

bluetongue in North America, has been collected up to 1000 feet (Glick and Noble 1961). The collection of a possible vector of bluetongue and ephemeral fever virus at 1950 m (450 m above ground level) lends support to the theory that wind carriage of *Culicoides* spp. is a means of disease dissemination within the ITCZ.

The authors are grateful to Dr. M.J. Reardon and Dr. R.A. Ward for review of the manuscript and to the Kenya Meteorological Department for their assistance in interpreting the synoptic chart and Meteosat 2 data. The results are published with the approval of Dr. A.R. Njogu, Director, Kenya Trypanosomiasis Institute, Government of Kenya. This work was supported by Research Grant No. DAMD17-84G-4002 from the U.S. Army Medical Research and Development Command, Ft. Detrick, MD 21701.

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EVIDENCE OF INCREASED DEVELOPMENTAL PERIOD IN LARVAE OF HOMOZYGOUS PYRETHROID-RESISTANT *CULEX* *QUINQUEFASCIATUS*

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The development of insecticide resistance in a population is a dynamic process influenced by many variables. Georghiou and Taylor (1976) have enumerated three main factors which influence the evolution of resistance: genetic, biological and operational (how the pesticide is applied). They pointed out that only the operational factors can be manipulated for the pur-

pose of delaying the onset of resistance. One of the strategies that has emerged from this line of thought is the use of insecticides in optimal rotational sequences (Georghiou et al. 1983). Among the requirements for this approach is the absence of cross resistance between the insecticides that are used, and a lower biotic fitness in the resistant individuals when selection pressure by the respective insecticides is not applied.

Differences in the reproductive potential between resistant and susceptible strains of some species have been found to be small or absent (Roush and Hoy 1981, Roush and Plapp

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² This study was supported by Special Funds for Mosquito Control Research appropriated annually by the California Legislature.

1982). In adult *Anopheles gambiae* Giles, individuals possessing the semi-dominant but not the dominant dieldrin resistance gene emerge slower than susceptible individuals (Emeka-Ejiofor et al. 1983). Ferrari and Georghiou (1981), studying organophosphate-resistant larvae of the southern house mosquito *Culex quinquefasciatus* Say, found some of the classical deleterious effects associated with the homozygous resistance phenotype: lowered fecundity, reduced viability and a longer developmental time.

Pyrethroid resistance in *Cx. quinquefasciatus* is due mainly to *kdr* (knockdown resistance). This incompletely recessive gene confers greater than 4000-fold resistance to homozygous individuals (Priester and Georghiou 1979). In the present study we compare the development time of *Cx. quinquefasciatus* larvae which are heterozygous or homozygous for the *kdr* gene.

The criterion used in this experiment to detect differences in the developmental rate of genotypes was the percent survival of backcross progeny in each of two bioassays conducted on successive days. This is actually an indirect way of measuring developmental time. It is indirect because it does not exactly measure the length of time from egg laying or hatch to eclosion. Instead, it measures the time it takes an individual to reach a certain morphological condition. The larvae were reared under standard conditions (Georghiou et al. 1966). F₁ crosses were carried out using either of two pyrethroid susceptible strains, S-Lab or *ypl*, followed by backcrosses to the homozygous pyrethroid-resistant strain, Perm-R (see Table 1). S-Lab is a susceptible strain collected in 1950 in the San Joaquin Valley of California and has been maintained in the laboratory free of insecticidal pressure. The second susceptible strain, *ypl*, is a marker strain homozygous for the recessive genes *yellow larva* (*y*) on the second chromosome and *plum-eye* (*pl*) on the third chromosome. This strain was kindly supplied by Dr. A. R. Barr, University of California, Los Angeles. Perm-R is the homozygous pyrethroid-resistant strain that has been selected to greater than 4000-fold resistance by Priester and Georghiou (1979) with (1*R*)-*trans*-permethrin. The genotypes of mid-fourth instar larvae of the backcross generation were determined by using a discriminating dosage (DD) of 1.0 ppm (1*R*)-*trans*-permethrin. This concentration is in the middle of a wide plateau occurring at the 50% mortality level of the 1d-p line obtained when progeny from a backcross of an F₁ to a strain homozygous for *kdr* are bioassayed. Therefore, the percent mortality produced by this DD indicates the frequency of heterozygous individuals in the sample.

The larvae tested in this experiment were raised in two large enameled pans, one for each backcross. Although the survivors were not specifically sexed, similar experiments have found that there is no significant deviation from the expected 1:1 male:female ratio when all the hatched larvae are tested (Halliday et al., unpublished data). Furthermore it has previously been shown that pyrethroid resistance is not sex-linked in this species (Priester and Georghiou 1979). Another factor that is known to affect developmental time is the density at which the larvae are reared. This was not a factor in this experiment since all the larvae from each backcross were reared at the same density.

Bioassay of all 1140 progeny of the backcross ♀ Perm-R X ♂ (♀ Perm-R X ♂ S-Lab) indicated a 1:1 ratio of heterozygous to homozygous-resistant individuals as shown by the overall 47.9% mortality (Table 1). However, the percentage of individuals surviving the DD was significantly different in each of the two test days. On day one there was a surfeit of *kdr* heterozygotes while on day two there was an excess of *kdr* homozygotes. Similar results were obtained when the *ypl* strain was used, i.e., ♀ Perm-R X ♂ (♀ *ypl* X ♂ Perm-R) (Table 1). Overall, in this cross there appeared to be a slight excess of *kdr* homozygotes to heterozygotes (52.9% vs. 47.1%) but this difference was not statistically significant ($\chi^2 = 2.45$, 1 df, $P > 0.05$). In this second cross there was also a similar increase in the percentage of survivors as developmental time increased.

Roush and Plapp (1982) used relative development time as an indicator of biotic potential in resistant and susceptible house flies and found that development time was longer with certain homozygous-resistant genotypes. Similarly, Emeka-Ejiofor et al. (1983) reared several F₂ populations of *Anopheles gambiae* derived from susceptible and either DDT resistant or DDT and dieldrin resistant strains. Bioassays of newly emerged adults showed that the semidominant dieldrin resistance gene was associated with approximately a half day delay in growth. The dominant dieldrin and DDT resistance genes showed no effect on delaying development.

Ferrari and Georghiou (1981) observed a similar, significantly longer developmental time in organophosphate-resistant and susceptible larvae of *Cx. quinquefasciatus*. These authors proposed that the lack of effect in their heterozygous resistant strain was due to heterosis. Although the data presented here do not preclude heterosis as being the cause of the observed increased developmental time, the two cases are not strictly analogous since

Table 1. Results of discriminating dose tests with permethrin on *Culex quinquefasciatus* larvae indicating slower developmental rate in *kdr/+* vs *kdr/kdr* individuals.

Total	♀ Perm-R × ♂ (♀ Perm-R × ♂ S-Lab)			♀ Perm-R × ♂ (♀ <i>ypl</i> × ♂ Perm-R)		
	No. alive/ no. tested	% alive ^a	χ ²	No. alive/ no. tested	% alive ^a	χ ²
Day 1	321/769	41.7*	11.5 ^b	167/379	44.1*	11.5 ^c
Day 2	225/371	60.6*	25.5 ^b	233/377	61.8*	11.7 ^c
Total	546/1140	47.9	1.94 ^d	400/756	52.9	2.45 ^d

^a An asterisk indicates a significantly different mortality from the expected value.

^b Chi-square value based on an expected survival of 47.9%.

^c Chi-square value based on an expected survival of 52.9%.

^d Chi-square value based on an expected survival of 50%.

organophosphate-resistance in the strain of Ferrari and Georghiou is a dominant trait while *kdr* resistance is recessive. Because of this difference in penetrance the phenotypes expressed by the heterozygotes are different, one expressing resistance the other susceptibility. The results reported here extend the findings of Ferrari and Georghiou (1981) and Roush and Plapp (1982) to pyrethroid resistance and should be of value in the design of predictive models on the evolution of resistance.

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