Theoretical and Applied Genetics 46, 25-32 (1975)

Population Control of Caged Native Fruitflies in the Field by Compound Autosomes and Temperature-sensitive Mutants*

M. Fitz-Earle **, D.G. Holm and D.T. Suzuki

Department of Zoology, The University of British Columbia, Vancouver (Canada)

Summary. A genetic technique for insect population control has been tested in cages under field conditions at two different locations in British Columbia. The method entails the population replacement of standard insects by those bearing compound autosomes using the principle of negative heterosis, thus permitting control or elimination through conditional mutations. Both native- and laboratory-derived compound strains of the fruitfly *Drosophila melanogaster* were tested in population cages against standards in the laboratory and at the two field sites. Those compound-bearing insects originating from the wild were the most successful, both in the laboratory and the field, in displacing standards from the cages down to a minimum initial ratio of 5 compounds to 1 standard. The importance is stressed of collecting strains from the wild, and performing the necessary genetic manipulations as rapidly as possible, prior to releasing the rearrangement in the field for control purposes.

Introduction

Following the successful application of the sterile insect technique to the control of the screwworm fly, *Cochliomyia hominivorax*, in the southern United States, considerable attention has been focussed upon more sophisticated genetic techniques for the suppression of pest insects. One such method involves the replacement of individuals in a population bearing standard chromosomal arrangements by those carrying chromosomal rearrangements termed compound autosomes, which may provide a transport mechanism for various controlling factors such as conditional mutations (Foster et al., 1972; Childress, 1972; Fitz-Earle et al., 1973).

Compound autosomes differ from standard chromosomes in that their homologous arms are attached to common centromeres rather than to different centromeres (Holm, 1974). The meiotic behaviour of a compound strain of the fruitfly, *Drosophila melanogaster*, is such that the zygotic frequency is one quarter that of standards, though the surviving zygotes are quite competitive. However, there is complete genetic isolation between compounds and standards, suggesting that in a mixed population there is an intra-fertility but inter-sterility of the two forms. An unstable genetic equilibrium (Li, 1955) can be obtained in a mixed population by adjusting the relative frequencies of the rearrangements and standards according to their fitnesses. By increasing the initial frequency of the compounds beyond the equilibrium point, the standards would be displaced from the population. The efficiency with which compounds could be fixed in this way would be dependent upon the initial frequencies and relative fitnesses of the strains. Compound autosome strains have been generated in *D. melanogaster* and are being actively sought in insects of both economic and hygienic importance.

If a compound-bearing strain that also carried a factor for eradicating the pest or rendering it innocuous were introduced into a target pest population, it would be possible to combine replacement with control. The introduction of mutants that would render pests less harmful to man, such as inability to transmit disease, may in some circumstances be more desirable than the introduction of factors that would completely eradicate the insect. However, for those pests that affect man's agriculture, complete eradication (through the agency of conditional lethal factors) may be quite acceptable. Temperature-sensitive (ts) mutations that permit survival and fertility at a permissive temperature but lead to death or sterility at a high or low restrictive temperature, would seem to be ideally suited to schemes for population elimination. In *D. melanogaster*, ts mutants have been detected throughout the genome and fall into three main groups: (i) ts lethals, in which, following a temperature shock during development, the insect dies at a later stage; (ii) ts paralytics, in which prolonged

* This research was supported by Canada Council Grant S71-1687 to M.F-E and by National Research Council of Canada Grants, A5853 to D.G.H. and A1764 to D. T.S.

** Canada Council Killam Special Postdoctoral Research Scholar.

exposure of adult individuals to restrictive temperatures sufficient to cause paralysis, leads to lethality; (iii) ts steriles, in which a temperature stress during development causes adult sterility (i.e., genetic death) (Suzuki, 1970). Additionally, it should be noted that up to one third of all ts lethals are both heat- and cold-sensitive (Tasaka and Suzuki, 1973). The strategy would be to replace, at permissive temperatures, a native pest population by a compound strain carrying a ts lethal, paralytic or sterility mutation. Genetic lethality would then occur when the temperatures either rise or fall to restrictive levels. Lethal ts mutations have been detected in the wasp, *Habrobracon serinopae* (Smith, 1971) and the housefly, *Musca domestica* (McDonald and Overland, 1972) and are being sought in pests of veterinary and agricultural significance.

In earlier papers (Fitz-Earle et al., 1973; Fitz-Earle, 1974a), laboratory cage populations of compound and standard chromosome strains of *Drosophila* were used to show that, (a) compounds can displace standards in populations with continuous reproduction, although considerable variation exists in the ability of compound strains to achieve replacement; (b) the minimum initial ratio of compounds to standards required to subsequently fix compounds in a population was 4:1, a ratio that compared favourably with data from other genetic techniques; and (c) it is important to select strains prior to release in competitive situations, using various fitness component criteria.

The present study examines native- and laboratory-derived compound strains for their ability to replace standards in cages both in the laboratory and at two distinct field locations. Subsequent papers will examine the behaviour of compounds carrying temperature-sensitive mutations to test the combined principles of population replacement and elimination.

Materials and Methods

Strains and their Derivation

The strains of *Drosophila melanogaster* used in the experiments are listed in Table 1. All compound autosome lines are reversed metacentric and are designated by initials for location of derivation (P - Pasadena; S - Storrs; V - Vancouver), discoverer (FE - Fitz-Earle; H - Holm; K - Kiceniuk) and a number.

Native standard insects were collected from an isolated fruit dump near Summerland, British Columbia and several lines were established. To generate compound autosomes in native lines, virgin females were treated with 2000r of γ-radiation and crossed either to compound stocks bearing markers ri and e^s (compound 3) or lt and px (compound 2) (Fig. 1a, b). A complete description of the markers is to be found in Lindsley and Grell (1968). Two generations later, unmarked native compounds of either the third (C(3L)VFE1,+;C(3R)VFE1,+) or second (C(2L)VFE5,+;C(2R)VFE5,+ and C(2L)VFE6,+;C(2R)VFE6,+) chromosomes were then derived.

Table 1. The compound and standard strains of *Drosophila melanogaster* used in the experiments

Strain	Origin	Mutations
C(2L)VFE5,+;C(2R)VFE5,+	Native	none
C(2L)VFE6,+;C(2R)VFE6,+	Native	none
C(3L)VFE1,+;C(3R)VFE1,+	Native	none
C(2L)VFE1,H28;C(2R)VFE5,+	Left arm: Laboratory Right arm: Native	H28 - heat-sensitive egg lethal
C(2L)VFE2,H28;C(2R)P,px	Laboratory	H28 - heat-sensitive egg lethal; plexus wing
C(2L)VH2,lt;C(2R)P,px	Laboratory	light eye; plexus wing
C(3L)VH2,ri;C(3R)VK1,e^s	Laboratory	radius incompletus wing; ebony sooty body
$para^{ts}$ C(3L)SH2,+;C(3R)SH19,+	Laboratory	$para^{ts}$ - adult paralysis at 29° C normal at 22°C
b	Laboratory	black body
e	Laboratory	ebony body
bw	Background native*	brown eye

* either C(2L)VFE5,+;C(2R)VFE5,+
or C(2L)VFE6,+;C(2R)VFE6,+

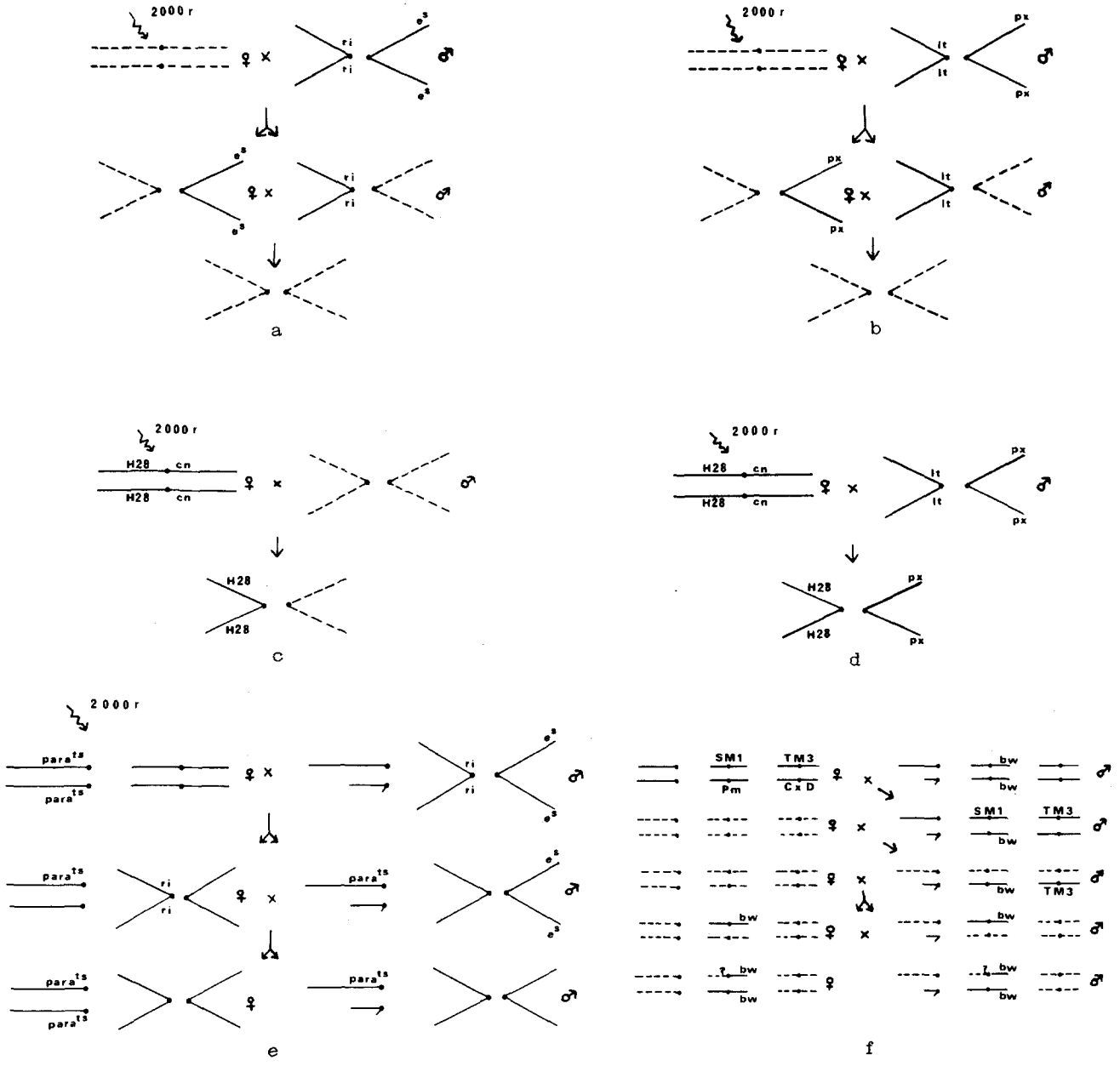

Fig. 1. Derivations of the compound and standard strains of *Drosophila melanogaster* used in the studies. Solid lines - laboratory-derived chromosomes; broken lines - native-derived chromosomes

Males of one of the native compound 2 lines were crossed to similarly irradiated virgin females bearing an ethyl methanesulfonate-induced heat-sensitive ts lethal mutation that dies in the egg stage (designated H28) on the left arm of chromosome 2 and the marker cn on the right arm. The mating thus yielded an unmarked native compound line containing a ts mutant (C(2L)VFE1, H28; C(2R)VFE5, +) (Fig. 1c). Similarly, treated H28 cn females were mated to a compound stock carrying lt and px to obtain a marked ts compound strain (C(2L)VFE2, H28; C(2R)P, px) (Fig. 1d). Irradiated virgins of a strain carrying the X-linked ts paralysis mutant, $para^{ts}$, (Suzuki et al., 1971) were crossed to compound 3 males marked with ri and e^s, to produce, two generations later, a line of compounds associated with an adult paralysis gene ($para^{ts}$; C(3L)SH2, +; C(3R)SH19, +) (Fig. 1e). All strains derived in these ways were tested for the presence of compound autosomes by crossing to known compound stocks. In addition, those lines putatively carrying a ts mutation were tested at both 22°C (permissive temperature) and 29 °C (restrictive temperature) for the expression of the ts phenotype.

A marked standard chromosome in a native background was derived in the following way. Virgin females heterozygous for the marked chromosome 2 and 3 balancers In(2LR)SM1, al^2 Cy cn^2 sp^2 and In(3LR)TM3, ri p^p sep bx^{34e} e^s Sb Ser, respectively, were crossed to males homozygous for the mutant bw linked to chromosome

2 (Fig. 1f). Phenotypically Cy Sb Ser males were mated to virgin native females; their Sb Ser male progeny were recovered and again crossed to virgin native females. Non-Sb Ser progeny were then mated in single pairs in sufficient numbers to yield a homozygous bw line of flies having a background that was for the most part co-isogenic to either the C(2L)VFE5,+;C(2R)VFE5,+ or C(2L)VFE6,+;C(2R)VFE6,+ strains.

Cages and Growth Conditions

The cages used in the laboratory studies were 46 cm Plexiglas® cubes, having air vents covered with nylon screening on the top and a sleeved port at the front to facilitate access to the food dishes and flies. Open food dishes containing 50 ml standard cornmeal-agar medium were introduced every three days until a maximum of seven were in the cage at any time. A covered dish of water was retained in the cage to ensure high humidity and the temperature was held at 24.5 ± 0.5°C.

For the field experiments, the cages were constructed of a cubical wood framework of side 31 cm with nylon screening on all sides except the base, and a sleeve at the front. The construction thus permitted exposure of the contained flies to prevailing weather conditions. The food-changing regimen was identical to that of the laboratory situation, with the exception that the lids were kept on the dishes and small access holes were cut in the sides to reduce the desiccation rate of the medium.

The field experiments were conducted in two locations:

1) Trout Creek in the Okanagan Valley of British Columbia; the area is a Ponderosa Pine Parkland and is semi-desert in nature. Precipitation is sparse throughout the year. Temperatures exceed 100° F in the summer and there are appreciable diurnal temperature fluctuations during this period.

2) South Campus of The University of British Columbia in a West Coast rainforest region. Precipitation is usually heavy during spring and fall but is light in the summer months. Temperatures rarely exceed 80° F and are not as extreme as at the Okanagan site. Temperature and precipitation records were obtained from the Meteorological Office, The University of British Columbia (in relation to the South Campus site) and from the Canada Department of Agriculture, Summerland, British Columbia (for the Trout Creek location).

Design of Experiments

Unmated compound and standard males and females were aged for 3-4 days and then released into cages in the initial ratios given in Tables 2 and 3 for laboratory and field experiments, respectively. The flies were permitted to increase in abundance over continuous generations.

Sampling Regime

About two weeks after releasing flies into a cage, and every 3 days thereafter until fixation, a random sample of approximately 300 flies was extracted with an aspirator. The flies were anesthetized with CO_2, scored for a marker and then returned to the cage. For the laboratory experiments, fixation was defined as being reached when three consecutive 3-day samples gave exclusively standard or compound flies. In the case of the field trials, fixation was defined as being reached when one such sample was obtained. The frequency of compound flies in each sample was calculated and recorded. The number of days to fixation was subsequently deduced.

Results

Laboratory experiments

Three compound autosome stocks derived from native material, C(2L)VFE5,+;C(2R)VFE5,+, C(2L)VFE6,+;C(2R)VFE6,+ and C(3L)VFE1,+;C(3R)VFE1,+ were extremely vigorous in laboratory culture. As anticipated, they were successful, at almost all ratios tested, in displacing marked standards under continuous reproduction in laboratory cages (Table 2). In general, the higher the initial frequency of native compounds released into a laboratory cage, the more rapid the replacement. Conversely, for those laboratory cages in which compounds and standards were competed at near-equilibrium ratios (i.e, 6:1, 5:1 and 4:1), a longer time was required for fixation of the compounds.

Two of the native compounds (C(2L)VFE5,+;C(2R)VFE5,+ and C(2L)VFE6,+;C(2R)VFE6,+), were additionally tested against non-compound flies marked with bw, but having the same genetic backgrounds as the native insects from which the compounds were synthesized (Table 2). The compounds were successful in some instances in displacing from the cages bw flies of native background, but not at such low levels as when the same compounds had been competed against b standards of laboratory origin. Indeed, C(2L)VFE5,+;C(2R)VFE5,+ compounds replaced b standards at all ratios tested down to 4:1 but were unable to displace bw standards below 5:1. Furthermore, C(2L)VFE6,+;C(2R)VFE6,+ compounds replaced b standards to a minimum initial ratio of 4:1, but when competed against bw standards, they failed to go to fixation at ratios below 6:1.

Field trails

The native-derived compound line C(2L)VFE5,+;C(2R)VFE5,+ was competed against standards in field cages in the initial ratios of 5:1 at the Trout Creek field site and 9:1 and 8:1 at the South Campus station (Table 3). For each ratio tested, the compounds were fixed and the standards were replaced. The time of fixation was quite long (70-120 days) compared to comparable laboratory experiments; no doubt this was due to the fact that the compound and standard flies were competed during the cool fall months.

A second compound strain derived from native material, C(3L)VFE1,+;C(3R)VFE1,+ was tested against standards in a field cage at the Trout Creek site in the initial ratio of 11:1 (Table 3). After about a month, the compounds had displaced a significant proportion of the standards; complete fixation of compounds was not, how-

Table 2. The results of competitions between compound and standard strains at various release ratios: laboratory cage experiments

Compound strain	Standard strain	Ratio*	Fixation of compound+	Days to fixation
C(2L)VFE5,+;C(2R)VFE5,+	b	10:1	S	32
		9:1	S	58
		7:1	S	76
		6:1	S	59
		5:1	S	86
		4:1	S	174
C(2L)VFE6,+;C(2R)VFE6,+	b	9:1	S	48
		7:1	S	68
		6:1	S	159
		5:1	S	107
		4:1	S	175
C(3L)VFE1,+;C(3R)VFE1,+	e	14:1	S	40
		9:1	S	28
		7:1	S	27
		6:1	S	52
		5:1	S	90
		4:1	S	32
C(2L)VFE5,+;C(2R)VFE5,+	bw**	10:1	S	80
		9:1	S	97
		6:1	S	102
		5:1	S	57
		4:1	F	100
C(2L)VFE6,+;C(2R)VFE6,+	bw**	10:1	S	78
		9:1	S	86
		6:1	S	92
		5:1	F	118
		4:1	F	69

* Compounds to standards

** Has same background as standard from which competitor derived

+ S - success; F - failure

ever, observed since the cage population was reduced in size by the low fall temperatures.

Many of the populations of flies established during the early- or mid-summer months at the Trout Creek site were reduced in numbers by the intense heat. The insects clearly died of desiccation and the culture medium was completely dried up. Two cages that were affected by this problem contained the compounds C(2L)VFE1,H28;C(2R)VFE5,+ that were native-derived and also carried a ts lethal gene and the b standards, established in the initial ratios of 17:1 and 5:1 (Table 3). The same competitions were conducted later in the season at the South Campus station using the ratios 12:1 and 5:1 and showed convincing replacement of the standards by the compounds (Table 3). Again, due to the lower temperatures, the replacement was prolonged (99-125 days) but fixation of compounds was ultimately observed.

A compound strain originally synthesized in the laboratory and bearing a ts lethal factor (C(2L)VFE2,H28;C(2R)P,px) was tested against an unmarked standard line in various ratios at both field locations. All flies died because of the summer heat in those cages established in the ratios of 7:1 and 6:1 at the Trout Creek station. However, cages set up later in the season at the same site in the ratios of 35:1, 30:1 and 12:1 were all fixed in favour of the compounds at the time of termination of the experiment (Table 3). Even after 34 days for the 30:1 cage and 64 days for the 12:1, samples of 300 flies were found to contain only compound individuals. Two further competitions between C(2L)VFE2,H28;C(2R)P,px and + strains in the ratios 10:1 and 8:1, conducted at the South Campus location in early fall, were most successful (Table 3). Within 46 days the compounds had displaced the standards from the 10:1 cage, while for the 8:1 test, fixation of compounds took 73 days.

A laboratory compound strain marked with lt and px (C(2L)VH2,lt;C(2R)P,px) was competed against standards at the Trout Creek site. A cage established in the ratio of 8:1 compounds to standards in the fall was found to be fixed in favour of the compounds after 65 days

Table 3. The results of competitions between compound and standard strains at various release rations: field cage trials

Compound strain	Standard strain	Initial* ratio	Location	Fixation of compound	Days to fixation	Notes
C(2L)VFE5,+;C(2R)VFE5,+	b	9:1	S.C.	S	116	Late fall experiment
		8:1	S.C.	S	71	Late fall experiment
		5:1	T.C.	S	91	Late fall experiment
C(2L)VFE6,+;C(2R)VFE6,+	b	11:1	T.C.	P	36	Late fall experiment
C(2L)VFE1;H28;C(2R)VFE5,+	b	17:1	T.C.	-	-	Summer desiccation death
		12:1	S.C.	S	125	Late fall experiment
		5:1	T.C.	-	-	Summer desiccation death
		5:1	S.C.	S	99	Late fall experiment
C(2L)VFE2,H28;C(2R)P,px	+	35:1	T.C.	S	111	Late fall experiment
		30:1	T.C.	S	34	Late fall experiment
		12:1	T.C.	S	64	Late fall experiment
		10:1	S.C.	S	46	Early fall experiment
		8:1	S.C.	S	73	Early fall experiment
		7:1	T.C.	-	-	Summer desiccation death
		6:1	T.C.	-	-	Summer desiccation death
C(2L)VH2,lt;C(2R)P,px	+	8:1	T.C.	S	65	Late fall experiment
		5:1	T.C.	-	-	Summer desiccation death
$para^{ts}$ C(3L)SH2,+;C(3R)SH19,+	b	12:1	S.C.	F	47	

* Compounds to standards

S = Success, F = Failure, P = Potential

S.C. = South Campus, T.C. = Trout Creek

(Table 3). Another cage that had been set up in early summer in the ratio of 5:1 gave no data due to the desiccation death of the flies (Table 3).

Compounds of the genotype $para^{ts}$; C(3L)SH2,+;C(3R)SH19,+ (containing the ts paralysis factor) failed to displace b standards from a cage established in the ratio of 12:1 at the South Campus station; indeed, within 47 days, the flies bearing standard chromosomes had gone to fixation (Table 3).

Discussion

Native compound flies were successful in displacing laboratory standards at ratios as low as 4:1. The same degree of success was obtained when comparable experiments were conducted in the field. Indeed, throughout these and other laboratory and field tests, native compound strains were found to be far superior to laboratory compound strains. The time to fixation of compounds in the field situation was considerably longer than in the laboratory, however, no doubt due to the lower fall temperatures to which the flies were subjected. Two of the native compound strains, although extremely vigorous compared to laboratory material, when competed in the laboratory against essentially native standard lines carrying the bw marker, were less successful in terms of the minimum ratio to achieve fixation, than when they were tested against laboratory standards carrying the b marker. These findings are supported by the experiments of Cantelo and Childress (1974), who observed that a laboratory compound line marked with se could replace laboratory standards in a cage when the initial ratio of compounds to standards was in the order of 5:1. However, when the same compound strain was tested under cage conditions in the laboratory against native standards, the ratio for success was appreciably increased and the necessary ratio was higher still when the same experiment was conducted under field conditions.

It should be noted that the native compound strains used in the present experiments have entirely native second chromosomes, and backgrounds that are 50 % native and 50 % laboratory-derived, whereas the bw standards have primarily laboratory-derived second chromosomes and all native backgrounds. The ideal test would be to match unmarked compounds and standards whose genetic constitutions were completely of native origin but the mechanics of obtaining the compound stocks would be prohibitive.

As an extension of the field cage experiments, unsuccessful attempts were made to demonstrate replacement under open field conditions. Several piles of culled apricots and apples that were free of *Drosophila* were seeded with large numbers of compound flies bearing inconspicuous markers, in an attempt to establish 'colonies' of compounds that would resist 'invasions' by native standard flies. Although chilled fruit was used to minimize adult disposal and cultures containing all stages of development were used to inoculate the fruit, colonies were formed in none of the piles. It was speculated that dispersal of the released compounds, rapid displacement by in-migrating native standards or mortality under field conditions, all contributed to the failure of these trials (Fitz-Earle, unpublished.) Cantelo and Childress (1974) released se compounds into open tomato fields and monitored the plots for the presence of marked flies over several days. The frequency of the compounds decreased rapidly with time and was likewise attributed to dispersal and mortality of the laboratory-reared flies.

Of those competitions in which a laboratory-derived compound bearing a ts lethal gene (H28;+ and H28;px) went to fixation, none did so prior to exposure of the flies to temperature fluctuations that met or exceeded the restrictive temperature of the ts mutant (29 °C). That is, the experiments conducted at the Trout Creek site, that gave replacement, were initiated so late in the summer that daytime temperatures were below the restrictive level and those tests at the South Campus location, even in high summer, were never subjected to the 29 °C temperature extreme. Thus, under the separate sets of field conditions, population replacement of standards by ts-bearing compound individuals was proven, but the corollary principle of population elimination mediated by the temperature-sensitive factor has yet to be demonstrated in the field. However, in the laboratory, elimination of similar strains has been achieved in approximately an equal length of time (40 days) as that required for replacement (Fitz-Earle, 1974b).

The laboratory-derived compound lt;px displaced standards from a field cage when the initial ratio was 8:1. In the laboratory, the same compounds were successful at ratios down to 9:1 (Fitz-Earle et al., 1973) but failed to give replacement at ratios approaching equilibrium (Fitz-Earle, 1974a). A further laboratory-derived compound that also carried the adult paralysis mutant $para^{ts}$ was unsuccessful in replacing standards in the field (12:1 initial ratio) and at all ratios tested in the laboratory (Fitz-Earle, 1974b), perhaps due to intrinsic properties of the compound or to viability effects associated with the paralysis gene.

It is apparent from the present and associated tests of compounds, that compound strains derived from laboratory stocks fared less well than native-derived compounds in their ability to displace standards, especially native ones. In a control programme, therefore, it is clearly important to collect native material from the field and perform the necessary genetic manipulations with as little exposure to laboratory conditions as is possible prior to re-introducing the insects into the wild.

Acknowledgements

The authors are most grateful to Dr. R.D. McMullen of the Canada Department of Agriculture, Research Station, Summerland, B.C., who contributed in many ways to the field aspects of the study. A.K. Junker, C.R. Reilkoff and W. Rublee assisted with the laboratory experiments.

Literature

Cantelo, W.W.; Childress, D.T.: Laboratory and field studies with a compound strain of *Drosophila melanogaster*. Theor. Appl. Genet. 45, 1-6 (1974)

Childress, D.: Changing population structure through the use of compound chromosomes. Genetics 72, 183-186 (1972)

Fitz-Earle, M.: Minimum frequency of compund autosomes in *Drosophila melanogaster* to achieve chromosomal replacement in cages. Genetica (in press) (1974a)

Fitz-Earle, M.: Elimation of fruitfly populations by using compound autosomes and temperature-sensitive mutations. (in preparation, 1974b)

Fitz-Earle, M.; Holm, D.G.; Suzuki, D.T.: Genetic control of insect populations: Cage studies of chromosome replacement by compound autosomes in *Drosophila melanogaster*. Genetics 74, 461-475 (1973)

Foster, G.G.; Whitten, M.; Prout, T.; Gill, R.: Chromosome rearrangements for the control of insect pests. Science 176, 875-880 (1972)

Holm, D.G.: Compound autosomes. In: Ashburner, M., Novitski, E. (Eds.), Biology of Drosophila Vol. 1, New York: Academic Press 1974

Li, C.C.: The stability of an equilibrium and the average fitness of population. Am. Nat. 89, 281-296 (1955)

Lindsley, D.L.; Grell, E.H.: Genetic variations of *Drosophila melanogaster*. Carnegie Inst. Wash. Pubn. No. 627 (1968)

McDonald, I.G.; Overland, D.E.: Temperature-sensitive mutations in the housefly: the characterization of heat-sensitive recessive lethal factors on autosome III. J. Econ. Entomol. 65, 1364-1368 (1972)

Smith, R.H.: Induced conditional lethal mutations for the control of insect populations. In: Sterility Principle for Insect Control or Eradication, pp. 453-465. Vienna: I.A.E.A. 1971

Suzuki, D.T.: Temperature-sensitive mutations in *Drosophila melanogaster*. Science 170, 697-706 (1970)

Suzuki, D.T.; Grigliatti, T.; Williamson, R.: Temperature-sensitive mutations in *Drosophila melanogaster*. VIII. A mutation (para ^{ts}) causing reversible adult paralysis. Proc. Nat. Acad. Sci. U.S. 68, 890-893 (1971)

Tasaka, S.E.; Suzuki, D.T.: Temperature-sensitive mutations in *Drosophila melanogaster*. XVII. Heat- and cold-sensitive lethals on chromosome 3. Genetics 74, 509-520 (1973)

Received August 8, 1974
Communicated by A. Robertson

Dr. M. Fitz-Earle
Dept. of Biology
Capilano College
N. Vancouver, B.C. (Canada)

Dr. D.G. Holm
Dr. D.T. Suzuki
Dept. of Zoology
The University of British Columbia
Vancouver, B.C. (Canada)