The Susceptibility to Insecticides of Disease-carrying Mosquitos in Fiji

G. F. BURNETT 1 & L. H. ASH 2

The larvae and adults of five species of vector mosquitos in Fiji have been tested for susceptibility to chlorinated hydrocarbon insecticides by standard techniques. Four species of Aëdes, three of them endemic to the South Pacific, gave results not differing greatly from those found for members of the genus in other countries. Culex fatigans Weid was unusually susceptible as a larva but as an adult was normal.

A strain of A. pseudoscutellaris Theo. resistant to DDT as a larva was readily obtained by selective pressure, the LC_{50} being increased to some 2000 times that of a susceptible wild strain. There was no cross-resistance to BHC or dieldrin but adults of this strain showed a slightly increased tolerance to DDT. It is suggested that inheritance is monofactorial, that the gene is present at a low frequency in wild populations and is favoured by domestication or urban conditions. There are indications of physiological differences between resistant and susceptible individuals.

Two mosquito-borne diseases occur in Fiji: filariasis (Wuchereria bancroftii var. pacifica) and dengue. The former may be transmitted by four species (Symes, 1955): Aëdes (Stegomyia) pseudoscutellaris Theo., A. (S) polynesiensis Marks., A. (Findlaya) fijiensis, Marks., and Culex (C) fatigans Weid. Dengue is assumed to be transmitted by A. (S) aegypti Linn. and it was included in these experiments because it is widespread and frequently used in laboratories, whereas the other Aëdes are endemic to the South Pacific and two of them to Fiji alone (A. pseudoscutellaris and A. fijiensis).

NORMAL LARVAE

These tests were started before the World Health Organization issued its recommendations on larval test procedure (WHO Expert Committee on Insecticides, 1958), but in order to make them comparable with at least some made elsewhere, the method described by Wharton (1955) was used as a model. Suspensions of insecticide in water were prepared by running from a pipette, with constant stirring, solutions in acetone (later, ethanol) into rain water. The concentrations of the solutions were such that 0.25-0.5 ml were required in 200 ml of

water. The necessary amount was mixed with 190 ml of water in half-pint glass tumblers, which gave about 30 cm² of surface. Twenty early fourth-stage larvae in 10 ml of water were added within five minutes of mixing. At the same time controls were set up with 0.5 ml acetone or ethanol. The larvae were left in the suspensions for 24 hours, after which mortality counts were made. If more than 10% of the controls had pupated the results of the experiment were rejected. It was found that if the larvae were removed to clean water and kept for another 24 hours, dieldrin often caused an increased mortality but this was irregular and many larvae pupated. and for this reason 24-hour mortalities were used for all insecticides. Larvae were counted as dead if they could not swim in a controlled manner when prodded by a blunt needle. Such insects rarely or never recovered whereas some which could not react to a light at 24 hours recovered later. Wild-caught larvae were used for the four Aëdes; Culex fatigans were reared from wild eggs. A minimum of six replicates was used at each concentration, except in the case of A. polynesiensis which was difficult to obtain in large numbers at this period, and for which only five replicates could be used for dieldrin and BHC. Laboratory temperatures could not be controlled but were recorded. Maxima varied from 25°C to 30°C and minima from 20°C to 26°C, the daily range not exceeding 5°C.

¹ Colonial Pesticides Research Unit, Arusha, Tanganyika. The work reported was carried out during the author's period of secondment as Officer in Charge, Filariasis Research, Fiji.

¹ Health Inspector, Medical Department, Fiji.

Results

Mortalities were corrected (Abbott, 1925) for control deaths, which were usually exceedingly low, before plotting on log-probit paper. In some species considerable batch variation (not necessarily seasonal) was encountered and this made it difficult to obtain good regression lines, because a range of concentrations which bracketed the LC₅₀ in a preliminary test might cover only one end of the dosagemortality curve of the next batch. The difference in LC₅₀ was not more than twofold and the probit regression lines appeared parallel, but the difficulty of obtaining several hundred larvae, all of species which, except for C. fatigans, are small-container breeders, prevented the regular extension of the range of concentrations tested. The principal reason for this batch variation is thought to be the physiological age of the larvae (Parker, 1957). It was absent in A. fijiensis, which has a very slow development and spends over a week as a fourth-instar larva, but pronounced in the others, which passed through the instar in some 48 hours. Because of these batch variations and the generally low degree of scatter of the data it was not thought worth while to calculate probit lines (except for particular comparisons) and LC₅₀'s and LC₉₀'s (Table 1) have been read from provisional lines drawn by eye (Fig. 1-3).

Discussion

Comparable figures for A. aegypti and C. fatigans are available from various parts of the world, and some are summarized in Tables 9 and 11 of Brown

TABLE 1

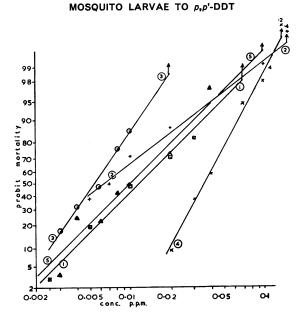
DOSAGE-MORTALITY DATA FOR LARVAE OF
FIVE SPECIES OF FIJIAN VECTOR MOSQUITOS,
EXPRESSED IN PARTS PER MILLION OF INSECTICIDE
SUSPENDED IN WATER⁴

Species	р-р'-	DDT	Die	ldrin	у-ВНС		
	LC50	LC90	LC50	LC90	LC50	LC90	
A. pseudoscutellaris	0.006	0.028	0.006	0.011	0.020	0.046	
A. polynesiensis	0.005	0.012	0.006	0.012	0.009	0.020	
A. fijiensis	0.36	0.65	0.005	0.018	0.007	0.029	
A. aegypti	0.012	0.036	0.008	0.010	0.010	0.026	
C. fatigans	0.012	0.027	0.004	0.008	0.008	0.024	

a Experiments conducted from January to April 1957 and from December 1957 to June 1958.

FIG. 1

DOSAGE-MORTALITY RELATIONS OF FIJIAN VECTOR



Line 1 and 🖸 = Aëdes aegypti.

Line 2 and + = Aëdes pseudoscutellaris.

Line 3 and \odot = Aëdes polynesiensis.

Line 4 and \times = Aëdes fijiensis.

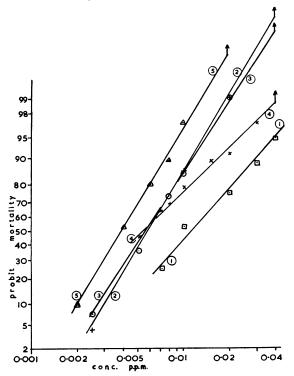
Line 5 and $\triangle = Culex fatigans$.

(1958). Fijian A. aegypti have a susceptibility to DDT and dieldrin of the same order of magnitude as susceptible strains elsewhere and are considerably more sensitive to γ -BHC. Fijian C. fatigans are extremely susceptible to DDT compared with all other strains reported except that from Lamir, Malaya (Wharton, 1958), which was about twice as susceptible. To dieldrin they have a normal susceptibility and to γ -BHC they are more susceptible than the majority of populations measured. The other three species are endemic to the South Pacific and no comparable figures have been seen. A. pseudoscutellaris and A. polynesiensis are closely related (their specific identity is not universally accepted), but although their response to dieldrin is almost identical (tested statistically by the method of Litchfield & Wilcoxon, 1949), they differ in their reaction to DDT and y-BHC. A. pseudoscutellaris readily develops a strong resistance to DDT (see later), and it is possible that the presence of the gene for this resistance is responsible for the much steeper regression line for this species. With γ -BHC the two

FIG. 2

DOSAGE-MORTALITY RELATIONS OF FIJIAN VECTOR

MOSQUITO LARVAE TO DIELDRIN



For key, see Fig. 1.

species give parallel lines and the difference in LC_{50} may be due in part at least to batch variation; another test on A. pseudoscutellaris, using only three replicates, gave the lower figure for LC_{50} of 0.016 p.p.m. A. fijiensis is naturally unusually tolerant to DDT but not to the other insecticides. Owing to its habitat (the leaf axils of large Pandanus palms) it is unlikely to be subjected to insecticide attack as a larva.

ADULTS

The Busvine-Nash technique was used (as modified by Busvine and advocated by the WHO Expert Committee on Malaria, 1954). Adult females 2-4 days after emergence were used, fed on 5% sugar-water but not blood, because blood-feeding gave much higher control mortalities, especially of *Culex fatigans*, which was in any case a shy blood-feeder in cages.

Three species were tested with both DDT and dieldrin. C. fatigans was raised from wild eggs,

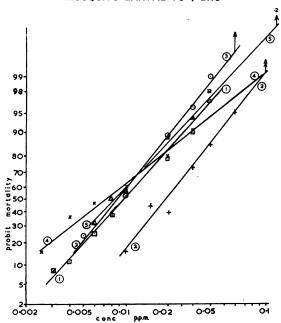
A. pseudoscutellaris from wild larvae and A. fijiensis from wild pupae because of heavy mortality on emergence of adults collected as larvae. Large numbers of pupae were not easy to obtain in a short period and only 200-300 adults of this species were available for each test. Adult females of A. polynesiensis, the fourth vector of filariasis (Symes, 1955) cannot be distinguished with certainty from those of its sister species A. pseudoscutellaris, and it was difficult to obtain at this time in its immature stages. Only one test was made, with DDT, using small numbers of insects. Neither of these two species is likely to be attacked as an adult with insecticides. A. aegypti, from wild larvae, was tested against DDT. BHC was not included in the tests; its use in control in Fiji is unlikely.

Results

Results after adjustment for control mortalities (Abbott, 1925) were plotted on log-probit paper and regression lines drawn by eye (Fig. 4). The lines have been analysed by the nomographic method of Litchfield & Wilcoxon (1949). The results of this analysis are given in Table 2.

FIG. 3

DOSAGE-MORTALITY RELATIONS OF FIJIAN VECTOR MOSQUITO LARVAE TO γ -BHC



For key, see Fig. 1.

TABLE 2						
DOSAGE-MORTALITY DATA	FOR ADULTS (OF FIVE SPECIES OF FIJIAN	VECTOR MOSQUITOS,			
EXPRESSED	AS PERCENTAG	GE INSECTICIDE IN RISELLA	OIL a			

Species	No. specimens (excl. control)	Control mortality		DDT		Dieldrin			Potency os	95 % FL	
		(%)	LC50	95 % FL ^c	LC:	LC50	95 % FL ¢	LC:	ratio	93 % FL	
A. pseudoscutellaris	569; 521	12	7	0.72	0.64-0.81	2.3	0.124	0.11-0.14	0.49	5.80	4.83-6.95
A. polynesiensis	92	4		0.70	0.52-0.95	1.9					
A. aegypti	238	0		1.28	1.07-1.53	4.4ª					
A. fijiensis	185; 224	0	0	0.24	0.17-0.33	0.96	0.054	0.041-0.071	0.21	4.35	2.83-6.70
C. fatigans	641; 822	4	0	9.8 đ	6.5-10.4	150 d	0.68	0.58-0.80	6.2 d	14.4	1.1-1.95

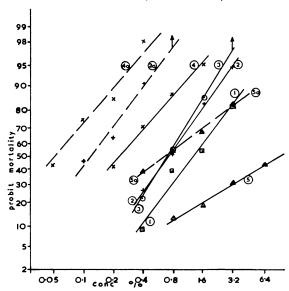
a Experiments, using the Busvine-Nash technique, conducted from February to July 1959.

FIG. 4

DOSAGE-MORTALITY RELATIONS OF FIJIAN VECTOR

MOSQUITO ADULTS TO DDT (CONTINUOUS LINES)

AND DIELDRIN (BROKEN LINES) ^a



 a A concentration of 6.4 % DDT in Risella oil is not obtainable, and the mortality illustrated at this concentration was obtained by 2 hours' exposure to 3.2 % DDT.

Line 1 and 🖸 = Aëdes aegypti.

Lines 2 & 2a and + = Aëdes pseudoscutellaris.

Line 3 and \odot = Aëdes polynesiensis.

Lines 4 & 4a and X = Aëdes fijiensis.

Lines 5 & 5a and $\triangle = Culex \ fatigans$.

Discussion

All the regression lines for the four species of Aëdes to both insecticides are parallel statistically; the two lines for C. fatigans are also parallel. All potency ratios (i.e., ratio of the LC₅₀'s for the two insecticides) for individual species are significant at P=0.05. The responses of A. pseudoscutellaris and A. polynesiensis to DDT are statistically indistinguishable. This is interesting in view of their different response as larvae (see previous section), for the adults and larvae used in these tests had the same origins. A. fijiensis is significantly more sensitive than A. pseudoscutellaris to both DDT and dieldrin (potency ratios 3.1 and 2.3; 95% fiducial limits 2.0-4.81 and 1.7-3.9 respectively) and than A. aegypti to DDT (potency ratio 5.6)—in fact this species is unusually susceptible for a culicine adult (Wharton, 1955; Busvine, 1956; Brown, 1958). The sensitivity of A. pseudoscutellaris to these two insecticides is very similar to that of susceptible A. aegypti in other parts of the world (Wharton, 1955; Busvine, 1956), but Fijian A. aegypti are rather less susceptible to DDT—and significantly less so than A. pseudoscutellaris (potency ratio 1.76; 95% fiducial limits 1.42-2.18). Culex fatigans is, as in most places, not susceptible to DDT (Wharton, 1955; Hamon et al., 1958; Brown, 1958). To dieldrin it is more susceptible although rather less so than the susceptible Malayan strain (Wharton, 1955, 1958), and about the same as Hamon et al. (1958) found in West Africa. In Tanganyika, Smith (1958) found C. fatigans considerably more susceptible to both DDT and

^b The left-hand column represents the percentage mortalities in the DDT series controls, and the right-hand column those in the dieldrin series controls.

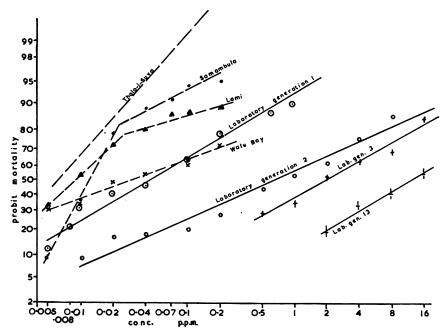
c FL = Fiducial limits.

d Extrapolated.

FIG. 5

DOSAGE-MORTALITY RELATIONS TO DDT OF VARIOUS SAMPLES OF DDT-RESISTANT AËDES

PSEUDOSCUTELLARIS LARVAE, WITH A SUSCEPTIBLE STRAIN (THOLO-I-SUVA) FOR COMPARISON 4



a Continuous lines are used for the laboratory strain and broken lines for wild strains.

dieldrin. The two regression lines for C. fatigans are parallel, but steeper than those for the species of Aëdes. The high LC₉₀, even for dieldrin (6.2%), suggests that there is a good chance of survivors among C. fatigans which enter houses treated with this insecticide, the LC₉₉ being of the order of 250% (if that were possible). If a small proportion of each generation of insects survives entrance to treated houses there is scope for the appearance of that type of resistance most frequently produced in the laboratory and which requires selection over a number of generations before it becomes marked (see the discussion in Brown, 1958, p. 25 et seq.). The steeper response of the other species tested makes it easier to obtain complete kills. Thus it appears possible that Fijian C. fatigans may have the potentiality of becoming resistant to dieldrin, as the species has elsewhere (Wharton, 1958; Floch & Fauran, 1958; Smith, 1958; Hamon et al., 1958).

DDT-RESISTANT AEDES PSEUDOSCUTELLARIS

In January 1957 some preliminary tests were done on the larval susceptibility to insecticides of the

Aëdes pseudoscutellaris colony maintained at the Filariasis Research Unit, Fiji, by Mr C. B. Symes (Symes, 1955). These gave good probit-mortality/ log-dosage regression lines, but that for DDT was unusually steep, and a concentration of 1 part per million gave only 90% kill (Fig. 5, laboratory generation 1; cf. Fig. 1, line 2). A number of samples of wild larvae from places near Suva (the locality of the laboratory) gave peculiar lines, some being straight but steep (Fig. 5, Walu Bay), others kinked in a way one would expect if the population tested was a mixture of two strains with very different responses to DDT (Fig. 5, Lami, Samambula). It was some time before apparently pure susceptible strains were found in the forest at Tholo-i-Suva (in the mountains some 15 km from the city of Suva), at Nukui (also 15 km away at the tip of the Rewa delta), and on Makogai, a small island 65 km from the main island of Viti Levu, on which Suva is situated (Fig. 5, Tholo-i-Suva).

The laboratory strain was selected for resistance to DDT by exposure to water suspensions of the insecticide as described at the beginning of this

Generation	LCso to DDT (p.p.m.)	Selection ^a	Mortality (%)	Remarks
1 "Laboratory"	0.044	at 0.1 p.p.m.	65	See Fig. 5.
2	0.65 (0.84) ^b	at 0.2 p.p.m.	27	See Fig. 5.
3	1.9	none	_	
4-7		none	_	0.1 p.p.m. killed 82 % of genera-
8, 9		0.2 in part		tion 7.
10		0.2	63	
11		2 p.p.m.	40 (approx.)	
12		not selected		
13	12.0	2 p.p.m.	19	See Fig. 5. Tested against DDT
14		2 p.p.m.		and BHC.
15		2 p.p.m	80, 16	In two batches of 2276 and 597
16		not selected		larvae.
17		2 p.p.m.	67, 67	In two batches of 826 and 233 larvae.
18		2 p.p.m.	51	Adults tested.

TABLE 3
HISTORY OF STRAIN OF AËDES PSEUDOSCUTELLARIS RESISTANT TO DDT AS LARVAE

paper. Details are given in Table 3. Dosagemortality regression curves were estimated when the condition of the colony permitted and at other times tests were made with samples at a single concentration of insecticide. Concentrations of over 16 p.p.m. were not used because of the rapid separation of crystals of insecticide. Some tests were made for cross-resistance to dieldrin and BHC and the last generation was tested for resistance as adults. The investigation was hampered by lack of facilities for laboratory work and the necessity of fitting in work on the colony with field work which had priority. Selection was interrupted for the 3rd to 7th generations by the absence from Fiji of one of the authors (G.F.B.) and on his return had to be halted at times in order to save the stock. This occurred for various reasons, sometimes for reasons of hygiene, sometimes on account of poor laying (generation 11), and sometimes on account of delayed death of larvae after removal to clean water. This was particularly important when attempts were made (twice) to increase selection pressure to 4 p.p.m. The expected 30% mortality was greatly exceeded in the sample tested (but see below). Work was brought to a close with the disbanding of the research unit in July 1959.

Results and discussion

Mortalities have been plotted on log-probit paper and regression lines drawn by eye and tested statistically by the method of Litchfield & Wilcoxon (1949). They are shown in Fig. 5 together with those of various wild samples, including the most susceptible strain found (Tholo-i-Suva). None of the resistant generations parallels this line but there are kinks in the lines of some of the wild samples and of generations 1 and 2 of the laboratory strain, and the lower portions of these lines are approximately parallel to the Tholo-i-Suva line. The angles of intersection of the segments of the kinked lines are too obtuse to give more than an approximate idea of the proportion of fully susceptible larvae in them, but the Samambula and Lami populations seem to be about 80% susceptible, the original laboratory stock about 35% and the 2nd generation about 16%. These last two lines show, rather indefinitely, a double break such as that found by Elliott for dieldrin-resistant Anopheles gambiae Giles when assessed with BHC (Elliott, 1959), but statistically these mosquitos were not significantly heterogeneous, perhaps because of the low percentage of sus-

a Selection on generation of larvae indicated, not its offspring.

^b Figure obtained when considering only upper, straight, portion of the curve.

ceptibles. The lines for generations 1, 3 and 13 are parallel statistically, and of course the differences in LC₅₀ are highly significant. It is easy to draw a line through the upper points of the curve for generation 2 which is parallel to the other three lines, and this gives an LC₅₀ of 0.84 p.p.m. The LC₅₀ in the 13th generation was 273 times that of the first (95%) fiducial limits 197-376). It is 2000 times that of the susceptible Tholo-i-Suva strain. The rapid increase in resistance with selection (virtually accomplished in three generations with increasing pressure) plus the discontinuity in the lines of generations 1 and 2 suggest that we have here a case of simple monofactorial inheritance of the type found by Davidson (1958) in dieldrin-resistant A. gambiae, but the fully resistant genotype was not isolated. Hoskins & Gordon (1956) have collected data to show that under selective pressure the regression line should become flatter in succeeding generations, followed by a steepening as the population becomes homogeneous for resistant individuals until the regression line for fully susceptible and fully resistant strains are parallel. In this case presumably the line will parallel that of the Tholo-i-Suva strain but if so it is difficult to account for an increase of nearly 300 times in LC₅₀ without change of slope, which was already considerably and significantly flatter than that of the susceptible strain. It is possible that this is because we are already well over the saturation point of DDT in water and the effective concentration of the insecticide is not the true one but a parameter of it. This may have the effect of extending the apparent range of LC₅₀'s but does not, of course, mean that there is not a very considerable degree of resistance; the sight of larvae vigorously swimming after 24 hours in a milky suspension of DDT was impressive.

There were insufficient larvae to spare in generation 13 to determine complete regression lines against dieldrin and γ -BHC. Instead, tests were done at a few concentrations, using about 300 larvae for each insecticide, which were expected to give about 50% and 90% mortalities with susceptible insects. The results (corrected for control mortalities) were:

Insecticide concentration	Percentage mortality				
(p.p.m.)	Dieldrin	γ-BHC			
0	2	2			
0.006	21				
0.02	93	16			
0.04	98				
0.1		100			

In all cases the mortalities fall within the range found for different batches of susceptible larvae, although some are lower than would be expected from the examples given in the first section of this paper.

Adult susceptibility to DDT was tested by the Busvine-Nash method (WHO Expert Committee on Insecticides, 1958). It had to be carried out on the adults from 18th generation larvae already exposed to DDT at 2 p.p.m. Only 174 females were available and the results were as follows:

This line is parallel to that of the normal susceptible strain (see under "Adults" above). The LC_{50} is 1.75 and the potency ratio 2.43 (95% fiducial limits 1.84-3.20), which is significant. There is quite probably a cumulative effect of the DDT from the larval exposure (see Hadaway, 1956) which has lowered the apparent resistance, and we are justified in accepting at least a moderate degree of DDT resistance in the adult.

Presumably some initial selection from the normal wild strain had taken place before or after the colony was brought into the laboratory. Its origin seems to have been mixed, in part from Lami and in part from Kasese. Lami is outside Suva and was once a city rubbish dump. It has never been treated with insecticides, but in 1957 the local A. pseudoscutellaris included resistant individuals (Fig. 5). Kasese is a residential district on the fringe of Suva and the area has been treated with insecticide in the past for the control of ground-breeding pest mosquitos only. Some DDT was used up to about 1954, but since then only dieldrin, to which our strain shows no cross-resistance. Other places where resistant insects were discovered (Samambula, Walu Bay; Fig. 5) have never been treated with insecticides. Even the Tholo-i-Suva strain showed signs of developing resistance under laboratory culture entirely free from exposure to insecticides. When originally taken in it gave 100 % mortality with 0.4 p.p.m. and 99.1 % mortality with 0.1 p.p.m. DDT. The fifth laboratory generation showed a 9 % survival to 1 p.p.m. The two strains could not be reared in isolation but contamination by the resistant strain is extremely unlikely on this scale, and we believe this degree of resistance to be the result of selection by laboratory conditions on a comparatively rare gene present in the original wild population and which incidentally confers resistance

to DDT. All susceptible strains of A. pseudo-scutellaris discovered were completely rural in origin, whereas the partly resistant ones were urban or semi-urban, and this may be significant. Incidentally, the Lami strain comprised both the normal and hairy varieties of larvae (Rosen & Rozeboom, 1954). These were treated separately and gave almost identical results, which have been pooled for the line in Fig. 5.

There is evidence of a physiological difference in the two strains—namely, that the resistant adults take longer to start laying than the susceptible. The eggs obtained from the 14th generation adults were divided into three batches: those laid in the first, second and third weeks of life. The first and third batches were hatched on the same day and the early fourth-instar larvae exposed to 2 p.p.m. DDT in water for 24 hours. At the end of the exposure period 80% of the first batch were dead and only 16% of the second. On the other hand, there appears to be no difference in the rate of development. The total eggs produced by the 16th generation were hatched together and those reaching fourth stage first were treated with 2 p.p.m. DDT separately from those reaching this stage on the next day. The mortality of both batches was 67%.

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RÉSUMÉ

Les épreuves standard de résistance aux hydrocarbures chlorés ont été appliquées à cinq espèces de moustiques vecteurs, aux îles Fidji. Les larves ont été mises en présence de suspensions aqueuses de DDT, de dieldrine et de HCH. Culex fatigans était extrêmement sensible aux trois insecticides. La sensibilité des souches d'Aëdes aegypti ne différait pas de celles d'autres souches, ailleurs dans le monde. Il en était de même des trois espèces endémiques dans la région du Pacifique sud, si ce n'est que A. fijiensis était anormalement résistant au DDT et A. pseudoscutellaris au HCH.

Quant aux formes adultes, celles d'A. polynesiensis réagissaient au DDT comme celles d'A. pseudoscutellaris. Les A. aegypti des îles Fidji sont plus difficiles à détruire que les souches non résistantes d'autres régions. Culex fatigans n'est pas sensible au DDT, et bien qu'il soit plus sensible à la dieldrine, la dose CL_{90} est élevée (6,2%). Les larves d'une souche de laboratoire d'A. pseudoscutellaris, qui n'avait jamais été soumise à la pression sélective d'un insecticide, présentaient une résistance cor-

respondant à une ${\rm CL}_{50}$ 7 fois plus forte que celle d'une souche sauvage sensible. Par sélection en suspension de DDT, la ${\rm CL}_{50}$ s'est rapidement élevée, jusqu'à atteindre 2000 fois celle de la souche sensible, sans que la courbe de régression en soit affectée. Il est probable que la résistance est un caractère génétique monofactoriel. On n'a observé aucune résistance croisée avec la dieldrine ou le HCH gamma. Les adultes provenant de larves résistantes accusaient un léger degré de résistance au DDT.

Les populations sauvages d'A. scutellaris des zones urbaines ou semi-urbaines présentaient une certaine résistance, contrairement aux souches rurales. On a des raisons de supposer que le gène responsable de la résistance existe, à un taux très faible, parmi au moins une des populations étudiées, et que la vie « domestique » favorise la manifestation de ce gène. Il semble que la ponte des moustiques résistants soit plus prolongée, mais la vitesse de développement des larves est la même, chez les souches sensibles et les souches résistantes.

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