Table 1 *Per cent inhibition of photosynthesis by simazine, butachlor and glyphosate in rice, maize, soybean and groundnut leaf discs*

Herbicide	Concentration (ppm)	Rice (IET-7633)	Maize (VL-16)	Soybean (Lee)	Groundnut (JL-24)
Simazine	0	—	—	—	—
	3	—	25	33	—
	6	—	37	50	30
	9	20	45	60	60
	12	50	50	70	70
Butachlor	0	—	—	—	—
	80	20	35	20	20
	160	40	45	50	50
	400	70	50	70	60
	800	90	60	100	70
Glyphosate	0	—	—	—	—
	80	—	35	60	—
	160	30	45	70	—
	400	40	50	80	20
	800	60	60	100	60

Butachlor showed a decreasing order of inhibition in soybean, rice, groundnut and maize at higher concentrations. However, at 80 ppm the adverse effect was maximum in maize leaf disks. Similarly the total weed killer glyphosate showed the highest degree of inhibition in soybean (80%). Inhibition in these cases is mainly at the PS II system through uncoupling or inhibition of electron acceptance and transport mechanisms as well as inhibition of CO_2 uptake[4].

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1. Moreland, D. E. and Hitlon, J. L., *Herbicides—Physiology, biochemistry and ecology*, 1976.
2. Bielecki, K., Doroszeweez, H., Grzys', E. and Szuwalaska, Z., *Acta Agron. Bot.*, 1985, 35, 123.
3. Ashton, F. M. and Crafts, A. S., *Mode of action of herbicides*, 1973.
4. Ciannopolitics, C. N. and Ayers, G. S., *Weed Sci.*, 1978, 26, 440.
5. Ashton, F. M., Gifford, E. M. and Bisalputra, T., *Bot. Gaz.*, 1963, **124**, 336.
6. Hill, E. R., Putala, E. C. and Vengris, J., *Weed Sci.*, 1968, **16**, 377.
7. Baird, D. D. and Upchurch, R. P., *Proc. 23rd southern weed control conference*, 1970, p 101.

GENETIC VARIATION AT ALCOHOL DEHYDROGENASE LOCUS IN SOME DROSOPHILIDS

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MEASURING the patterns and amounts of genic variation in natural populations of diverse organisms is the major thrust of experimental population genetics[1-3]. Allozymic (allelic isozyme) variations detected by gel electrophoresis have been used to assess the extent of genetic variability in species populations. Alcohol dehydrogenase (ADH, EC 1.1.1.1) constitutes an important gene–enzyme system in *Drosophila* because of its role in detoxification and/or utilization of alcohol in the natural habitat of the organism[4]. Several field and empirical studies have been made on ADH polymorphism in *D. melanogaster* but information about this enzyme in other drosophilids is scanty[5-7]. The present investigation was undertaken to examine the extent of electrophoretic variation of ADH in some drosophilids.

Individuals of species *D. melanogaster*, *D. takahashii*, *D. nepalensis*, *D. malerkotliana*, *D. bipectinata*, *D. ananassae*, *D. jambulina*, *D. punjabiensis*, *D. immigrans*, *D. busckii* and *Zaprionus indianus* were bait-trapped from Delhi, Rohtak, Pinjore, Jammu, Hasimara, Bagdogra and Dhulabari (Nepal). Labo-

ratory cultures of *Z. sepsoides* and *Z. tuberculatus* were also employed. Wild caught males and F_1 individuals from species-specific isofemale lines were analysed electrophoretically. In order to compare electrophoretic patterns, individuals belonging to different subgenera (*Sophophora*, *Dorsilopha* and *Drosophila*) were included in the same gel. Each horizontal 12% starch gel slab measured 15 × 10 × 1 cm and could accommodate 12–14 samples. Homogenates of single individuals were subjected to electrophoresis at 250 V and 25 mA at 4°C for 3.5 h. Gel slices were stained for the related and overlapping enzyme systems ADH, octanol dehydrogenase (ODH) and aldehyde oxidase (AO) by standard staining procedures[8,9]. The gel slices stained for ADH revealed three zones of activity due to non-specificity and overlapping band patterns of alcohol-oxidizing enzymes (ADH, AO and ODH). On the basis of comparison of gel slices stained for ADH, AO and ODH, it was found that ODH and AO constitute the two anodal zones while the single cathodal zone is true ADH. Genetic control of ADH electromorphs or banding patterns in each species was interpreted from the segregation patterns of ADH electromorphs of parents, and F_1 and F_2 progeny of several single-pair matings. The genetic interpretation of banding patterns and calculation of genetic indices such as allelic frequency, heterozygosity and effective number of alleles were done following a standard source[10]. The log-likelihood χ^2 test (*G*-test) was used to assess whether the observed genotypes were in agreement with those expected on the basis of Hardy–Weinberg equilibrium.

The electrophoretic mobility patterns of ADH are species-specific (figure 1). The ADH zymograms of three species (*D. jambulina*, *D. punjabiensis* and

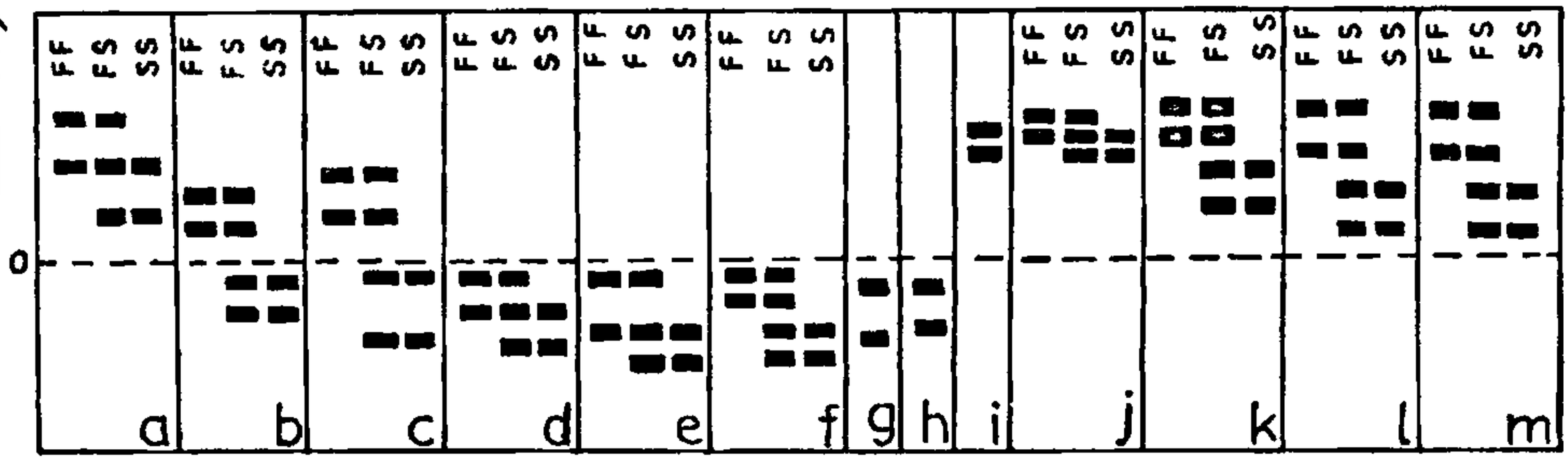

Figure 1. Electrophoretic phenotypes of ADH in homogenates of single individuals of drosophilids (a–m). In species polymorphic for ADH, band patterns in first and third slots represent different homozygous genotypes (FF and SS) while that of the second slot represents heterozygous ADH genotype (FS). Differential binding of coenzyme (NAD) causes two-band patterns in homozygotes. a, *D. melanogaster*; b, *D. takahashii*; c, *D. nepalensis*; d, *D. malerkotliana*; e, *D. bipectinata*; f, *D. ananassae*; g, *D. jambulina*; h, *D. punjabiensis*; i, *D. immigrans*; j, *D. buschii*; k, *Z. indianus*; l, *Z. sepsoides*; m, *Z. tuberculatus*.

Table 1 *Inheritance patterns of polymorphic alcohol dehydrogenase electromorphs in ten drosophilids. Genetic crosses were intra-species*

ADH phenotype of genetic cross	No. of matings	ADH phenotype of progeny			Sample size	Test for Mendelian ratios	χ^{2*}
		FF	FS	SS			
FF × SS	2	—	46	—	46	—	—
FS × FS	3	28	66	34	128	1:2:1	0.75
FS × SS	2	—	38	44	82	1:1	0.43
SS × FF	1	—	27	—	27	—	—
FS × FF	2	33	29	—	62	1:1	0.26
FS × FS	2	35	79	38	152	1:2:1	0.47
SS × FS	1	—	18	22	40	1:1	0.40

FF and SS are fast and slow electrophoretic variants represented by two-banded patterns; *Non-significant at 5% level.

Table 2 *Observed ADH genotypes, allelic frequencies, heterozygosities, effective numbers of alleles (n_e) and G values (log-likelihood χ^2 test) for Hardy–Weinberg expectations at the ADH locus in different drosophilids*

Species	ADH genotypes							Sample size	Allelic frequencies				Heterozygosity		n_e	G value
	1,1	2,2	3,3	4,4	1,2	2,3	3,4		1	2	3	4	Obs.	Exp.		
D. melanogaster	8	60	—	—	40	—	—	108	0.26	0.74	—	—	0.37	0.38	1.62	0.14
D. takahashii	—	84	6	—	—	24	—	114	—	0.84	0.16	—	0.28	0.27	1.36	2.85
D. nepalensis	—	116	12	—	—	48	—	176	—	0.80	0.20	—	0.27	0.32	1.47	4.3
D. malerkotliana	—	—	8	70	—	—	36	114	—	—	0.23	0.77	0.31	0.36	1.55	1.10
D. bipectinata	—	—	12	54	—	—	40	106	—	—	0.30	0.70	0.38	0.42	1.73	1.19
D. ananassae	—	—	16	60	—	—	48	124	—	—	0.32	0.68	0.38	0.44	1.77	1.61
D. jambulina	—	—	109	—	—	—	—	109	—	—	1.0	—	—	—	1.0	—
D. punjabiensis	—	—	102	—	—	—	—	102	—	—	1.0	—	—	—	1.0	—
D. immigrans	121	—	—	—	—	—	—	121	1.0	—	—	—	—	—	1.0	—
D. busckii	4	92	—	—	4	—	—	100	0.06	0.94	—	—	0.04	0.11	1.13	18.4*
Z. indianus	6	113	—	—	86	—	—	205	0.24	0.76	—	—	0.41	0.38	1.57	3.91
Z. tuberculatus	16	32	—	—	40	—	—	88	0.41	0.59	—	—	0.45	0.48	1.94	0.31
Z. sepsoides	16	26	—	—	30	—	—	72	0.43	0.57	—	—	0.41	0.49	1.96	1.71

*Significant at 1% level; Other G values are non-significant.

D. immigrans) show two-banded phenotypes. Electrophoretic analysis of parents and progeny of several single-pair matings in these species revealed that the two-banded ADH phenotypes do not show any segregation behaviour and thus represent a monomorphic zone of ADH activity. In the other ten species, the species-specific homozygous phenotypes are represented by two-banded ADH patterns of either faster mobility (FF) or slower mobility (SS) (figure 1). Segregating two-banded (FF and SS, with one band of each having the same mobility) and three-banded patterns were observed in four species (*D. melanogaster, D. malerkotliana, D. bipectinata* and *D. busckii*). Genetic crosses involving segregating two-banded patterns in these species resulted in three-banded patterns in F_1 and a 1:2:1 ratio of segregating two-banded and three-banded patterns in F_2 progeny. The other six species showed two-banded (FF and SS, with both bands of each having non-overlapping mobilities) and four-banded patterns (figure 1). In these species, genetic crosses involving segregating two-banded patterns resulted in four-banded patterns in F_1 and a 1:2:1 ratio of segregating two-banded and four-banded patterns in F_2 progeny (table 1). The electrophoretic data for these crosses are in agreement with monogenic control of ADH pattern. Thus homozygous individuals showing different two-banded patterns/electromorphs are allozymic variants. The observed ADH isozyme patterns are in sharp contrast to many other gene–enzyme systems where a single band represents an allelic isozyme or allozyme[2,3]. The present observations on ADH patterns in different drosophilids agree with other reports on *D. melanogaster*, i.e. in homozygous strains more than one electromorphs/bands may arise because of differential binding of the coenzyme NAD[11–15].

The distribution of ADH genotypes, allelic frequencies, observed and expected heterozygosity, effective number of alleles and log-likelihood χ^2 test for fit to Hardy–Weinberg expectations at the ADH locus in various drosophilids are given in table 2. The ADH locus is effectively polymorphic in ten drosophilids on the basis of the criterion that the most common allele does not exceed 0.95. Except *D. busckii*, all the species polymorphic at the ADH locus show a fit to Hardy–Weinberg equilibrium and do not reveal rare alleles. Most of the species show occurrence of two common ADH alleles and high heterozygosity value. The maintenance of two common alleles at the ADH locus in several drosophilids may be explained on the basis of balancing natural selection. However, both field and laboratory studies on several eco-geographical populations of these drosophilids need to be analysed to assess the role played by evolutionary forces in the maintenance of genic diversity at the ADH locus.

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1. Karlin, S. and Nevo, E., *Evolutionary Processes and Theory*, Academic Press, New York, 1986.
2. Oxford, G. S. and Rollinson, D., *Protein Polymorphism: Adaptive and Taxonomic Significance*, Academic Press, New York, 1983.
3. Nevo, E., *Theor. Pop. Biol.*, 1978, **13**, 121.
4. Van Delden, W., *Evol. Biol.*, 1982, **15**, 187.
5. Kohane, M. and Parsons, P. A., *Heredity*, 1986, **57**, 289.
6. Parsons, P. A., *Evol. Biol.*, 1981, **14**, 297.
7. Parsons, P. A., *The Evolutionary Biology of Colonizing Species*, Cambridge University Press, New York, 1983.
8. Shaw, C. R. and Prasad, R., *Biochem. Genet.*, 1970, **4**, 297.
9. Chambers, G. K., McDonald, J. F., McElfresh, M. and Ayala, F. J., *Biochem. Genet.*, 1978, **26**, 757.
10. Hartl, D., *Principles of Population Genetics*. Sinuaer Associates, Sunderland, USA, 1980.
11. David, J., *Biochem. Genet.*, 1982, **20**, 747.
12. Cavener, D. R., and Clegg, M. T., *Proc. Nat. Acad. Sci.*, 1981, **78**, 4444.
13. Kreitman, M., *Genetics*, 1980, **95**, 467.
14. Sampsell, B. and Sims, S., *Nature* (*London*), 1982, **296**, 853.
15. Oakeshott, J. G., Gibson, J. B., Anderson, P. R., Knibb, W. R., Anderson, D. G. and Chambers, G. K., *Evolution*, 1982, **32**, 86.