) was used to assess the differences between frequencies of gene arrangements individually, between populations and years. Bonferoni multiple test correction was applied to adjust for multiple pairwise comparisons. Inversion polymorphism parameters (Degree of Heterozygosity - HZ and Index of Free Recombination - IFR) were derived from karyotype frequencies according to the description of KRIMBAS (1993).

RESULTS

The frequencies of gene arrangements on five acrocentric chromosomes, Degree of Heterozygosity (HZ) and Index of Free Recombination (IFR) in *D.subobscura* populations, from two habitats in four years, are presented in Table 1., and the obtained differences in the frequencies of individual gene arrangements between years within both habitats are summarized in Table 2.

Table 1. Gene arrangement frequency (%) and inversion polymorphism parameters in four years, in beech and oak populations of *Drosophila subobscura*.

YEAR	BEECH WOOD				OAK WOOD			
	1998	2003	2005	2006	1998	2003	2005	2006
GENE ARRANGEMENT (%)	n=44	n=30	n=30	n=44	n=43	n=30	n=30	n=56
A _{st}	20,46	53,33	70,00	65,91	18,60	66,67	60,00	39,29
A ₁	52,27	30,00	16,67	25,00	69,77	26,67	26,67	57,14
A ₂	27,27	16,67	13,33	9,09	11,63	6,67	13,33	3,57
J _{st}	43,18	30,00	30,00	18,18	25,58	23,33	25,00	2,68
J ₁	56,82	70,00	70,00	81,82	74,42	76,67	75,00	97,32
U _{st}	12,50	8,33	10,00	10,23	5,81	8,33	13,33	7,14
U ₁					1,16			
U ₁₊₂	42,00	58,34	56,67	42,05	45,35	50,00	53,33	22,32
U ₁₊₂₊₆	45,50	33,33	33,33	47,73	47,67	41,67	33,33	70,54
E _{st}	40,91	40,00	20,00	17,05	37,21	26,67	51,67	16,07
E ₈	12,50	21,67	33,33	29,55	23,26	28,33	20,00	15,18
E ₁₊₂	1,14	3,33						
E ₁₊₂₊₉	45,45	35,00	43,34	53,41	39,53	45,00	26,67	66,07
E ₁₊₂₊₉₊₁₂			3,33				1,67	2,68
O _{st}	18,18	13,33	26,67	10,23	24,42	23,33	21,67	10,71
O ₃₊₄	50,00	46,67	55,00	51,14	44,19	51,67	63,33	39,29
O ₃₊₄₊₁	31,82	38,33	15,00	34,09	31,99	21,67	11,67	41,96
O ₃₊₄₊₂		1,67	3,33	4,55		3,33	3,33	8,04
HD	2,41	2,17	2,57	2,48	2,05	2,40	2,13	1,64
IFR (%)	79,94	82,99	78,98	80,29	82,09	80,28	83,05	86,08

heterozygosity (HZ); index of free recombination (IFR); n = number of males in the analysis

Analysis of gene arrangement frequencies on all five chromosomes during four years of study shows that within each habitat, frequencies of inversions and inversion complexes varied at certain degree ($G_{\text{Beech}} = 103.292$; $p < 0.001$, $G_{\text{Oak}} = 171.190$; $p < 0.001$).

In *beech* wood population significant difference was found between years 1998/2005, for the frequency of arrangements on chromosome A between years 1998/2005 ($G_{1998/2005} = 18.998$; $p < 0.0036$) and 1998/2006 ($G_{1998/2006} = 19.580$; $p < 0.001$). Those differences are associated with significant changes in the frequencies of gene arrangements A_{St} and A_1 , while the frequency of arrangement A_2 has not significantly changed in the period of study (Table 2.). The frequencies of both arrangements on chromosome J (J_{St} and J_1) show significant changes between years 1998/2006, which is reflected at the level of overall variability in the frequency of this chromosome ($G_{1998/2006} = 13.218$; $p < 0.0102$). The significant overall variability in gene arrangement distribution was found for chromosome E between years 1998/2005 ($G_{1998/2005} = 17.031$; $p < 0.0245$), 1998/2006 ($G_{1998/2006} = 17.119$; $p < 0.05$) and 2003/2006 ($G_{2003/2006} = 14.155$; $p < 0.0864$). These differences primarily result from the significant changes in the frequencies of gene arrangements E_{St} and E_8 in the period of study (Table 2.). Gene arrangements at chromosome U did not show significant changes in frequencies during the period of study. Although gene arrangements O_{St} and O_{3+4+1} show significant changes in frequencies between years 2003/2005 and 2005/2006 (Table 2.), the overall distribution of gene arrangement frequencies at chromosome O did not significantly change.

Significant difference in the overall distribution of gene arrangements between first and last year of study (1998/2006) in *beech* wood population of *D.subobscura* is found for chromosome A as sex chromosome and autosomes J and E, as well. Thus, the G-test result, for all autosomes (J, U, E and O), after Bonferroni correction, gave highly significant overall difference between given years ($G = 41.765$; $p < 0.01$).

Degree of heterozygosity (HZ) in *beech* wood population of *D.subobscura* for the period of study (Table 1.) ranges between 2.17 (year 2003) and 2.57 (year 2005). If arbitrary criteria is used, that difference of $\geq 10\%$ is significant in the pairwise comparisons of HZ values, we can say that differences in the degree of heterozygosity exist between years 1998/2003, 2003/2005 and 2003/2006.

In the *oak* wood population of *D.subobscura* significant difference was found between years 1998/2003 and 1998/2005, for the frequency of arrangements on chromosome A ($G_{1998/2003} = 17.879$; $p < 0.0036$ and $G_{1998/2005} = 15.297$; $p < 0.0175$). These differences are primarily associated with significant changes in the frequencies of gene arrangements A_{St} and A_1 (Table 2.). If each year is separately compared with year 2006 for the overall distribution of gene arrangements, on all chromosomes, the highly significant difference is found for chromosome J in all comparisons ($G_{1998/2006} = 24.728$; $p < 0.001$; $G_{2003/2006} = 18.166$; $p < 0.001$; $G_{2005/2006} = 20.185$; $p < 0.001$). Since there are only two gene arrangement of this chromosome

registered in the oak wood population (J_{St} and J_1), the observed differences are due to their changes in frequency (Table 2.). For chromosome U, the significant difference is found only between years 2003/2006 and 2005/2006 ($G_{2003/2006} = 14.642$; $p < 0.0175$; $G_{2005/2006} = 22.504$; $p < 0.001$). Considering the frequencies of all gene arrangements of chromosome U, the observed differences are due to significant changes in the frequencies of arrangements U_{1+2} and U_{1+2+6} (Table 2). Five gene arrangements of chromosome E are registered in the oak wood population of *D. subobscura*, and within those, arrangements E_{St} , E_8 and E_{1+2+9} show significant differences in frequencies over the years of study (Table 2.). It is also reflected at the level of overall gene arrangement frequencies and the significant differences are obtained between years 1998/2006 ($G = 20.125$; $p < 0.01$) and 2005/2006 ($G = 29.959$; $p < 0.001$). All four gene arrangements of chromosome O which are present in oak wood population of *D. subobscura*, show significant changes in frequencies during period of study, either if compared between successive years or between longer periods (Table 2.). Those differences are reflected at the level of overall gene arrangement frequencies and the significant differences are obtained between years 1998/2006 ($G = 17.451$; $p < 0.05$) and 2005/2006 ($G = 22.534$; $p < 0.001$).

If overall frequencies of gene arrangements at four autosomes are analysed, the significant changes result in significant differences in all comparisons at the level of individual chromosomes. The highly significant difference is obtained for all autosomes between years 1998/2006 ($G = 58.790$; $p < 0.001$), 2003/2006 ($G = 80.379$; $p < 0.001$) and years 2005/2006 ($G = -118.776$; $p < 0.001$).

Degree of heterozygosity (HZ) in oak wood population of *D. subobscura* for the period of study (Table 1) ranges between 1.64 (year 2006) and 2.40 (year 2003). If arbitrary criteria is used, that difference of $\geq 10\%$ is significant in the pairwise comparisons of HZ values, we can say that differences in the degree of heterozygosity exist between years 1998/2003, 1998/2006, 2003/2005, 2003/2006 and 2005/2006. Significant difference is not registered only between years 1998/2005.

DISCUSSION

Our previous results (ANDJELKOVIĆ et al., 2003, SAVKOVIĆ et al., 2004) clearly show that studied populations of *D. subobscura* from two distinct habitats at mountain Goč (*beech* and *oak* wood) differ significantly in the frequencies of approximately 40% of total gene arrangements. The observed differences can partly be associated with microclimate differences between two habitats. The average daily light intensity and the average temperature was lower in *beech* wood than in *oak* wood, and relative average humidity was higher (GAJIĆ, 1984, and *personal observation*). All these ecological abiotic factors vary during day, but the variations were of the smaller range in *beech* woods.

The papers concerned with inversion polymorphism of *D.subobscura* from Serbia region (ANDJELKOVIĆ and SPERLICH, 1973, ŽIVANOVIĆ et al., 1994; 1995; 1998; 2002, ANDJELKOVIĆ et al., 1998; 2003, SAVKOVIĆ et al., 2004) reveal that the obtained frequencies of gene arrangements are consistent with the hitherto registered frequencies in the Balkan region, as well as, with the values observed for populations of Central Europe (generally summarized by KRIMBAS 1992, 1993). However, while heterozygosity and IFR values obtained in the several years long study of two populations of *D.subobscura* from mountain Goč, generally fit into the pattern of the respective geographic distribution, the frequencies of particular gene complexes evidently differ over the whole or a period of study. That indicates that biological and ecological specificities of Central Balkan area (STEVANOVIĆ, 2005) reflect through the genetic structure of populations of organisms which inhabit the region. On the other side, the obtained results undoubtedly indicate the temporal variability in gene pools of the studied populations of *D.subobscura*, which is of importance because majority of inversion polymorphism studies of *D.subobscura* in Europe to date is based on short term studies.

Analysis of the observed genetic changes over years reveals that duration of time period reflects through the range of changes in gene pool of populations. Thus, the majority of significant differences among the frequencies of individual gene arrangements appear between years 1998/2006, in the samples from both habitats, being much higher in the *oak* wood. Such interpopulation differences are certainly generated by higher daily and yearly oscillations of abiotic ecological factors in *oak* wood than in *beech* wood (ANDJELKOVIĆ et al., 2003). This is confirmed by comparing the years 2005 and 2006, when significant differences in gene arrangement frequencies are found in *oak* wood at the level of each autosome, while none is obtained in *beech* wood.

These interpopulation differences contain interchromosomal ones. In the population of *D.subobscura* from *beech* wood, gene arrangements on chromosome U and O, do not show significant changes in the period of study, while in the population from *oak* wood, all five chromosomes vary significantly in certain periods. The study reveals that within individual chromosomes, the number of cases when significant changes in the frequencies of some gene arrangements are registered is not equal. In the population from *beech* wood at chromosome E, significant changes of gene arrangements are registered in three comparisons between years, at chromosome A in two, while only in one comparison at chromosome J. In the population from *oak* wood at chromosome J, significant changes of gene arrangements are registered in three comparisons between years, and at other chromosomes in two comparisons.

Differences in temporal variability of gene pools of two studied populations are reflected in the change of the overall heterozygosity. The range of the HZ values is wider and fluctuation over years is larger, for the population from *oak* wood than in the population from *beech* wood. While in the population of *D.subobscura* from *beech* wood there is no overlapping of the values from the comparisons between years in which significant changes within gene arrangements

on autosomes are registered and arbitrary stated differences in HZ, in the population from *oak* woods the changes at these two aspects of polymorphism overlap in the most cases. All the obtained differences, within temporal dynamics of gene pool of two studied populations of *D.subobscura*, indicate that inversion polymorphism of this species represents, in the adaptive sense, more sophisticated system than the one classified as "semi rigid" or "semi flexible" (SPERLICH and FEUERBACH, 1966).

As pointed out by ENDLER (1986) long-term directional trends suggest that the traits are not at selective equilibrium, but they are not drifting either. A long-term change can arise from directional selection, or an approach to an equilibrium that is shifting due to environmental changes. Determining the causal relation between individual or complex of environmental factors and temporal changes in gene pools of natural populations of organisms, is very difficult and more or less speculative. The general approach is analysis of the effect of climatic changes on genetic structure of populations and species as well. The starting point of this approach is the fact that climatic changes influence geographic range, abundance, phenology and biotic interactions of organisms (LOVEJOY and HANNA, 2006). Data shows that inversion polymorphism of *D.subobscura* is relatively sensitive to climate changes (PREVOSTI et al., 1988), and primarily temperature changes (ORENGO and PREVOSTI, 1996, RODRÍGUEZ-TRELLES and RODRIGUEZ, 1998). Results of the long - term, (but not successive over several years) survey of genetic changes in 13 natural populations of *D.subobscura* from Mediterranean, Atlantic and Central Europe regions (SOLÉ et al., 2002, BALAÑYÁ et al., 2004), shows that significant changes occurred in the frequency of particular gene arrangements during the last 15 to 35 years. This changes could be due to a shift in temperature or to other climatic factors that are correlated to geographic latitude. Generally, it is indicative that the gene arrangements which were more frequent in the north tend to decrease in frequency in the new samples of the previously analysed populations, whereas the arrangements typical of the southern populations show the opposite behavior. These can be related to global warming phenomenon which makes inversion polymorphism of *D.subobscura* as a very good indicator for monitoring the effects of climatic changes on genetic structure of populations (RODRÍGUEZ-TRELLES et al., 1998, BALAÑYÁ et al., 2006).

The decrease in frequencies, or presence in the lower frequencies than expected for Central Balkan area of *D.subobscura*, of some gene arrangements (A_1 , J_{St} , U_{St} , E_{St} , O_{St}) and the increase in frequencies or presence in the higher than expected of other arrangements (J_1 , U_{1+2} , U_{1+2+6} and O_{3+4}), go in favour to the hypothesis that changes at the level of inversion polymorphism are related to global warming.

The assumption that global warming is responsible for all changes observed is rather likely. Of course, it is not known whether the temporal changes of chromosomal polymorphism of these populations are a consequence of a local adaptation, or they were produced by migration from the south. Still, little is known about evolutionary temperature adaptation which influences organism

performance and fitness. The microecological pattern has powerful consequences for life-history and probably also for biotic response to climate change although the relationships among evolution, temperature and ecology are multivariate, hierarchical and complex (CLARKE, 2003). Having these in mind, the results of our study, including simultaneous surveillance of genetic changes in gene pools of *D.subobscura* populations over longer period of time, in two ecologically and mainly microclimatically distinct habitats, reveal that inversion polymorphism of this species proves to be a good indicator of environmental change, because it is not too sensitive so that microclimatic differences and/or seasonal fluctuations could mask general long term changes.

ACKNOWLEDGEMENTS

The authors feel honoured to dedicate this paper to the memory of Prof. Janko Dumanovic, a respected scientist, who in the 80 years of his life gave an exceptional contribution to the development and promotion of genetics in Serbia.

This work was supported by Ministry of Sciences of Republic of Serbia, Grant No. 143014.

Received July 11th, 2007
Accepted August 17th, 2007

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**STUDIJA HROMOZOMSKOG INVERZIONOG POLIMORFIZMA
Drosophila subobscura TOKOM VIŠE GODINA U DVA RAZLIČITA
STANIŠTA NA PLANINI GOČ**

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Analizirane su promene u genetičkoj strukturi dve ekološki odvojene populacije *Drosophila subobscura*, određivanjem parametara inverzionog polimorfizma tokom više godina.

Učestalosti genskih aranžmana na svih pet hromozoma pokazuju varijabilnost u svakoj od populacija. Nekoliko aranžmana se pojavljuje po prvi put u obe populacije. Značajna razlika u ukupnoj distribuciji genskih aranžmana između prve i poslednje godine istraživanja (1998/2006) dobijena je u populaciji *D.subobscura* iz bukove šume za hromozom A (polni hromozom) i za autozome J i E, dok se u populaciji iz hrastove šume ukupna učestalost genskih aranžmana razlikuje za autozome J, E i O. Dobijene značajne promene učestalosti određenih genskih aranžmana specifične su za svaku populaciju i rezultuju u značajnim razlikama u poredjenjima na nivou pojedinačnih hromozoma između godina istraživanja. Mada ukupna heterozigotnost ostaje nepromenjena tokom više godina u populaciji iz bukove šume, ona se značajno smanjuje u populaciji iz hrasta u četvrtoj godini istraživanja.

Dobijeni rezultati pokazuju da genetička struktura populacije može značajno da zavisi od kratkoročnih i dugoročnih mikroklimatskih promena u staništima. Na osnovu dosadašnjih rezultata, monitoring mikroevolutivnih promena korišćenjem *D.ubobscura* i srodne vrste predstavlja dobar put u istraživanjima efekta globalnih promena.

Primljeno 11 VII 2007.

Odobreno.17 VIII.2007.