

## CLIMATE CHANGE EFFECT ON THE GENETICS OF A MEXICAN POPULATION OF *Drosophila pseudoobscura*

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The chromosomal polymorphism present in populations of several species of *Drosophila* could be related with changes in time or ecological parameter. The aim of this work is to evaluate the long-term effect of climatic changes on the frequencies of *D. pseudoobscura* chromosomal arrangements. The population studied is located in a forest near Tulancingo, México, the chromosomal analysis has been studied for more than 35 years. The relative frequencies found in that period were used to evaluate the changes. The climatic data of the National Meteorological Service were gathered for the period from 1974 to 2011. A multiple analysis of variance was used to analyze the relationship between the changes in the chromosomal arrangement frequencies and the different climatic variables (maximum and minimum temperature, evaporation and pluvial precipitation). Results showed a significant correlation of several chromosome gene arrangements with one or more hydro-climatic variables modifying the genetic structure of the natural population. Comparisons with other populations shown and allow the establishment of the effect of climate change on the genetic structure of natural populations.

*Keywords:* Inversion polymorphism, *D. pseudoobscura*

### INTRODUCTION

Chromosome polymorphism represent changes in structure known as inversions that appear as mutations and allow adaptation to different ecological condition in such a way to

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increase the possibility of expansion of the population. In the case of *Drosophila pseudoobscura* it has a geographic distribution that extends from British Columbia in Canada, through western USA, Mexico, Guatemala, and the Colombian Highlands, and it lives in sites of temperate climate.

This fly has polytene chromosomes with paracentric inversions that prevent alleles to be exchanged by crossing over forming "super genes", there are different types of chromosomal arrangements formed by multiple inversions on the third chromosome of *Drosophila pseudoobscura* ANDERSON *et al.* (1979).

Chromosomal inversions are rare sequences that occur as unique events and because of this, they are considered to be carrying more historical information than mutations DOBZHANSKY and STURTEVANT (1938), AQUADRO *et al.* (1991).

With few exceptions, differences in the genetic makeup of two populations increase as the distance between them increases forming gradients which can be gentle or abrupt as noted by DOBZHANSKY and EPLING (1944), WALLACE *et al.* (2011), OLVERA *et al.* (1979) and LEVINE *et al.* (1995).

On the other hand, the climatic changes of the past decades have led to genetic changes in the constitution of the populations, BRADSHAW and HOLZAPFEL (2006).

Modifications for long-term in the chromosomal polymorphism in *Drosophila* suggest that the genetic constitution of the population is responding to climate variations VAN HEERWAARDEN and HOFFMANN (2007). This suggestion is supported by the fact that genes located within the inversions are associated with a variety of characters, including those involved in adapting to the climate HOFFMANN and RIESEBERG (2008).

Chromosomal polymorphisms are exposed to intense selective pressure, and they are very sensitive to environmental changes. In the fly, *D. subobscura*, thermal preference and tolerance to high temperatures have been associated with inverted chromosomal polymorphisms as reported in the studies done among others by ORENGO and PREVOSTI (1996), DOLGOVA *et al.* (2010), REZENDE *et al.* (2010), ZIVAROVIC and MESTRES (2011), GALLUDO *et al.* (2018), ZIVAROVIC *et al.* (2021), KHADEM *et al.* (2023). In addition, once a new inversion is formed this stays in the population in later generations, which makes polymorphisms a useful tool for the study of the environmental effects.

In Mexico the presence and distribution of chromosomal polymorphisms, as well as seasonal and geographical variations in natural populations of *D. pseudoobscura* have been studied; in addition, the role they have had in the evolution of the species has been analyzed demonstrating that they present a cyclical variation GUZMÁN *et al.* (2005, 2006), OLVERA *et al.* (2005), SALCEDA and ESPINOZA-VELAZQUEZ (2006), SALCEDA *et al.* (2007a, b), SALCEDA *et al.* (2008), SALCEDA (2009).

Given that climate change is altering the geographical distribution, abundance, phenology and the interactions of organisms ROOT and HUGHES (2005), POUNDS *et al.* (2005), PARMESAN (2006), we wanted to assess the response of the species to environmental effects biosphere-atmosphere. Therefore, the aim of this study was to quantify the impact of environmental conditions on the frequencies of chromosomal arrangements, as well as seasonal and geographical variations and their role in the evolution of *D. pseudoobscura* in a natural population of a forest near Tulancingo, Hidalgo, México.

## MATERIALS AND METHODS

Flies were collected in a forest near Tulancingo, Hidalgo, over baits of fermenting banana, and transported to the laboratory for genetic analysis: each female was placed in a separated culture bottle with the regular medium used in the laboratory prepared basically with corn flour, sugar, sucrose and added with propionic acid and tegosept to prevent infections, while each male was crossed to several virgin females from a laboratory stock homozygous for TL gene arrangement. All cultures were maintain in fresh food at  $24^{\circ} \text{C} \pm 1$ . Chromosomes were analyzed by making squash of salivary glands dissected from third instar larvae and stained with 5 % aceto-carmin. Larvae, one from each culture, were studied using all the flies captured that correspond to the sample size shown in the tables. The inversion types were classified according to the descriptions in DOBZHANSKY and STURTEVANT (1938), KASTRITSIS and CRUMPACKER (1966, 1967) and OLVERA *et al.* (1979). The results obtained and their relative frequencies were calculated.

The chromosomal arrangement frequencies obtained from the data gathered in 2011 as well as those previously reported for the population of Tulancingo, published in GUZMÁN *et al.* (2006) were analyze as a single group. Gathered weather data (maximum and minimum temperature, evaporation and pluvial precipitation), covered the period 1974-2011 from the National Meteorological Service (SMN) stations: Presa La Esperanza (code 00013082), Sinóptica Meteorológica Automática station (ESIME) “Tulancingo” (code 76634) and Santa María Asunción (00013130 code) station all of which are near Tulancingo. Graphics were built to observe the trend of chromosomal arrangements and environmental conditions over all those years and for statistical diagnosis. A linear correlation analysis was perform specifically involving the months of sampling or collection of the species and the frequencies of different chromosome arrangements. The MANOVA analysis were used to make proper differentiations.

## RESULTS

The data obtained for the hydro-climatic variables: evaporation (EVP), rainfall (RF), maximum temperature (Tmax) and minimum temperature (Tmin) in three sampling stations close to the city of Tulancingo is shown in Table 1.

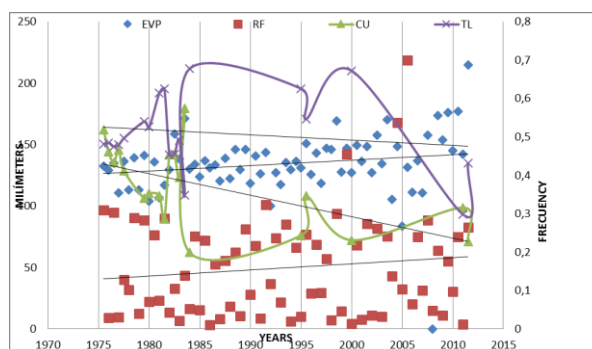


Figure 1. Relative frequency of the main chromosomal arrangements TL and CU and the trends in climate variables, evaporation and rainfall.

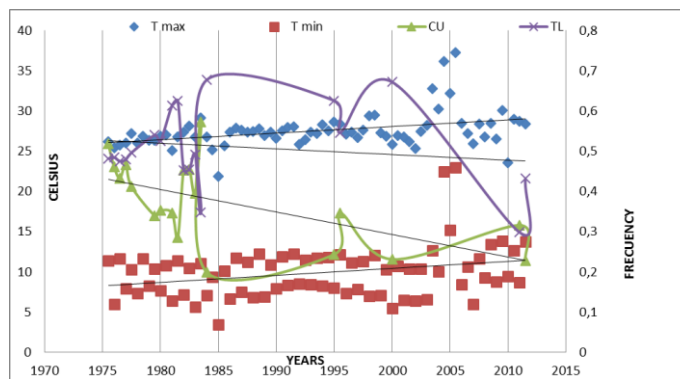


Figure 2. Relative frequency of the main chromosomal arrangements TL and CU and the trends in maximum and minimum temperatures.

Table 1. Data grouped by rainy and dry seasons of hydro-climatic variables, and chromosomal arrangement frequencies. (Also shown are the chromosome frequencies that correspond to the same season)

Year	EVP	RF	Tmax	Tmin	CU	TL	EP	OL	SC
1975 (RS)	132.600	96.750	26.188	11.376	0.519	0.481	0	0	0
1976 (DS)	128.933	8.833	25.419	5.975	0.461	0.485	0.017	0.008	0.021
1976 (RS)	134.733	94.917	25.734	11.623	0.433	0.475	0.031	0.009	0.057
1977 (DS)	110.817	9.417	25.978	7.878	0.466	0.479	0.024	0.020	0.004
1977 (RS)	136.500	40.083	27.200	10.293	0.412	0.496	0.012	0.031	0.012
1979 (RS)	140.967	88.583	26.370	10.356	0.340	0.540	0.010	0.060	0.040
1980 (DS)	103.833	22.000	26.901	7.638	0.353	0.526	0.012	0.046	0.035
1981 (DS)	106.867	22.833	25.100	6.372	0.347	0.614	0.005	0.005	0
1981 (RS)	117.183	89.633	26.767	11.343	0.286	0.625	0	0.054	0
1982 (DS)	129.350	13.150	27.359	7.114	0.453	0.453	0.013	0.060	0
1982 (RS)	158.797	32.533	28.107	10.467	0.455	0.455	0.045	0	0.045
1983 (DS)	138.500	6.817	26.809	5.627	0.395	0.491	0.009	0.061	0.018
1983 (RS)	171.350	43.600	29.138	11.025	0.574	0.348	0.015	0.029	0.005
1984 (DS)	129.950	16.083	26.754	7.045	0.199	0.678	0.017	0.056	0.010
1995 (DS)	131.237	9.950	28.677	8.021	0.243	0.626	0.046	0.058	0.013
1995 (RS)	150.735	76.983	28.387	12.149	0.347	0.547	0.013	0.053	0.027
2000 (DS)	127.202	4.117	25.845	5.448	0.231	0.672	0.063	0.025	0
2011 (DS)	141.967	3.800	28.686	8.688	0.316	0.298	0.053	0.175	0.088
2011 (RS)	214.550	82.550	28.362	13.763	0.227	0.432	0.023	0.114	0.068

Year	HI	PO	CH	SA	OA	PP	TA	n
1975 (RS)	0	0	0	0	0	0	0	54
1976 (DS)	0.017	0	0	0	0	0	0.0034	180.5
1976 (RS)	0.016	0	0.003	0	0.0103	0	0	245
1977 (DS)	0.008	0.001	0	0.0005	0	0.0005	0	991.5
1977 (RS)	0.031	0	0	0	0.0039	0.0030	0	156
1979 (RS)	0.010	0	0	0	0	0	0	100
1980 (DS)	0.029	0	0	0	0	0	0	173
1981 (DS)	0.025	0	0	0	0	0.0049	0	202
1981 (RS)	0.036	0	0	0	0	0	0	56
1982 (DS)	0.020	0	0	0	0	0	0	150
1982 (RS)	0	0	0	0	0	0	0	22
1983 (DS)	0.026	0	0	0	0	0	0	114
1983 (RS)	0.029	0	0	0	0	0	0	204
1984 (DS)	0.031	0	0	0	0.0096	0	0	518
1995 (DS)	0.006	0	0	0	0.0171	0	0	178
1995 (RS)	0	0	0	0	0.0133	0	0	75
2000 (DS)	0.004	0	0	0	0.0042	0	0	238
2011 (DS)	0	0	0	0	0.0702	0	0	57
2011 (RS)	0	0	0.091	0	0.0455	0	0	44

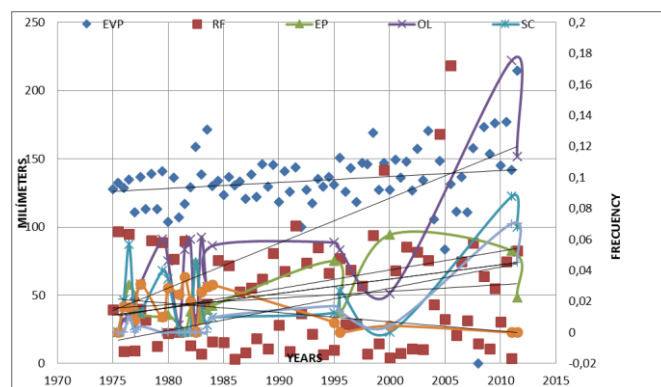


Figure 3. Relative frequency of the minor chromosomal arrangements EP, OL and SC, and the trends of climatic variables, evaporation and rainfall.

The distribution of values for EVP and RF, as well as their tendency can be seen in Figure 1. It is remarkable that both factors have systematically increased during the period of time studied. On the other hand, when analyzing the frequencies for CU and TL chromosome arrangements, both values show a significant decrease over the same time period.

Figure 2. shows the Tmax and Tmin values as well as the frequencies of CU and TL gene arrangements over the 38 years included in this study. The trends for the different data showed that climatic variables increased while the chromosomal frequencies decreased.

Figure 3. shows the trends of the data for EVP and RF as well as their relationship with minor arrangements such as SC, CH, OL and OA. One observes that both, climatic factors and frequencies of minor chromosome arrangements increased over the time period studied.

Similar results can be seen in Figure 4, which compares the values of the Tmax and Tmin with frequencies of the minor gene arrangements (EP, OL, SC, and HI). In both cases there is a positive trend, suggesting that the increase in both, Tmax and Tmin, results in an increase in the frequencies of minor gene arrangements.

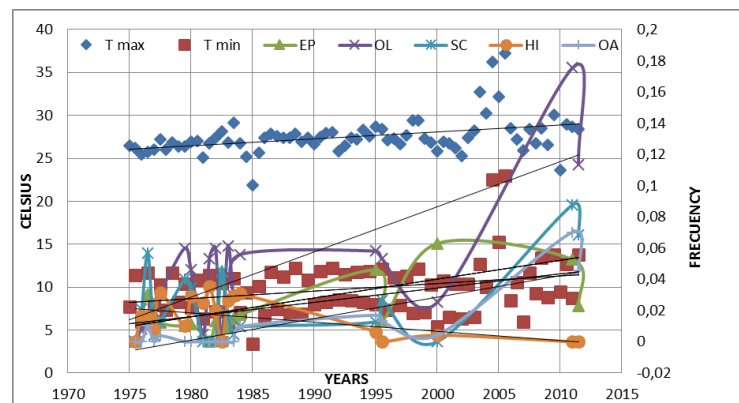


Figure 4. Relative frequency of the minor chromosomal arrangements EP, OL, SC and HI, and trends in maximum and minimum temperatures.

The correlation analysis between hydro-climatic variables (EVP, RF, Tmax and Tmin) and frequencies observed for different chromosomal arrangements are show in Table 2. The The statistical analysis suggests that the EVP presents a significant correlation to TL ( $p=0.0457$ ), SC ( $p=0.0358$ ), and OA ( $p=0.0490$ ), arrangements showing a negative correlation for the first case ( $r=-0.4633$ ) and a positive one for SC and OA ( $r=0.4838$  and  $0.4571$ , respectively). RF was significant for EP ( $p=0.0714$ ), with a negative correlation ( $r=-0.4226$ ). The correlation with Tmax was significant for all the arrangements analyzed ( $p<0.1$  for all cases). The major arrangements CU, TL and HI showed a negative correlation ( $r=-0.0537$   $-0.4454$  and  $-0.2210$ , respectively), while the minor ones EP, OL, SC and OA showed a positive one ( $r=0.2579$ ,  $0.5502$ ,  $0.3529$  and  $0.4977$ , respectively).

Table 2. Relationship between chromosomal arrangements and hydro-climatic variables of the natural population of Tulancingo, Hidalgo (*r* stands for Pearson Correlation Coefficient).

Chromosomal Arrangement	EVP		RF		Tmax		Tmin	
	r	p	r	p	r	p	r	p
CU	-0.028546	0.9076	0.0916	0.7089	-0.05371	8.27E-01*	0.1162	0.6356
TL	-0.4633	0.0457*	-0.0364	0.8823	-0.4454	5.60E-02*	-0.3321	0.1646
EP	0.1488	0.5430	-0.4226	0.0714*	0.2579	2.86E-01*	-0.1848	0.4486
OL	0.3552	0.1355	-0.1061	0.6654	0.5502	1.46E-02*	0.1210	0.6216
SC	0.4838	0.0358*	0.1687	0.4899	0.3529	1.38E-01*	0.3818	0.1066
HI	-0.3813	0.1071	-0.1198	0.6251	-0.2210	3.63E-01*	-0.2607	0.2809
OA	0.4571	0.0490*	-0.0395	0.8723	0.4977	3.01E-02*	0.2508	0.3003

\* Significant correlation (p<0.1)

### DISCUSSION

Chromosomal polymorphism in the genus *Drosophila* have been studied to detect climate and temporal changes in the frequency of different inversions in populations of these flies. Among others we have the works of VALENTE and ARAUJO (1989) in natural populations of *Drosophila willistoni* from Brazil and more recently those done in European populations of *D. subobscura* by ORENCO and PREVOSTI (1996), BALANYÁ *et al.* (2009), REZENDE *et al.* (2010), ZIVANOVIC and MESTRES (2011), GALLUDO *et al.* (2018), KHADEM *et al.* (2022) and ZIVANOVIC *et al.* (2023), or results show resemblance with the ones of these authors as seen below.

We analyzed four hydro-climatic variables (Tmax, Tmin, RF and EVP); three of them (EVP, RF and Tmax) showed a significant relationship ( $p < 0.1$ ) with at least one chromosomal arrangement. Tmin did not correlate with any, suggesting that it did not affect the frequency of inversions. All chromosomal arrangements significantly correlated with Tmax. A multiple analysis of variance test (MANOVA) demonstrated that EVP and Tmax proved to be the factors that most affected the relative frequency of the different chromosomal arrangements, since they are both correlated to TL, SC, and OA arrangements.

When the trend lines for the major arrangements (CU and TL) were analyze, we noted that their slopes were negative (see tables and figures), indicating that their frequencies decreased with time; however, when we applied the same analysis to the hydro-climatic variables we found that the four parameters tended to increase (Figs. 1, 2). On the other hand, minor arrangements, as OA and SC, presented an increase in their frequencies (Figs. 3 and 4) directly correlating with the change in the climatic variables.

At northern latitudes although the proportion of minor arrangements in the total population was very low with respect to the main arrangements and the detected increases were not enough to change their condition as minor chromosomal arrangements, they are of importance to the genetic composition of the population, probably due to the fact that the alleles which are trapped inside the structure of those arrangements possibly had a greater opportunity of adapting to the conditions emerging with environmental changes.

Global climate change (GCC) is linked to biotic impacts at species level, including physiological, phenological and distributional changes ROOT and HUGHES (2005), PARMESAN

(2006). There is also evidence that these impacts exceeded initial estimates. There is evidence that the rate of movement in terrestrial animals is two or three times higher than the prediction made, that is, animals move to higher latitudes or higher places CHEN *et al.* (2011). In this regard, it would be convenient to analyze populations of *D. pseudoobscura*, covering regions further north from their geographical distribution, and to check whether the distribution of the arrangements moves consistently with the results reported by CHEN *et al.* (2011).

For *Drosophila subobscura*, CESPEDES (2006) reported a negative relationship between the rate of chromosomal diversity of experimental populations and the evolutionary effect of temperature, with a decreasing trend of the chromosomal diversity in response to an increase in temperature.

Previously reported studies of thermal evolution in *D. subobscura* show the loss of chromosomal diversity in response to an increase in temperature KRIMBAS (1967), QUINTANA and PREVOSTI (1991). Change in chromosomal diversity seems to be related to the current climate change RODRIGUEZ-TRELLES and RODRÍGUEZ (1998) and the decrease in frequency of the most frequent chromosomal systems of some populations probably arise as a response to the global warming of the planet SOLE *et al.* (2002).

Although the results indicated that the maximum temperature significantly affected the frequency of several chromosomal arrangements in *D. pseudoobscura*, POUNDS *et al.* (2005) suggest that climate change could be affecting other natural populations through various mechanisms that carry significant implications which could often be indirect.

In the case of *Drosophila*, the abundance of food, predators or pathogens in the population could be responsible, at least partly, for our observed changes.

This study demonstrated that environmental changes altered the genetic structure of a natural population of *Drosophila pseudoobscura*. The impact that some environmental conditions had on the frequencies of chromosomal arrangements of *D. pseudoobscura* was positive for the minor chromosomal arrangements OA and SC, but negative for the main ones TL and CU, showing that as T<sub>max</sub> increased, the main arrangements decreased, while minors increased. The remaining inversions EP, OL and HI did not show significant changes.

A further study on the relationship of chromosome polymorphisms with the environmental conditions in other natural populations would be desirable.

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**UTICAJ KLIMATSKIH PROMENA NA GENETIKU MEKSIČKE POPULACIJE**  
***Drosophila pseudoobscura***

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Izvod

Polimorfizam hromozoma prisutan u populacijama nekoliko vrsta *Drosophila* može biti povezan sa promenama u vremenu ili ekološkom parametru. Cilj ovog rada je da se proceni dugoročni efekat klimatskih promena na frekvencije hromozomskih aranžmana *D. pseudoobscura*. Ispitivana populacija se nalazi u šumi u blizini Tulansinga, Meksiko, a hromozomska analiza se proučava više od 35 godina. Za procenu promena korišćene su relativne frekvencije pronađene u tom periodu. Klimatski podaci Nacionalne meteorološke službe prikupljeni su za period od 1974. do 2011. godine. Višestrukom analizom varijanse analiziran je odnos između promena u frekvencijama hromozomskog rasporeda i različitih klimatskih varijabli (maksimalne i minimalne temperature, isparavanja i pluvijalnih padavina). Rezultati su pokazali značajnu korelaciju nekoliko rasporeda gena sa jednom ili više hidroklimatskih varijabli koje modifikuju genetsku strukturu prirodne populacije. Poređenja sa drugim populacijama su prikazana i omogućavaju utvrđivanje uticaja klimatskih promena na genetsku strukturu prirodnih populacija.

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