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Four decades of inversion polymorphism in *Drosophila pseudoobscura*

(evolution/genetic change/chromosome inversions)

WYATT W. ANDERSON[a], JONATHAN ARNOLD[a], DAVID G. BALDWIN[b], ANDREW T. BECKENBACH[c], CELESTE J. BROWN[a], STEPHEN H. BRYANT[d], JERRY A. COYNE[e], LAWRENCE G. HARSHMAN[f], WILLIAM B. HEED[b], DUANE E. JEFFERY[g], LOUIS B. KLACZKO[h], BETTY C. MOORE[i], JEAN M. PORTER[a], JEFFREY R. POWELL[j], TIMOTHY PROUT[f], STEPHEN W. SCHAEFFER[k], J. CLAIBORNE STEPHENS[l], CHARLES E. TAYLOR[m], MONTE E. TURNER[n], GABRIEL O. WILLIAMS[g], AND JOHN A. MOORE[io]

[a]Department of Genetics, University of Georgia, Athens, GA 30602; [b]Department of Ecology and Evolution, University of Arizona, Tucson, AZ 85721; [c]Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6, Canada; [d]Department of Biology, California Polytechnic University, Pomona, CA 91768; [e]Department of Ecology and Evolution, The University of Chicago, Chicago, IL 60637; [f]Department of Genetics, University of California, Davis, CA 95616; [g]Department of Zoology, Brigham Young University, Provo, UT 84602; [i]Department of Biology, University of California, Riverside, CA 92521; [j]Department of Biology, Yale University, New Haven CT 06511; [m]Department of Biology, University of California, Los Angeles, CA 90024; [n]Department of Biology, University of Akron, Akron, OH 44325; [h]Departamento de Genetica, Universidade Estadual de Campinas, Campinas, Brazil; [k]Department of Biology, Pennsylvania State University, University Park, PA 16802; and [l]Laboratory of Viral Carcinogenesis, National Cancer Institute, Frederick, MD 21702

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ABSTRACT **We report data that continue the studies of Dobzhansky and others on the frequencies of third-chromosome inversions in natural populations of *Drosophila pseudoobscura* in North America. The common gene arrangements continue to be present in frequencies similar to those described four decades ago, and the broad geographic patterns also remain unchanged. There is only one pronounced trend over time: the increase in frequency of the Tree Line inversion in Pacific coast populations.**

For more than 40 years Dobzhansky and his associates have monitored the frequencies of third-chromosome inversions in natural populations of *Drosophila pseudoobscura* (1–5). This species, like many others in the genus, has an extraordinary amount of chromosome polymorphism. *D. pseudoobscura* and its sibling species *Drosophila persimilis* are polymorphic for several dozen third-chromosome inversions (with only one in common) and are fixed for single-inversion differences on the X, second, and fourth chromosomes. Since polymorphism must be a transient stage in the establishment of interspecific differences, long-term monitoring of gene arrangement frequencies may be useful in understanding this process. In addition, such surveys offer the possibility of documenting balancing selection as well as stasis or microevolution over long periods of human observation.

The third-chromosome inversions of *D. pseudoobscura* are identified by differences in the banding patterns of polytene chromosomes in the larval salivary glands. Molecular data suggest that each inversion has arisen only once and that the polymorphism is at least 1 million years old (6). Because the inversions are overlapping and show very little recombination in heterokaryotypes, they form semi-isolated gene pools and, hence, have become genetically differentiated (6). The inversions also differ in fitness, as documented by laboratory experiments and observations in nature of seasonal cyling and differential mating success of males (1, 7–9). However, the ecological interactions that maintain the polymorphisms in nature are unknown.

Almost all of the data on inversion frequencies in this species have come from Dobzhansky's studies of seasonal, annual, and geographic variation. Many localities (mainly in the western United States) were monitored at roughly 10-year intervals between 1936 and 1973, and a three-decade overview was published in 1975 (4). We report here the results of the latest survey, conducted in the early 1980s and covering 48 localities in the northern part of the species range. Our methods were the same as those employed in previous studies: freshly collected females were allowed to oviposit on medium, and the salivary gland polytene chromosomes were analyzed in one to eight larvae from each female. Occasionally, wild-caught males were mated to tester females and chromosomes were analyzed in a sample of larvae (4).

Table 1 gives the data from our survey, along with a summary of previous observations from these localities, which are described in previous surveys (1–4). Eight gene arrangements reach a frequency of at least 10% in some localities: ST, AR, CH, PP, TL, SC, OL, and EP. Inversions OL, SC, and EP are rare in many localities but consistently appear in large samples. Eighteen rare arrangements have been described, and two more are undescribed, giving a total of 28 inversions segregating in North America. Fig. 1 shows the diversity of gene arrangements within localities, given as a contour map, whereas Fig. 2 summarizes the common inversions in each population.

The most important conclusion to be drawn from these data is that during half a century the common inversions have continued to segregate within populations at fairly similar frequencies. The general geographic pattern has also remained similar. ST is in highest frequency in Pacific Coast populations, especially west of the Sierra Nevada, where AR, CH, and TL are also common. AR becomes the predominant inversion between the Sierra Nevada and the Rocky Mountains and shares prominence with PP at the eastern edge of the species distribution. CH is predominant in southern California. Finally, western California has remained the region of highest diversity.

Superimposed on this temporal stability are significant fluctuations in frequencies in some populations. These fluctuations, which have been seen in previous surveys (4), should be viewed with caution, for most populations were sampled only once in a given survey and seasonal variation has been seen in some localities (refs. 7 and 8; J.A.M., B.C.M., and C.E.T., unpublished data). This source of error does not apply, however, to broad regional changes over time. Dobzhansky (ref. 3, p. 823) noted that the frequency of the PP

Abbreviations: ST, standard; AR, arrowhead; CH, Chiricahua; PP, Pike's Peak; TL, Tree Line; SC, Santa Cruz; OL, Olympic; EP, Estes Park.

[o]To whom reprint requests should be addressed.

Table 1. Frequencies (in percent) of gene arrangements in *D. pseudoobscura* populations and *n*, the effective number of chromosomes on which they are based

Locality	Year	*n*	Frequency, %								
			ST	AR	CH	PP	TL	SC	OL	EP	Others
1. Lillooet, BC	1982	246	33.6	20.8	3.1	19.7	20.8			1.9	
2. Port Coquitlam, BC	1981	162	13.2	13.8	9.6	1.8	58.7		1.8	1.2	
3. Okanagan, BC	1940	30	36.7	46.7	10.0	3.3	3.3				
	1964	80	55.0	30.0	1.2	8.8	5.0				
	1972	160	54.4	31.9		0.6	13.1				
	1981	180	31.7	36.7	0.5	1.7	28.3		0.5	0.5	
4. Victoria, BC	1983	83	19.3	10.0	16.1	1.2	40.2		1.2	12.0	
5. Bellingham, WA	1980	92	20.7	19.6	8.7	9.8	39.1			2.2	
6. Methow, WA	1940	100	52.0	47.0	1.0						
	1964	208	79.3	17.8			2.9				
	1972	320	60.6	34.4		0.9	4.1				
	1981	228	46.1	34.2	0.9	1.3	15.8		0.4	1.3	
7. Seattle, WA	1940	44	52.3	11.4	29.5		6.8				
	1981	156	7.1	12.2	29.5	0.6	43.6		1.3	5.8	
8. Gaston, OR	1982	79	17.1	27.3	11.4	1.1	38.6			4.6	
9. Spray, OR	1940	88	25.0	56.8	11.4	4.5	2.3				
	1965	70	44.3	27.1	5.7	8.6	14.3				
	1972	148	17.6	29.1	5.4	10.8	37.2				
	1981–1982	185	12.1	46.5	2.3	6.1	24.7	0.5	0.5	7.4	
10. Kerby, OR	1940	64	18.8	53.1	18.8		7.8	1.6			
	1965	30	43.3	30.0	13.3	3.3	6.7	3.3			
	1981–1982	125	17.8	44.5	4.8	6.2	22.6		1.4	0.7	2.1 (KE)
11. St. Helena, CA	1940	108	35.2	20.4	11.1		17.6	12.0	2.8		0.9 (new)
	1957	200	51.0	19.5	2.0	5.0	13.5	7.5	1.5		
	1963	362	51.4	14.9	2.5	6.1	22.9	1.1	0.3	0.8	
	1971–1972	166	51.8	12.1	1.8	0.6	32.5	1.2			
	1980–1981	70	28.6	17.1	4.3	4.3	37.1	2.9	4.3	1.4	
12. Spieth Reserve, Davis, CA	1980	144	30.6	13.9	18.7	2.8	30.6		2.1	1.4	
	1981	180	41.1	10.0	5.0	1.7	33.3	1.1	4.4	3.3	
13. Georgetown, CA	1981	106	25.5	33.0	3.8	3.8	24.5		9.4		
14. Placerville, Camino, and Apple Hill,	1940	108	26.9	26.9	6.5		13.9	18.5	7.4		
CA	1957	300	57.0	15.0	1.3	12.0	4.3	9.0	1.3		
	1963	206	49.5	24.8	3.4	4.9	16.5		1.0		
	1979	82	11.0	9.8		14.6	37.8		12.2	14.6	
	1980–1982	242	30.2	19.4	5.3	9.9	22.7	0.8	7.8	4.8	
15. Berkeley, CA	1962–1964	5221	46.6	9.1	19.1	2.8	14.0	1.4	0.7	6.2	0.04 (EB, BE)
	1980–1981	202	34.2	6.4	14.9	1.5	31.2	1.0	2.5	8.4	
16. Mather, CA	1945	308	35.7	35.7	17.2		10.4	0.7	0.3		
	1957	316	45.3	33.2	3.8	9.8	6.3	1.6			
	1963	446	54.7	22.0	6.3	6.7	9.9		0.4		
	1971	390	34.3	33.1	11.5	2.8	17.2	0.3	0.5	0.3	
	1972	576	22.2	37.5	17.0	6.3	15.1	0.5	1.4		
	1974	746	29.5	32.6	6.6	6.4	19.2	3.2	2.6		
	1975	204	23.5	30.4	12.2	8.3	20.1	3.9	1.5		
	1976	222	18.0	38.3	14.0	4.5	21.6	1.4	1.8	0.4	
	1981	62	14.5	25.8	21.0	12.9	25.8				
17. Tassajara Hot Springs, Santa Lucia	1940	104	51.0	20.2	12.5		1.9	13.5	1.0		
Mountains, CA	1957	200	54.0	23.0	4.0	9.0	2.0	7.5	0.5		
	1962–1963	640	40.6	18.0	23.6	5.2	8.9	2.2	1.1	0.5	
	1972	296	52.3	11.1	26.6	0.3	7.4	2.0	0.3		
	1980	212	36.8	9.4	25.9		24.1	0.9	1.9	0.9	
18. Lone Pine Canyon, Inyo National	1938	94	21.3	56.4	18.0		3.2		1.1		
Forest, CA	1957	78	25.6	51.3	5.1	9.0	7.7	1.3			
	1963	38	65.8	13.2	7.9	5.3	7.9				
	1983	95	28.4	54.7	7.4	3.2	6.3				
19. Death Valley National Monument, CA											
19a. Wildrose Canyon, Panamint	1937	224	13.8	67.4	18.8						
Mountains	1940	360	30.8	44.4	21.1		3.1				0.6 (MA)
	1957	224	25.5	58.9	11.2	0.9	2.7	0.4			0.4 (MA)
	1963	132	24.3	40.9	5.3	12.9	16.7				
	1968	142	33.1	45.1	11.3	6.3	4.2				
	1972	96	37.5	38.5	13.6	3.1	7.3				
	May 1980	134	26.9	39.6	23.9	3.7	4.5		0.7	0.7	
	July 1980	124	48.4	30.6	16.9	0.8	3.2				

Table 1. (*Continued*)

Locality	Year	*n*	Frequency, %								Others
			ST	AR	CH	PP	TL	SC	OL	EP	
19b. Furnace Creek	1980	334	8.7	78.4	7.8	3.0	1.2			0.6	0.3 (FC)
20. China Ranch, Tecopa, CA	1981	234	15.8	67.5	7.7	3.4	4.7		0.4	0.4	
21. Santa Barbara, CA	1940	438	47.5	20.8	16.2		7.3	7.8	0.5		
	1963	332	56.6	15.1	7.2	7.2	11.4	2.4			
	1973	204	52.9	10.8	16.7	0.5	18.1	1.0			
	1981	312	22.4	6.4	35.3	1.0	24.7	1.0	2.6	6.7	
22. Santa Cruz Island, CA	1936	42	54.8	16.7				28.6			
	1940	72	43.1	18.1	6.9			31.9			
	1963	400	62.2	12.8	9.8	1.2	4.8	7.2		2.0	
	1970	204	41.2	14.2	15.2	1.0	10.8	13.2	1.0	3.4	
	1980–1981	612	38.4	5.9	14.5	0.8	6.6	20.2	0.3	13.2	
23. San Gabriel Mountains, CA	1936–1937	101	34.7	27.7	26.7		10.9				
	1963–1964	134	68.7	16.4	7.5	0.8	6.7				
	1973	72	38.9	18.1	18.1	2.8	20.8				1.4 (SJ)
	1980–1981	155	26.5	3.9	52.9	3.2	12.3			1.3	
24. Riverside, CA	1963	124	68.5	10.5	8.1	2.4	5.6	4.0	0.8		
	1980–1981	386	32.9	11.6	37.8	2.1	14.8	0.2	0.2	0.1	
25. San Jacinto Mountains, CA											
25a. Pinyon Flats	1939–1942	3021	40.9	26.4	28.0		4.0	0.6			
	1952–1956	5702	47.7	21.5	15.4	8.7	5.3	0.7	0.6	0.1	
	1963	604	72.7	10.9	3.5	6.3	5.8	0.8			
	1970	1080	65.3	20.1	4.5	2.8	6.9	0.1	0.3		
	1978	201	58.2	18.4	10.5	2.0	9.5			1.5	
	1980	146	69.9	10.3	11.6	2.7	5.5				
25b. Keen Camp	1939–1940	4368	29.9	26.1	40.2		3.6	0.2			
	1948–1949	571	44.5	19.8	35.7						
	1955–1956	1838	33.6	25.8	32.5	5.3	2.8				
	1966	438	48.2	24.2	14.2	3.2	10.3				
25c. Indian Mountain	1974–1975	666	44.7	17.0	22.7	2.3	8.9	0.8	0.6	0.6	
25d. James Reserve	1978–1979	414	44.9	13.5	30.7	1.9	8.5	0.2		0.2	
25e. Andreas Canyon	1940–1942	782	58.7	25.8	12.5		2.9				
	1978–1979	86	55.8	16.3	11.6		16.3				
26. Anza Borrego State Park, CA	1938	132	53.8	30.3	13.6			2.3			
	1941	42	59.5	35.7	4.8						
	1966	200	69.5	16.0	3.0	2.0	9.0	0.5			
	1973	450	75.3	16.4	2.7	0.4	5.1				
	1981	223	76.7	5.8	6.3	0.5	10.3			0.5	
27. Lamoille Canyon, NV	1982	139	3.4	79.3	3.4	6.9	5.5				1.4 (TX, LA)
28. Lehman Caves National Monument,	1950	100	7.0	84.0	6.0	1.0				2.0	
NV	1963	318	7.5	86.5	0.6	4.1				1.3	
	1973	264	1.9	96.2	1.1	0.4	0.4				
	1980	241	3.5	94.2	0.6	1.2	0.3				0.3 (new)
29. Charleston Mountains, NV	1937	256	12.1	68.8	19.1						
	1955	126	24.6	55.6	9.5	6.3	4.0				
	1963	372	19.1	69.4	2.4	7.5	1.6				
	1972	200	23.0	64.5	10.5	1.0	1.0				
	1980	174	17.8	58.6	13.8	4.0	2.9		0.6	1.7	0.6 (CM)
30. Ferron, UT	1950	110	6.4	87.3	4.5	1.8					
	1965	54	5.6	81.3	1.9	9.3	1.9				
	1980	132		94.1	3.7						2.2 (EM, FE)
31. Bryce Canyon National Park, UT	1940	100	2.0	96.0	2.0						
	1950	84	4.8	92.9	2.4						
	1957	190	2.6	93.2	1.6	2.6					
	1965	200	2.5	92.0	4.0	1.5					
	1973	136	0.7	99.3							
	1978	880	0.6	97.6	1.6		0.1				0.1 (BR)
32. Betatakin, AZ	1957	200	3.0	96.5		0.5					
	1980	191	2.0	91.3	4.1	0.5	2.0				
33. Grand Canyon National Park, AZ	1940	100	1.0	98.0	1.0						
	1957	200	5.5	91.0	2.5	1.0					
	1965	200	2.5	96.5		0.5	0.5				
	1973	244	2.5	94.3	2.5	0.8					
	1980	245	0.8	98.4		0.4	0.4				
34. Flagstaff, AZ	1940	100	1.0	97.0	1.0	1.0					
	1957	200	6.5	89.0	2.0	2.5					

Table 1. (*Continued*)

Locality	Year	*n*	Frequency, %								
			ST	AR	CH	PP	TL	SC	OL	EP	Others
	1965	200	0.5	96.0	1.5	1.5					0.5 (new)
	1973	206		95.1	4.9						
	1980	132		95.3	4.0	0.7					
35. Prescott, AZ	1940	100	11.0	79.0	9.0	1.0					
	1957	200	23.0	71.5	3.5	2.0					
	1963	412	10.4	82.3	5.1	2.2					
	1973	238	5.0	86.6	8.0		0.4				
	1980	178	4.5	91.6	3.9						
36. Tempe, AZ	1981	203	0.5	90.7	8.8						
37. Organ Pipe National Monument, AZ	1971	42	7.1	90.5		2.4					
38. Sonoita, AZ	1941	42	7.1	59.5	33.3						
	1957	200	2.0	80.0	15.0	3.0					
	1965	200	6.5	77.5	11.5	4.0	0.5				
	1973	122	0.8	86.1	9.0	3.3					
	1980	159	4.8	78.6	12.5	4.2					0.8 (SO)
39. Chiricahua Mountains, AZ	1940	192	0.5	88.5	6.3	4.2	0.5				
	1957	400	0.2	85.0	11.5	2.5	0.2				0.5 (CC)
	1959	200		84.0	11.5	4.0					0.5 (CC)
	1964	198	1.5	88.9	6.1	3.0	0.5				
	1973	262	0.4	92.4	4.9	2.3					
	1980	275		85.1	11.4	2.8		0.5			0.3 (EM)
40. Muggins Gulch and Rist Canyon, CO	1941	64	4.7	17.2		57.8	7.8			12.5	
	1965	449	4.7	49.9		28.5	10.9			5.1	0.9 (CH, OL, SC)
	R 1968–1970	450	6.4	34.9		29.3	14.9			9.6	4.9 (CH, OL, SC)
	M 1969–1970	410	3.4	34.6		37.3	15.4			6.3	2.9 (CH, OL, SC)
	1980	41	4.7	46.5		16.3	25.6		2.3	4.7	
41. Black Canyon of the Gunnison National Monument, CO	1950	152	3.3	81.6		8.6	1.3			5.3	
	1964	182	5.0	94.4		0.6					
	1981–1982	399	1.2	72.5	0.5	11.4	5.9	0.2		8.3	
42. Rocky Mountain Biological Lab., CO	1970	48	4.2	83.3		6.2	4.2			2.1	
	1980	128		94.5	1.6	2.3	0.8	0.8			
	1981	74	2.7	73.0		12.2	9.5			2.7	
43. Hayden Creek, CO	1950	24		41.7		20.8	29.2		4.2	4.2	
	1964	180	17.2	47.2	2.2	25.0	1.7			6.7	
	1982	122	0.7	67.1	2.1	26.7	2.1				1.4 (HC)
44. Mesa Verde National Park, CO	1940	100		100.0							
	1957	200		96.5		1.5				0.5	1.5 (CC)
	1964	206	1.9	97.6		0.5					
	1980–1981	147		98.5		1.5					
45. Raton, NM	1940	100		78.0	1.0	20.0	1.0				
	1964	200	0.5	78.0	1.5	19.0	1.0				
	1980	184		72.6	3.7	22.0	0.6				1.2 (CU)
46. Capitan, Hondo, Ruidoso, and Lincoln, NM	1941	142		56.3	7.0	35.2	1.4				
	1964	82	2.4	69.5	1.2	25.6	1.2				
	1965	200	2.5	42.0	1.0	47.5	2.0			5.0	
	1969	376	0.3	57.7	2.9	35.9	1.1		1.9	0.3	
	1970	310	1.6	68.7	3.2	25.5			0.6	0.3	
	1980	247	0.7	81.1	4.2	11.7	0.7	0.4		0.4	0.8 (SO, RU)
47. Marfa and Davis Mountains, TX	1939–1941	148	1.4	33.8	3.4	56.1	4.7			0.7	
	1964	200		15.0	1.5	82.5				1.0	
	1973	224	0.5	32.6	2.2	61.6	2.7		0.4		
	1982	288		33.0	4.6	57.8	3.0	0.7	0.3	0.7	
48. Austin, TX	1939–1941	1279		20.6		71.0	6.3		1.5	0.7	
	1953	200	2.0	38.5		54.5	4.0			0.5	0.5 (TX)
	1964	300	2.6	16.4		72.0	3.5		4.3	1.3	
	1982	176		21.0	0.6	66.3	5.5	0.6	5.5		0.6 (HI)

See refs. 10 and 11 for discussion of *n*. In addition to the eight principal gene arrangements [Standard (ST), Arrowhead (AR), Chiricahua (CH), Pike's Peak (PP), Tree Line (TL), Santa Cruz (SC), Olympic (OL), and Estes Park (EP)], others in low frequency are listed under "Others." These include some previously described: Berkeley (BE), Cochise (CO), Cuernavaca (CU), East Bay (EB), Hidalgo (HI), Mammoth (MA), San Jacinto (SJ), Sonoita (SO), and Texas (TX). Many new arrangements were encountered and some of these have been given working names: Bryce (BR), Charleston Mountains (CM), Emory (EM), Fort Collins (FC), Ferron (FE), Hayden Creek (HC), Lamoille (LA), Ruidoso (RU). Other undiagnosed new arrangements were from St. Helena (locality 11), Lehman Caves (locality 28), and Flagstaff (locality 34).

inversion increased in many California localities in earlier surveys, but its frequency has since declined (4). The one clear directional trend in our data is the continuing increase in the frequency of TL along the entire Pacific coast, a pattern noted in 1975 (4). As Fig. 3 indicates, this trend has continued in 13 of our 16 west coast populations. With the exception of PP,

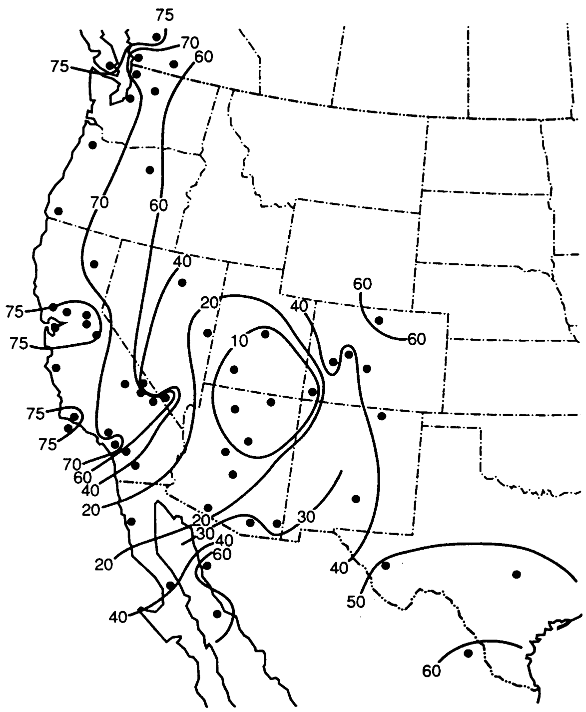

FIG. 1. Inversion diversity measured as $H = 1 - \Sigma p_i^2$, where p_i is the frequency of the *i*th inversion. The Mexican sites indicated are from earlier surveys and are not in Table 1.

none of the other common gene arrangements has shown such a trend over the four decades of sampling.

Apart from the recent change in the frequency of TL, inversions in North American populations of *D. pseudoobscura* constitute many locally stable polymorphisms with pronounced differentiation across the species range. The field and laboratory evidence that the inversions differ in fitness implies that the local stability probably results from

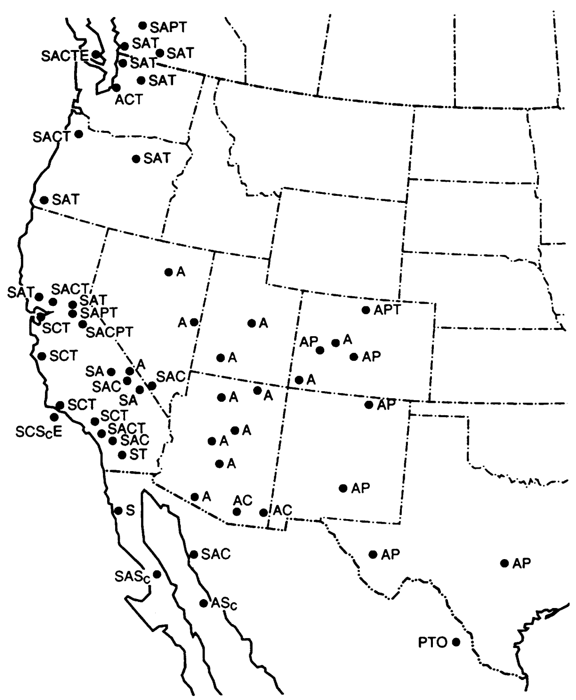

FIG. 2. Inversions >10% in each site. Inversion identity is given by the first letter of the two-letter acronym except for SC, which is denoted by Sc. For Mexican sites, see Fig. 1 legend.

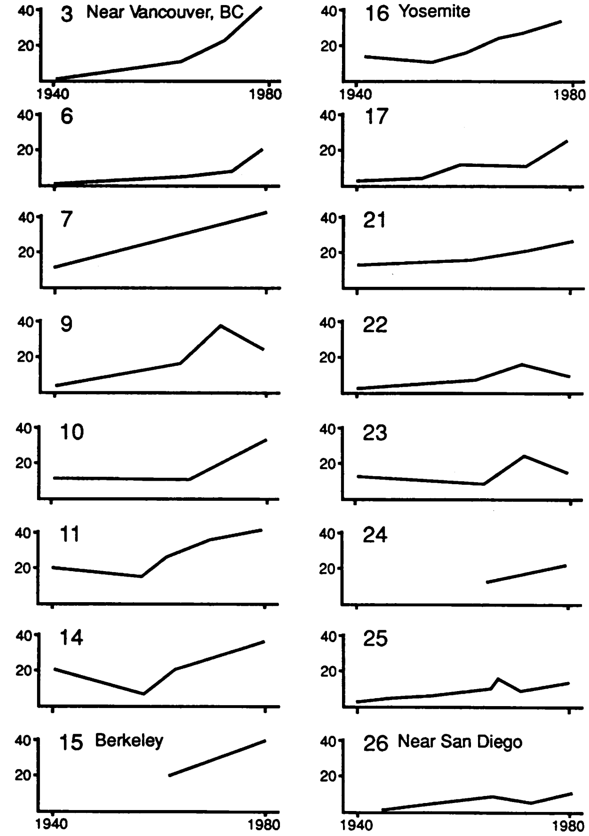

FIG. 3. Frequency of TL on the west coast. On each graph the ordinate is % TL and the abscissa is years with 1940 and 1980 as indicated. Site numbers from Table 1 are given.

balancing selection. The relative stability is also indicated by the 1- to 2-million-year age of the system estimated from molecular analysis (6). The causes of the differentiation among populations remain a mystery.

The increase in frequency of TL may be due to an environmental change favoring carriers of TL or to the occurrence of a new favorable mutation linked to the arrangement. Further monitoring of natural populations combined with laboratory experiments may reveal the bases for stable polymorphism, geographic variation, and temporal changes in the frequency of these inversions.

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