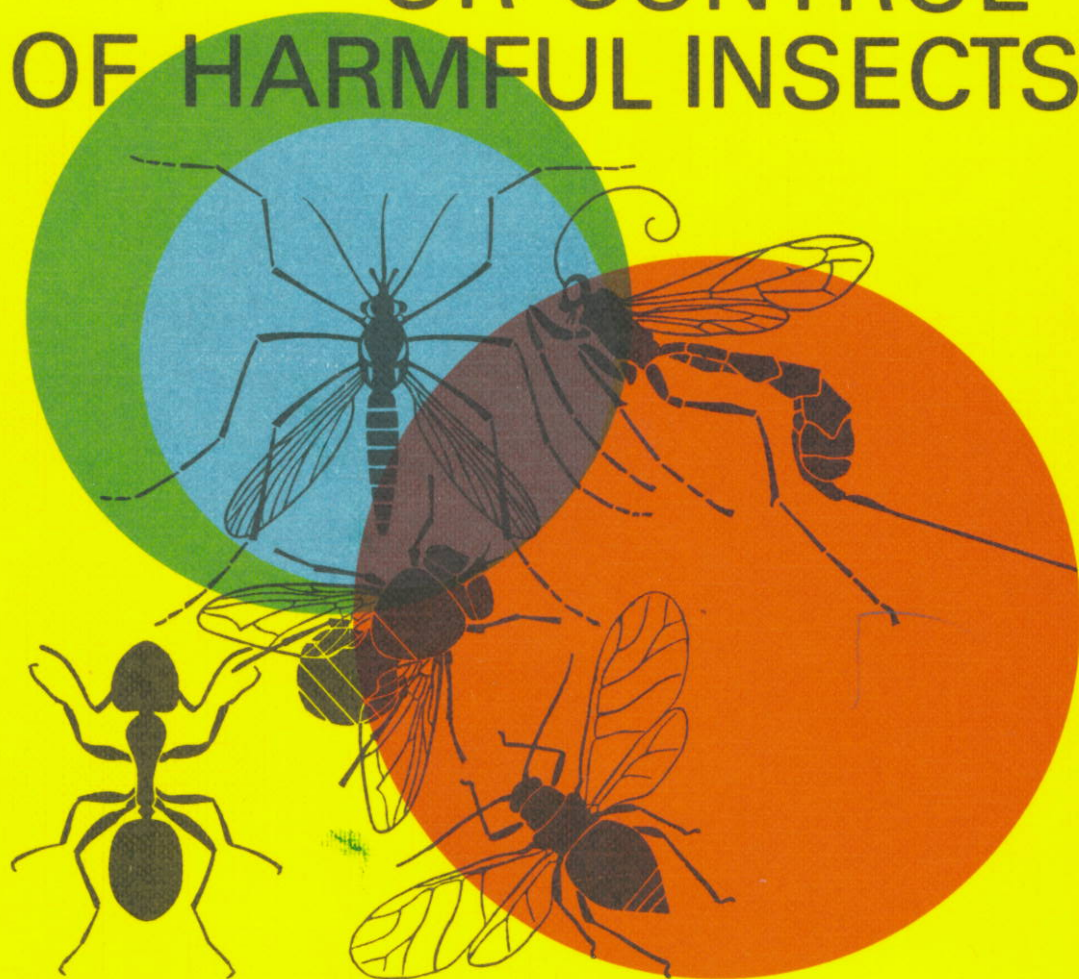


PROCEEDINGS OF A
PANEL, VIENNA,
27-31 MAY 1968
ORGANIZED
BY THE JOINT
FAO/IAEA DIVISION
OF ATOMIC ENERGY
IN FOOD AND
AGRICULTURE



STERILE-MALE TECHNIQUE FOR ERADICATION OR CONTROL OF HARMFUL INSECTS



INTERNATIONAL ATOMIC ENERGY AGENCY, VIENNA, 1969

STERILE-MALE TECHNIQUE
FOR ERADICATION OR CONTROL
OF HARMFUL INSECTS

PANEL PROCEEDINGS SERIES

STERILE-MALE TECHNIQUE
FOR ERADICATION OR CONTROL
OF HARMFUL INSECTS

PROCEEDINGS OF A PANEL
ON APPLICATION OF THE STERILE-MALE TECHNIQUE FOR THE
ERADICATION OR CONTROL OF HARMFUL SPECIES OF INSECTS,
ORGANIZED BY THE
JOINT FAO/IAEA DIVISION OF ATOMIC ENERGY
IN FOOD AND AGRICULTURE
AND HELD IN VIENNA, 27 - 31 MAY 1968

INTERNATIONAL ATOMIC ENERGY AGENCY
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OR CONTROL OF HARMFUL INSECTS
IAEA, VIENNA, 1969
STI/PUB/224

Printed by the IAEA in Austria
September 1969

FOREWORD

A Panel on the Application of the Sterile-Male Technique for the Eradication or Control of Harmful Species of Insects was organized by the Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture and held in Vienna, 27 - 31 May 1968. Previous panels on this and related subjects resulted in the publication by the Agency of the following books in the Technical Reports Series (TRS) and the Panel Proceedings Series (PPS):

- TRS 21: "Insect population control by the sterile-male technique"
- TRS 44: "Advances in insect population control by the sterile-male technique"
- PPS: "Radiation, radiosotopes and rearing methods in the control of insect pests" (1968)
- PPS: "Control of livestock insect pests by the sterile-male technique" (1968)
- PPS: "Insect ecology and the sterile-male technique" (1969)

The sterile-male concept of insect control is based on the use of sexually sterilized males to seek out and mate with normal females in a field environment. No offspring will result from such matings, and if the number of sterilized males present is higher than the number of native males for successive generations, the target species will be eradicated or suppressed.

Although the sterile-male concept sounds simple it is not simple to implement and involves a vast amount of research on basic biology, field ecology, numbers of the species in the field on a seasonal basis, effective methods of trapping or of sampling a population before, during and after sterile insects are introduced, radiation dose to cause sterility, competitiveness of irradiated males, economical mass-rearing methods, release methodology, dispersion and mating behaviour of released specimens, and organization of men and materials for field trials. These are some of the important areas of research and it is obvious that much time and effort will be expended on them before completely satisfactory results are obtained.

Good progress has been made in basic laboratory research on various facets of the sterile-insect methods of insect control such as mass rearing, release procedures, and the biology of numerous insects in various parts of the world for possible use in sterility programs. Small-scale field experiments to test the applicability of the methods and to identify problems that need further investigation have not kept pace with the basic work. This is due almost entirely to lack of funds. Small-scale field trials require extra funds which are usually not available to laboratory research organizations.

This publication contains the summary of the meeting and the recommendations of the Panel, which are intended to serve as a guide to the Joint FAO/IAEA Division and to others engaged in this work. Included is a list of in-

sects that appear to be suitable as candidates for investigations on the applicability of the sterile-male method to their control, and a further list of insects that have been studied in the laboratory, in field cage tests or small field trials and require further testing on a larger scale in the field. The papers presented by panel members are also included.

CONTENTS

SUMMARY OF THE PANEL

1. General	3
2. Insects on which research information is available and which are ready for field testing	3
3. Need for a research development and evaluation fund	7
4. List of insects on which basic and applied research is needed	8
5. Prior reduction of insect population to levels manageable by the release of sterile insects	10
6. Basic research on the population ecology of migratory insects considered as promising candidates for application of the sterile-insect release method	11
7. Sub-sterilizing doses of radiation	11
8. Increased studies of genetic mechanisms, biology and field ecology	12
9. Basic research on the prevention of diseases in mass-cultured insects	12
10. Work at Seibersdorf Laboratory	12
11. Research on the taxonomy, genetics and cytogenetics of medfly	13
12. The use of Research Contract funds should be concentrated on a few insects rather than on many	13
13. A co-ordinated research program for rice insect control	13
14. Use of sterility techniques for the suppression of vertebrate pests	13
15. Preparation and publication of two manuals on the sterile-male method of insect control for the guidance of scientists and administrators	14
16. Training	14

PAPERS PRESENTED AT THE PANEL

Concept and value of eradication or continuous suppression of insect populations	19
E. F. Knipling	
Biological information needed in the sterile-male method of insect control	33
A. W. Lindquist	
Potential of the sterile-male technique in integrated insect control programs	39
V. Delucchi	

Activities of the United States Atomic Energy Commission related to radiation techniques used in control of insects	45
R . R a b s o n	
Problems in large-scale sterile-male technique programs in developing countries	51
R . H . R h o d e	
Development of research in sterilization techniques for agricultural insect pests in the USSR	57
S . V . A n d r e e v , B . K . M a r t e n s a n d V . A . M o l c h a n o v a	
Sterile-male technique for control or eradication of the boll weevil, <u>Anthonomus grandis</u> Boh.	65
T . B . D a v i c h	
Significance of the sterile-male technique in pest management of the white grub (<u>Melolontha vulgaris</u> F.)	73
E . H o r b e r	
Present status and potential use of the sterile-male technique for control of rice stem borers	87
J a i S u n H y u n	
Sterile-male technique studies in Hungary	91
T . J e r m y a n d B . N a g y	
Experiments on Mediterranean fruit fly control with the sterile-male technique	97
D . J . N a d e l a n d G . G u e r r i e r i	
Status of the sterile-male technique for mosquito control	107
K . S . R a i	
Present stage of research into the eradication of the Mediterranean and South American fruit flies and the cotton stainer in Peru by the sterile-male technique	115
J . E . S i m o n F	
On the possibility of a new method for the control of insect pests	123
A . S . S e r e b r o v s k y	
APPENDIX : PANEL RECOMMENDATIONS	139
LIST OF PARTICIPANTS	141

SUMMARY OF THE PANEL

SUMMARY OF THE PANEL

1. GENERAL

Insects are among man's most important enemies, attacking and destroying food, fibres and forest commodities and, in addition, carrying and transmitting diseases of plants, humans and animals. The losses of food crops total many hundreds of million dollars annually.

Chemical control of harmful insects fails in many instances because these pests become resistant to chemicals, thus making effective control impossible. Of greater importance is the persistence of insecticide residues in food chains following use of these chemicals on plants and animals. Although the chemical residues are in most cases exceedingly minute, they are viewed with concern by health authorities because of possible harmful effects on man. In addition, the use of pesticides on a wide scale may be harmful to beneficial forms of life such as fish, wild mammals and birds.

In view of this, the Panel feels strongly that there is an urgent need to expand research on the use of the sterile-male technique for insect control and recommends that the Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture encourage and support such research.

2. INSECTS ON WHICH RESEARCH INFORMATION IS AVAILABLE AND WHICH ARE READY FOR FIELD TESTING

Research on some of the insects in this list is in an advanced stage while on others it will still entail much work. However, all these insects appear to be ready for further evaluation in either small- or large-scale field trials to determine the feasibility of the sterile-insect method of control and to identify problems that need more investigation. The list does not include all insects that are ready for field trials, but rather those that are known to the members of the Panel.

Anastrepha ludens (Loew) - Mexican fruit fly

Sterile Mexican fruit flies are currently being used in a localized area on the Southern California border as a caretaker population to prevent movement of wild flies into the citrus-growing areas of California.

Ceratitis capitata (Wied) - Mediterranean fruit fly

Although eradication trials are under way on Capri and in Central America, there seems to be a need for further field tests in different areas, for further studies on producing more vigorous flies and for more field ecological investigations.

Dacus cucurbitae Coq. - Melon fly and

Dacus dorsalis (Hendel) - Oriental fruit fly

These two species have been used in sterile-insect release trials on South Pacific islands. Large-scale eradication attempts should be considered.

Anastrepha suspensa - Carribean fruit fly

Successful mass rearing and sterilization studies warrant the initiation of field trials in the near future.

Anastrepha fraterculus Wied. - South American fruit fly

Mass rearing of this insect is being perfected. Determination of sterilizing dose and studies of competitiveness have been performed. The insect occurs in isolated coastal valleys of Peru which offer ideal locations for carrying out small-scale experiments.

Dacus tryoni (Froyg.) - Queensland fruit fly

The sterile-male technique has been successfully tested with this species in small isolated populations in Australia. Suppression of outbreaks appears to be possible but complete eradication seems to be more costly than could be justified by the problem.

Drosophila spp. - Vinegar flies

Information is available on the ecology, radiobiology and mass rearing of these insects. Results of small field tests in tomato fields and packing plants suggest larger field trials for the near future.

Dacus oleae (Gmelin) - Olive fly

The main obstacle is the lack of economical mass rearing. The implementation of the production through improvement of the diet is under consideration at various laboratories, and relatively expensive mass rearing may be envisaged in a few years. The production may be supplemented with rearings on olive fruits. A field test should be carried out in a sufficiently isolated small area, preferably an island, to determine the feasibility of the sterile-insect release method.

Glossina morsitans (Westwood)

and

Glossina austeni (Newstead) - Tsetse fly

Self-supporting laboratory colonies of these two species of tsetse fly exist. The feasibility of using the sterile-insect release method against G. morsitans is being studied. Sterilization by irradiation and chemosterilants is being evaluated for both species. A primary consideration should be to produce competitive insects in the laboratory on economical artificial diets.

Hylemya antiqua (Meig) - Onion fly

Semi-artificial rearing and the effects of radiation on the reproductive potential have been investigated. Basic biological studies such as dispersal and mating behaviour have been completed. Field tests are desirable.

Aedes aegypti - Yellow fever mosquito

Only one field test, in which gamma-ray sterilization was used, has been carried out with this species and it was unsuccessful, probably because

of too high a radiation dose and the fact that the treated males were not competing satisfactorily with wild males. Several genetic mechanisms are available and might be preferable to gamma irradiation. Mass rearing of this species is simple, efficient and economical. WHO is contemplating more research on the species (see WHO/VBC/ 67.47).

Aedes scutellaris - Vector of filariasis

Mass production techniques are available. Cytoplasmic incompatibility appears promising.

Culex pipiens fatigans Wied. - Vector of filariasis

A partially successful field test with insects sterilized by gamma radiation was conducted in India. Mass rearing is possible and ecological information is available. A successful test with cytoplasmic incompatible males has been conducted (see WHO/VBC/67.47).

Anopheles gambiae - Vector of malaria

Genetic mechanisms appear to offer promise. Ecological studies and current rearing procedures appear to make small-scale field experiments feasible (see WHO/VBC/67.47).

Dermatobia hominis (Linnaeus) - Torsalo, human bot fly

A fair amount of research on this species has been done in Central America. Work on ecology and behaviour was published. Progress was made on rearing larvae in an artificial medium but more research is needed. However, a small field test could be done by using larvae reared in living animals.

Haematobia irritans (Linnaeus) - Hornfly

Mass-rearing techniques have been developed which are usable for small-scale tests. Considerable biological information is available as well as data on radiation.

Musca domestica (Linnaeus) - House fly

Radiation and chemosterilant data were obtained. Ecological data and mass-rearing techniques are available. Several field trials were fairly successful, indicating a need for larger control programs.

Athonomus grandis (Bol.) - Boll weevil

Rearing methods are nearing perfection. Current sterility methods, although resulting in reduction of mating competitiveness and longevity, have enabled small-scale field tests to be carried out. Large-scale field tests are desirable.

Oryctes rhinoceros L. - Rhinoceros beetle

Damage is caused to coconut palms only by adults. Conventional ecological studies were conducted in South-East Asia and the South-Pacific region. Data on mass-production techniques and on sterilizing radiation

doses are now known for this and related dinastid species. Adults were trapped for sterilization and release studies. In view of the advanced stage of these investigations, which are supported by a UNDP(SF)/FAO/SPC project, a preliminary field test on a small infested South-Pacific island is encouraged.

Acanthoscelides obtectus Say - Bean weevil

Mass-rearing techniques and ecological and gamma-radiation studies have indicated that small field trials should be considered for this insect.

Melolontha vulgaris F. - Cockchafer

Methods of estimating population density in treated and control areas are known. Ecology, behaviour, population dynamics and other biological information suggest the feasibility of the sterile-male technique either alone or in combination with other control methods. Sterile-insect control methods would contribute decisively to long-term population regulation as a unique and efficient method. Areas of several hundreds or thousands of hectares of farmland might be protected, but technological improvements in collecting and irradiating several million adults (tons) in a few days are necessary.

Carpocapsa pomonella L. - Codling moth

Small-scale field tests indicate the feasibility of the sterile-male method. Large-scale tests are necessary to demonstrate the success of this technique on an economical basis for commercial application. Mass rearing is possible and the radiation sterilizing dose has been determined.

Diatraea saccharalis (F.) - Sugar cane borer

Many data on the biology, sterilizing radiation doses, seasonal population fluctuations and alternate host plants, such as Zea maize, are known for the sugar cane borer. The principal obstacle now is mass rearing; however, a field test might be possible with trapped wild insects.

Leucoptera coffeella - Coffee leaf miner

Mass-rearing methods and the sterilizing dose are known together with the habits of this insect. Field tests are foreseen for the near future.

Heliothia virescens (F.) - Tobacco budworm
and

Heliothia zea (Boddie) - Cotton bollworm

Rearing and testing of sterilized insects of these two species have progressed to the point that large isolated areas should be utilized.

Chilo suppressalis Walker - Rice-stem borer

The moth can be sterilized by irradiation without substantial alteration of behaviour. Economical rearing methods are under way. Small-scale field tests are necessary.

Pectinophera gonypiella (Saunders) - Pink bollworm

Rearing, although not yet perfected, has enabled field cage tests to be performed with sterilized insects and large-scale experiments are warranted.

Dysdercus peruvianus C. - Cotton red stainer

This species infests cotton in the coastal valleys of Peru. Since sterile insects cause damage, they should be released away from the crop area in spring before migration of the natural population to cotton. The natural history of this insect has been studied, mass rearing techniques have been developed and the radiation biology is currently being investigated. The natural habitat (isolated coastal valleys) offers an excellent opportunity for a pilot study to control a migratory insect.

Popillia japonica (Newm.) - Japanese beetle

Preliminary radiation and ecological information is available. There is a possibility that collected beetles can be used in small field tests.

Protoparce sexta (Ich.) - Hornworm

Information on ecology, mass rearing and radiation dose is available. The research is promising and field trials are planned.

Trichoplusia ni - Cabbage looper

Radiation data and ecological information are available. Mass-rearing techniques are progressing satisfactorily. A powerful attractant has facilitated field work and should be very useful in pilot tests with sterile insects.

See Panel Recommendation No. 1 in the Appendix.

3. NEED FOR A RESEARCH DEVELOPMENT AND EVALUATION FUND

The information necessary for application of the sterile-insect release method to a specific pest is by no means complete after basic research on an insect has shown that the method is likely to be feasible as a means of control. It is essential to conduct pilot experiments to demonstrate the effectiveness of the technique before the method can be applied in a practical project to control any given pest. Such tests must be conducted on a scale adequate to demonstrate the feasibility and practicability of mass rearing the insect. Efficient methods must be developed to reduce costs of materials and labour. Cost analyses must be made that can be used for practical application. Suitable test sites must be selected and basic data obtained on the population ecology of the insect in the test area. To demonstrate the feasibility of eradication, a test area must be found that provides complete isolation, such as an island or an isolated valley. If suppression of a population in a non-isolated area is the goal, the test site must be large enough to demonstrate effective suppression. The effectiveness of the released insect must be demonstrated by showing the rate of overflooding of native insects and by showing a suppression in insect populations in relation to previous history and/or in comparison with a comparable untreated area.

Facilities, funds, manpower and technical competence which suffice for basic and small-scale applied research are totally inadequate for the research development and evaluation required for the pilot stage of the sterile-insect release technique. Generally, the development of pesticides has been supported by the chemical industries that undertake this development themselves, but public funds must be provided for these phases in perfecting the sterile-insect release method. The funds needed to complete the research development and evaluation phases will vary with the insect and the location. However, experience with insects for which these phases have been completed indicates that such costs will probably range from about \$50 000 to \$500 000 per annum for each insect over a period of two to three years.

The report of the Panel shows that research on the pilot testing phase is needed for a dozen or more insect species and this number can be expected to increase each year as adequate basic information is obtained on other insects under investigation.

To proceed with the development of the technique with the wide range of insects for which the method shows promise, it is essential that a special research development fund first be established by international agencies to finance the pilot testing phase of the technique. It would be essential for such tests to be financed with international funds, since developing countries cannot be expected to finance such test programs. Furthermore, many insect pests cover large areas and are not limited by international boundaries. Money from such funds should be used only for development of the technique and not for practical suppression or eradication programs. As pilot tests for different insects are completed, which will probably require a minimum of two to three years for each test, the funds should revert back to the development fund and be employed for pilot testing of the method with other insects.

See Panel Recommendation No. 2 in the Appendix.

4. LIST OF INSECTS ON WHICH BASIC AND APPLIED RESEARCH IS NEEDED

Listed below are species of insects on which research should be encouraged with the goal of utilizing the sterile-male technique for eradication or control of these species. This inventory, suggested by the Panel, does not include all insects deserving further investigation. Some of these insects have been investigated to a limited extent, others have been used successfully in field trials while others have not been studied at all. All of them, regardless of stage of development, need research in certain areas to reduce costs or increase efficiency.

This list of pests of economic importance is proposed with priority for:

- (1) species which transmit diseases;
- (2) species which already have developed or are building up resistance to insecticides;
- (3) species which have a very low tolerance level of infestation on their host animals, host plants or on commodities;

- (4) species requiring chemical control that would result in intolerably high residue levels;
- (5) species for which no alternative control methods are available.

Order	Species	Common name
Diptera	<u>Aedes aegypti</u> (Linnaeus)	Yellow fever mosquito
	<u>Anastrepha fraterculus</u> (Wied)	South American fruit fly
	<u>Anastrepha ludens</u> (Loew)	Mexican fruit fly
	<u>Anastrepha scutellaris</u> (Walker)	Fruit fly
	<u>Anastrepha suspensa</u> (Loew)	Caribbean fruit fly
	<u>Anopheles gambiae</u> (Giles)	Mosquito
	<u>Ceratitis capitata</u> (Wied)	Mediterranean fruit fly
	<u>Ceratitis rosae</u>	Natal fruit fly
	<u>Cochliomyia hominivorax</u> (Coquerel)	Screw-worm fly
	<u>Culex fatigans</u> (Wied)	House mosquito
	<u>Dacus cucurbitae</u> (Coquerel)	Melon fly
	<u>Dacus dorsalis</u> (Hendel)	Oriental fruit fly
	<u>Dacus oleae</u> (Gmelin)	Olive fly
	<u>Dacus tryoni</u> (Frogg)	Queensland fruit fly
	<u>Dermatobia hominis</u> (Linnaeus)	Human bot fly, Torsalo
	<u>Drosophila spp.</u>	Vinegar flies
	<u>Glossina spp.</u>	Tsetse flies
	<u>Leptolytlemyia coarctata</u> (Fallen)	Wheat bulb fly
	<u>Lucilia (Phaenicia) spp.</u>	Blowfly
	<u>Musca autumnalis</u> (Degue)	Face fly
	<u>Musca spp.</u>	House flies
	<u>Myiopardalis pardalina</u> (Big)	Asian fruit fly
	<u>Pegomya hyoscyami</u> (Panzer)	Paug. beet fly
	<u>Phorbia antiqua</u> (Neigen)	Onion maggot
	<u>Phorbia brassicae</u> (Bouché)	Cabbage maggot
	<u>Phorbia ciliocrura</u> (Rondani)	Seed corn maggot
	<u>Phorbia floralis</u>	Turnip maggot
	<u>Psila rosae</u> (Fabricius)	Carrot fly
	<u>Rhagoletis cerasi</u> (Linnaeus)	Cherry fruit fly
	<u>Rhagoletis cingulata</u> (Loew)	Cherry fruit fly
	<u>Simulium spp.</u>	Black flies
	<u>Stomoxys calitrans</u> (Linnaeus)	Stable fly
	Coleoptera	<u>Acanthoscelides obtectus</u> (Say)
<u>Amphimallon majalis</u> (Razoumowsky)		European chafer
<u>Amphimallon solstitialis</u>		European chafer
<u>Anthonomus grandis</u> (Boheman)		Boll weevil
<u>Anthonomus vestitus</u>		Cotton square weevil
<u>Bothynoderes punctioentris</u> (Germ)		Sugar beet weevil
<u>Bruchus pisorum</u> (Linnaeus)		Tea weevil
<u>Costelytra zealandica</u>		Grass grub
<u>Diabrotica spp.</u>		Root worms
<u>Dynastid beetles (Oryctes spp.)</u>		Rhinoceros beetles
<u>Epilachna spp.</u>		Leaf beetles
<u>Hylotrupes bajulus</u>	Old house borer	

Order	Species	Common name
	<u>Leptinotarsa decemlineata</u> (Say)	Colorado potato beetle
	<u>Melolontha hippocastani</u> (Fabricius)	Cockchafer
	<u>Melolontha vulgaris</u> (Fabricius)	Cockchafer
	<u>Phyllopertha horticola</u>	Garden chafer
	<u>Popilla japonica</u> (Newm.)	Japanese beetle
	<u>Phyndites cupreus</u> var. <u>auratus</u>	Weevil
	<u>Sitophilus granaria</u> (Linnaeus)	Granary weevil
	<u>Tremuoctrypes solani</u> (Pierce)	Andean weevil
	<u>Scotytidae spp.</u>	
Lepidoptera	<u>Cacoecia promulana</u>	Daisy tortrix
Hemiptera	<u>Carpocapsa pomonella</u> (Linnaeus)	Codling moth
	<u>Centrogaster integriceps</u>	Grape phylloxera
	<u>Chilo suppressalis</u> (Walker)	Rice stem borer
	<u>Dactylosphera vitifolii</u> (Shimer)	Grape phylloxera
	<u>Dendrolimus spectabilis</u> (Butler)	Korean pine caterpillar
	<u>Diatraea saccharalis</u> (Fabricius)	Sugar cane borer
	<u>Distantiella theobroma</u> (Distant)	Cacao capsid
	<u>Dysdercus peruvianus</u> C.	Cotton red stainer
	<u>Grapholita tunebrana</u> Tr.	Plum fruit moth
	<u>Heliothis spp.</u>	Fruit worms
	<u>Hyphantrea cunea</u> (Drury)	Western fall webworm
	<u>Nezara viridula</u> (Linnaeus)	Southern green streak bery
	<u>Ostrinia nubilalis</u> (Hübner)	European corn borer
	<u>Pectinophora gossypiella</u> (Saunders)	Pink bollworm
	<u>Pectinophora malvella</u> (Hübner)	Mallow moth
	<u>Phylloxera vastatrix</u> (Planel.)	
	<u>Porthetria dispar</u> (Linnaeus)	Gypsy moth
	<u>Prodenia litura</u> (Fabricius)	Cotton leaf worm
	<u>Protoparce sexta</u> (Johansen)	Tobacco hornworm
	<u>Spodoptera spp.</u>	Army worms
	<u>Spodoptera exigua</u> (Hübner)	Cutworm moth
	<u>Trichoplusia spp.</u>	Loopers
	<u>Zeuzera pyrina</u> (Linnaeus)	Leopard moth
Other Phyla	Nematodes	Eelworms
	Vertebrateae	Rodents, birds
	Acari: <u>Ornithodoros tholozani</u>	Laboulleum and ticks

See Panel Recommendation No. 3 in the Appendix.

5. PRIOR REDUCTION OF INSECT POPULATIONS TO LEVELS MANAGEABLE BY THE RELEASE OF STERILE INSECTS

In view of the high natural densities of many major insects, the application of the sterile-insect release method alone is not likely to be economically feasible in most areas. An important part of research on the develop-

ment of the sterile-male method should therefore involve investigations on ways to reduce high natural populations drastically before contemplating the use of sterile-insect releases. A high level of suppression by chemical, biological, cultural or other means may be possible in a well co-ordinated program and thus reduce populations well within the range of practical management with sterile insects. Complete suppression of the populations below the economic threshold levels might then be achieved and maintained indefinitely in large areas by the release of sterile insects at a cost less than that of the usual methods employed for control.

The initial investment for such a program might be very high, but in the long run it could represent a temporary investment and result in the maintenance of sub-economic-threshold regional populations which would otherwise cause high losses in spite of conventional control methods.

See Panel Recommendation No. 4 in the Appendix.

6. BASIC RESEARCH ON THE POPULATION ECOLOGY OF MIGRATORY INSECTS CONSIDERED AS PROMISING CANDIDATES FOR APPLICATION OF THE STERILE-INSECT RELEASE METHOD

A number of lepidopterous insects of major importance as pests of cereals, other basic food crops and cotton in various parts of the world are known or suspected to disperse widely from their source of origin each season. The Heliothis species complex is of particular importance among the migratory insects.

In view of the high losses caused by these insects and the difficulties and high costs generally experienced in their control by conventional means, there is an urgent need to develop more effective, less costly and more selective means for their suppression on a regional basis.

The feasibility of employing sterile-insect releases as a means of population suppression on a regional, national or international basis cannot now be determined because of a lack of information in areas where the insects overwinter, their distance and rate of dispersion, and their density, especially during periods of scarcity and restricted distribution. Support for research on the population ecology of such insects will be essential before an intelligent approach to their control by the sterile-insect technique or by any other method can be formulated. Close co-operation by investigators in various contiguous countries may be necessary and should be facilitated wherever possible.

See Panel Recommendation No. 5 in the Appendix.

7. SUB-STERILIZING DOSES OF RADIATION

The Panel members discussed recent work on the effectiveness of sub-sterilizing doses of radiation on lepidopterous insects. It has been found that sub-sterilizing doses of radiation or chemicals can lead to a level of sterility in surviving F_1 progeny that is higher than the sterility level in the parent generation. Other work indicates that a sub-sterilizing dose may carry over into the F_2 , F_3 or F_4 generation. Obviously, sub-sterilizing

doses should make it possible to release moths that are stronger and more competitive than those receiving a 100% sterilizing dose.

See Panel Recommendation No. 6 in the Appendix.

8. INCREASED STUDIES ON GENETIC MECHANISMS, BIOLOGY AND FIELD ECOLOGY

The Panel discussed the possibilities of utilizing sterility mechanisms such as cytoplasmic incompatibility, hybrid sterility, chromosomal rearrangements, etc. for insect suppression or eradication. A good example of genetic manipulation is the highly successful use of a strain of cytoplasmic incompatible Culex pipiens fatigans males in a natural population. Many other genetic control possibilities exist with Aedes aegypti, Anopheles gambiae and possibly destructive insect plant pests. For both genetic and radiation-induced sterility there is a need for much research on reproductive biology and field ecology, especially for data on seasonal densities to exploit more fully the sterility methods of control. The WHO Scientific Group on Cytogenetics of Vectors of Disease of Man, 1967, discussed these items in considerable detail.

See Panel Recommendation No. 7 in the Appendix.

9. BASIC RESEARCH ON THE PREVENTION OF DISEASES IN MASS-CULTURED INSECTS

A major obstacle to the practical development of the sterile-insect technique for many of our most important insect pests is the occurrence of disease in the mass-cultured insects. Disease problems may occur in any kind of cultured insect, but they are especially difficult to deal with in the mass production of most lepidopterous species.

There is an urgent need to conduct basic studies on the nature, course, diagnosis and prevention of such diseases. The influence of nutritional deficiencies, unsuitable laboratory environments and other stresses may also be involved in such investigations.

A satisfactory solution to these insect disease problems is essential to advance the sterile-insect release technique to a practical stage and, in addition, the mass production of selective pathogens, selective parasites and selective predators for use in biological control alone or for integration with the use of sterile insects hinges on the control of diseases in mass-cultured insects.

See Panel Recommendation No. 8 in the Appendix.

10. WORK AT SEIBERSDORF LABORATORY

The Panel was pleased to see the substantial contributions of the Entomology Section of the Seibersdorf Laboratory to research on tsetse flies, the Mediterranean fruit fly and the olive fly. This research comple-

ments the Mediterranean fruit fly projects in Central America and Capri, the olive fly research in various Mediterranean countries and the tsetse fly research in European and African laboratories. An important contribution of the laboratory was the development of bagasse for use in the larval rearing medium which resulted in a saving of US \$100 000 in the Costa Rica project. Important information was acquired on Medfly release which has significantly assisted all Medfly projects. Current work on developing vigorous strains of Medflies and olive flies is very important.

The budget could justifiably be increased many times on the basis of the world's food and medical needs.

See Panel Recommendation No. 9 in the Appendix.

11. RESEARCH ON THE TAXONOMY, GENETICS AND CYTOGENETICS OF MEDFLY

Experience with the Mediterranean fruit fly (Ceratitis capitata) has shown that many strains exist. The question arises as to the taxonomic and genetic relationships of these strains. Studies on this subject could provide information useful for control programs. Anastrepha species should also be considered in this context.

See Panel Recommendation No. 10 in the Appendix.

12. THE USE OF RESEARCH CONTRACT FUNDS SHOULD BE CONCENTRATED ON A FEW INSECTS RATHER THAN ON MANY

Where possible, IAEA Research Contract funds should be expended on a co-ordinated regional basis, such as on the rice-stem borer in the Far East or the Heliothis complex or codling moth in North and South America and Europe.

See Panel Recommendation No. 11 in the Appendix.

13. A CO-ORDINATED RESEARCH PROGRAM FOR RICE INSECT CONTROL

Rice is one of the most important food crops in the world and rice-stem borers cause large losses in the production of this staple food. The establishment of an international co-ordinated program will foster more rapid research progress in utilizing the sterile-male method of insect control.

See Panel Recommendation No. 12 in the Appendix.

14. USE OF STERILITY TECHNIQUES FOR THE SUPPRESSION OF VERTEBRATE PESTS

The sterility principle for pest management should be applicable to vertebrate pest problems. Chemicals that induce sterility in both sexes of vertebrate pests, such as rodents and birds, without serious adverse

effects on length of life or mating behaviour, are potentially much more effective in suppressing reproduction than are chemicals that kill the organisms. The use of chemosterilants would effect a combined chemical and biological system for pest management. The pests directly affected by the sterilizing chemical could not reproduce, thus resulting in suppression of reproduction equal to a comparable level of kill. Furthermore, they in turn become biological agents for the suppression of reproduction among the animals not treated directly. Irreversibly sterilized animals in a population are capable of suppressing reproduction as long as they live. Thus, not only does the suppression of reproduction affect the treated (sterile) generation but substantial suppression of reproduction will continue in the untreated (fertile) population for several generations.

In addition to the potentially greater population suppression achieved by this approach to vertebrate pest management, there is another advantage, namely, it should be more acceptable to a public often strongly opposed to the killing of animals by conventional means.

There is an urgent need to develop effective chemical sterilants for use against vertebrate pests and to employ safe ways for selective control of the target pest.

See Panel Recommendation No. 13 in the Appendix.

15. PREPARATION AND PUBLICATION OF TWO MANUALS ON THE STERILE-MALE METHOD OF INSECT CONTROL FOR THE GUIDANCE OF SCIENTISTS AND ADMINISTRATORS

There are many requirements for the successful application of the sterile-insect release technique. An investigator new to this field is often confronted with problems on requirements and limitations and with other pitfalls. A manual describing methods and approaches would here be of great assistance. The manual would be aimed principally at the scientific worker beginning to work with the technique and should present the method in a realistic way. In addition, a shorter publication should be written to provide an explanation of the theory and application of the technique for administrators and other non-specialists.

See Panel Recommendation No. 14 in the Appendix.

16. TRAINING

Since sterile-insect control methods are often complex and involve such diverse disciplines as biology, radiology, physics, chemistry, economics and mechanical engineering, it is urgently necessary that the Joint FAO/IAEA Division give special consideration to the training of scientists and scientific administrators in the sterile-male technique. Training should be encouraged in several ways:

- (a) A continuation of the Joint Division Training Course on Use of Radiation and Radioisotopes in Entomology with some restructuring of

the material presented to place more emphasis on the various aspects of sterile-insect control methods and less on radioisotope methods.

(b) Every effort should be made to introduce potential senior project workers to the problems associated with the technique by placing them in a work-study situation. This could be done by having them participate for an extended period in an operational field sterile-male program.

(c) The Joint Division should encourage and support graduate training of promising young entomologists from developing countries who will provide the backbone for future eradication programs.

(d) From time to time the Joint Division should sponsor regional workshops and/or seminars for active workers in the sterile-insect technique for the purpose of exchanging information. The meetings should preferably be held at a laboratory where a program is in progress, and participants should come from both developing and developed countries.

See Panel Recommendation No. 15 in the Appendix.

PAPERS PRESENTED AT THE PANEL

CONCEPT AND VALUE OF ERADICATION OR CONTINUOUS SUPPRESSION OF INSECT POPULATIONS

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Abstract

CONCEPT AND VALUE OF ERADICATION OR CONTINUOUS SUPPRESSION OF INSECT POPULATIONS.
A general review of the sterile-male technique is followed by a discussion of the application of this technique to certain insect species such as the corn earworm, Heliothis zea (Boddie), the codling moth, Carpocapsa pomonella (Linnaeus), the pink bollworm, Pectinophora gossypiella (Saunders), the gypsy moth, Porthetria dispar (Linnaeus), the sugar-cane borer, Diatraea saccharalis (Fabricius), and others. The potential of F₁ sterility resulting from sub-sterilizing doses of gamma radiation administered to the P generation is discussed.

1. INTRODUCTION

This report considers some of the basic principles governing the role that the sterility technique can play in the suppression or elimination of insect populations. Although these principles have been considered in a number of publications, it seems desirable to discuss them again. The report also includes brief statements on research progress on several insect species in the United States and offers comments on the potential possibilities of employing the sterility technique for the suppression of certain lepidopterous insects.

1.1. Two basic sterility techniques

It should be made clear that there are two basic techniques involved in the application of the sterility methods to the management of pest populations. It seems important to discuss them and point out the basic differences in their application. The best known technique involves the rearing or collection of insects, which are made sterile or in which some other genetic deficiency is induced, and then releasing them into the environment on a sustained basis in numbers adequate to overwhelm the natural population. Various methods of causing sterility or other genetic defects in the insects prior to release may be used, including exposure to atomic radiation, exposure to chemical agents that cause sterility, the crossing of related strains that produce hybrid sterility, the development and release of strains that are somatically incompatible with the natural strain to be controlled, and the selection and release of strains that carry various lethal traits such as distorted sex ratios or conditional lethal factors.

The other basic technique involves the treatment of a portion of the natural population of a pest with a chemical that causes sterility rather than death. This method either ensures that the sterilization is irreversible or else it is applied frequently enough to maintain a high level of sterility and in such a way that it does not drastically change the normal mating behaviour or mating competitiveness of the sterilized animals. At present there is only one feasible means of achieving sterility in natural pest populations. This is by the use of chemical agents that cause sterility. These chemical agents are generally referred to as chemosterilants.

2. REVIEW OF THE POTENTIAL VALUE OF STERILIZATION OF NATURAL PEST POPULATIONS

The chemosterilant method of pest population suppression should be useful for any type of organism, invertebrate, or vertebrate, if a suitable means of applying the sterility treatment can be developed. The method is basically much more effective than the killing method. The technique of sterilizing organisms in the natural population should be particularly advantageous in the management of vertebrate pest organisms, such as birds, rodents, predators or any organism that may become a pest when present in large numbers. Chemical sterilization of natural pest populations actually combines two systems of population suppression: the chemical and the biological. The direct and immediate effect on the treated animals is caused by chemical action. If the degree of sterilization is equal to the degree of kill, this direct effect in limiting reproduction of a population is the same as that of a killing agent. For example, if an agent can sterilize 90% of the natural pest population, the immediate effect will be equivalent to killing 90% of the natural pest population, since only 10% of the original population will be capable of reproducing in each case. However, after 90% of the population is killed, no other population suppression effect can occur. On the other hand, if 90% is suitably sterilized, further suppression of reproduction can occur in the population because of competition for mates between the sterile and fertile organisms. All organisms that escape or survive exposure to a killing agent are not only capable of reproducing but they have the advantage of less competition for food and shelter, and perhaps less predation pressure than the original higher population. This can lead to a higher survival and reproductive rate per individual than was the case for individuals in the original population. The organisms that escape exposure to the sterilization treatment must not only compete for fertile mates on a chance basis, they must also compete with the sterile individuals for food, shelter and breeding sites as long as any of the sterilized organisms remain in the environment. The total impact of the sterilization treatment can be very great, especially among long-lived animals. If fully competitive in mating, the sterilized organisms can reduce the reproductive capability of the normal population proportionally to the ratio of sterile to fertile organisms in the population. If 90% of the natural population has been sterilized, this will mean that reproduction in the remaining fertile population can also be reduced by 90%. Moreover, the continuing effect of sterilized organisms on reproduction in subsequent generations is also a major deterrent to reproduction, especially for long-lived animals.

TABLE I. RELATIVE EFFECT OF STERILIZATION VERSUS KILLING IN THE SUPPRESSION OF REPRODUCTION IN NATURAL PEST POPULATIONS

Effect of killing	Effect of sterilization
<ol style="list-style-type: none"> 1. Potential reproduction in a population is immediately reduced proportionally to the percentage of the population killed. 2. Organisms that escape the killing treatment are immediately subject to less competition for food, shelter, breeding sites, and other density-dependent population suppression effects. 	<ol style="list-style-type: none"> 1. Potential reproduction in a population is immediately reduced proportionally to the percentage of the population actually sterilized. 2. Potential reproduction in the population that escapes direct sterilization is subsequently further reduced proportionally to the percentage of the population that is sterilized. 3. Potential reproduction in the population continues to be suppressed in subsequent generations proportionally to the ratio of sterile to fertile organisms in the environment. 4. Sterilized organisms continue to compete for food, shelter and nesting sites, and otherwise exert density-dependent suppression effects as long as they survive.

The relative advantages of sterilization over killing as a means of suppressing reproduction in natural animal populations are summarized in Table I.

To project the relative effect of sterilization versus killing into representative pest population models, one must consider the life history of the pest, its reproductive potential, normal survival rate and other factors. However, if we assume that the pest population has a normal capacity to increase at a rate of 50% in one generation, and if this population consists of half the previous parent population, the effect of the two methods can be projected as shown in Table II.

The potentially greater impact on pest population suppression afforded by sterilization, especially among long-lived animal pests, is readily apparent when the trends in the hypothetical models are noted. To achieve such effects it will be necessary to develop sterilization chemicals that are highly effective, which produce irreversible sterility, and which do not adversely affect mating competitiveness and length of life of the sterilized organisms. Such materials are not yet available, but their potential advantage over normal toxic agents are of such magnitude that a concerted research effort in this area is amply justified.

We are here concerned primarily with a consideration of progress and problems associated with the use of the first technique mentioned - the release of insects into the environment. However, it seemed desi-

rable to depart from this main theme to define clearly the types of sterility now under investigation and to explain the difference in the two methods for the suppression of pest populations.

Until effective chemosterilants are found that can be used safely in the environment, the technique involving the sterilization of the natural population cannot be put into practical use. However, research should continue in the search for effective and safe ways to sterilize pest insects and other animals. In this connection, some of the insect hormones or their derivatives may provide safe selective sterilants or growth-regulating effects that would achieve the same effect as conventional chemosterilants.

3. REVIEW OF THE POTENTIAL USE OF RELEASED STERILE ORGANISMS WITH PARTICULAR REFERENCE TO LEPIDOPTEROUS INSECTS

The release of sterile insects to compete with the natural population will not provide a feasible or practical control method for all insect pests. However, when basically feasible and properly used, the technique could provide a population suppression mechanism that would materially advance the control or eradication of some of our most important insect species. The potential of the sterile-insect release method is probably not yet fully realized by most scientists and scientist-administrators. Much research and development may be required to realize the potential for each insect problem amenable to control by the method. However, this should not deter us in fully exploring the potential.

We might list the situations in which sterile-insect releases are likely to be useful:

- (1) For use alone in the eradication of isolated established insect populations. Generally, such populations must exist at a low density level and/or be restricted in distribution at some period in the seasonal cycle.
- (2) To prevent the establishment and spread of insects into new areas.
- (3) To eliminate new incipient infestations in restricted areas before natural populations can build up and spread into larger areas.
- (4) To use as an adjunct with other methods to achieve complete suppression of large non-isolated populations or to achieve eradication of isolated populations.
- (5) To maintain continuous suppression of insect populations in areas subject to constant reinvasion, after established populations have been brought under control by various integrated means.

A number of factors must be considered and weighed before it can be determined whether the release of sterile insects is likely to be useful in the suppression or eradication of a given insect pest. How damaging is the pest to be controlled? How many insects occur in the natural population? What are the costs or potential costs of rearing the insects in large numbers? How competitive are the sterilized insects when released to compete with the natural population? What are the costs involved in using available methods and what are the alternative methods of control on a long-range continuing basis? These are just some of the questions that

must be answered in considering the justification for undertaking research to develop the sterile-insect release method.

3.1. Possible use of the sterile-insect technique for the suppression of certain lepidopterous insects

(a) Corn earworm - Heliothis zea

In my opinion, relatively few insect problems have been analysed from all aspects to determine if sterile-insect releases can serve a useful role in their control. In making such an appraisal, the potential value of the sterile-insect release technique as a major component in a control system should be considered in relation to alternative methods over a period of years, perhaps 10 years or longer.

TABLE II. THE ASSUMED TREND OF SIMILAR POPULATIONS, EACH STARTING WITH 1000 INDIVIDUALS, AFTER THEY HAVE BEEN SUBJECTED TO: 1. NO CONTROL; 2. 90% CONTROL OF THE INITIAL POPULATION WITH A KILLING AGENT; 3. 90% STERILIZATION OF THE INITIAL POPULATION WITH A STERILIZATION AGENT. THE NORMAL POPULATION IS ASSUMED TO STABILIZE AT A DENSITY OF ABOUT 2000 IN ITS ECOLOGICAL ENVIRONMENT.

Generation	No control	90% kill of initial population	90% sterilization of initial population
1	1000	1000 ----> 100	1000 --> (900 sterile; 100 fertile)
2	1500	150 ←	510 (a) (450 sterile; 60 fertile)
3	2000	225	262 (225 sterile; 37 fertile)
4	2000	337	136 (113 sterile; 23 fertile)
5	2000	505	72 (56 sterile; 16 fertile)
6	2000	758	40 (28 sterile; 12 fertile)
7	2000	1137	23 (14 sterile; 9 fertile)
8	2000	1705	15 (7 sterile; 8 fertile)
9	2000	2000	12 (4 sterile; 8 fertile)
10	2000	2000	11 (2 sterile; 9 fertile)
11	2000	2000	13 (1 sterile; 12 fertile)
12	2000	2000	17 (0 sterile; 17 fertile)

(a) According to the assumptions, 10 of the 100 fertile organisms would reproduce successfully and yield 10 progeny that survive to reproduce in the next generation. The 10 new progeny added to the 50% survivors of the 1000 original population would total 510. Of the 510 survivors in generation 2, 450 would represent survivors of the 900 sterile organisms, 50 would represent survivors of the original 100 fertile organisms remaining after treatment of the population, and 10 would represent progeny from the 10 animals that reproduced successfully. All calculations for subsequent generations were made in the same way.

We might select H. zea, which poses the most important insect problem in the United States, to illustrate an example of the type of analysis that should be made. Entomologists in the United States have been slow to suggest that the sterile-insect method could provide a practical solution to the problem caused by this insect pest when applied in regional or national programs. Admittedly, there are important gaps in our knowledge of the population ecology of this insect, which makes it difficult to make a good appraisal of the feasibility of using the sterile-insect release method. However, I believe that we have enough information to suggest that there are good chances for the sterility technique to be developed as a more effective and more economical long-range solution to this major insect problem than current control methods.

It is estimated that Heliothis zea causes losses, including control costs, totalling about \$400 million per year in the United States. It is the major pest of field corn. It rivals the boll weevil as a pest of cotton. It causes heavy losses in the production of sweet corn, tomatoes, field beans, leafy vegetables and a number of other crops. A wide variety of broad-spectrum insecticides are employed for its control that give rise to residue problems and have adverse effects on beneficial insects.

If we assume that, with current control methods, annual losses to United States agriculture caused by the insect is of the order of \$400 million, an effort should be made to appraise the potential value of sterile moths as a means of control or as a major component in integrated systems of control. If it is within the realm of feasibility to mass produce, sterilize and release large numbers of H. zea at a cost of \$5.00 per 1000 moths, which I regard as a good possibility, we can calculate that for \$400 million it would be possible to rear and release about 80 billion sterile moths. The question is: What are the chances that 80 billion sterile moths would have to achieve complete or virtually complete suppression of this pest throughout the United States? We cannot answer this question because we do not know how many H. zea overwinter in the United States each year. However, if the total overwintered population normally does not exceed a few hundred million, it may require far fewer than 80 billion moths to maintain suppression below the economic damage level even during the first year. If such circumstances do exist, this approach would be, from both an economic and an aesthetic standpoint, as good as or better than the methods of control now employed. However, the continuing costs over a 10-year period would provide the most realistic appraisal of the potential of this approach to H. zea control. If the insects were effectively suppressed for one year, the numbers of the starting population the following year might be expected to be substantially below normal. In that event, the number of sterile insects required, and hence the cost necessary to maintain suppression during the second and subsequent years, should be proportionally lower.

The continuing costs after the first year might be only a fraction of the cost for that year. Moreover, the insect might be virtually eliminated from certain regions of the nation and continuous suppression might involve the establishment of sterile moth barriers in strategic places, in the same way as the sterile screw-worm barrier is now being maintained along the United States-Mexico border. Thus, we might relegate our most important insect problem to one of little or no economic consequence at a continuing

cost that would be only a fraction of the losses under current control practices.

Obviously, a program of the nature suggested, if perfected, would be complex and require substantial financial support. Because of the magnitude of such a program, the sterility approach may be regarded in some quarters as impractical. Yet, when we consider control costs and losses as well as certain objectionable features of current methods of dealing with this insect in relation to the possible costs and advantages of the sterile-insect release method, there is every justification for a full exploration of the feasibility of the method. I may be overly optimistic in appraising the potential costs and benefits of the sterility method, but at the same time there is a possibility that my projections are too conservative.

I purposely selected H. zea in the United States as an example of one of the most difficult and costly insect problems to deal with. This was done to emphasize the need for a critical appraisal of an insect problem in all of its aspects before concluding that the sterile-insect technique would be an impractical solution. H. zea is perhaps the most widespread major insect pest in the United States. In the summer months it is present throughout the country and attains fantastic numbers at certain times of the year. It is known to disperse for long distances. It attacks a wide range of host crops, both cultivated and wild. The cost of rearing the insect can be expected to be quite high. Nevertheless, in spite of the many features that would seem to rule out the sterile-insect release technique as a practical means of control, a critical consideration of these factors in relation to the costs and limitations of alternative control methods leads me to believe that the sterility technique (combined with other prior population suppression measures if necessary) might eventually be the best long-range solution to this problem. A similar critical analysis should be made of other major insect problems throughout the world to judge whether research on application of the sterile-insect technique is justified.

I should emphasize that we cannot yet say that the sterility method will offer a practical solution to the H. zea problem in the United States. We need to make a complete seasonal study of H. zea abundance in the country. Basic information is needed on early season host plants, both cultivated and wild. We need to determine what crops produce the larvae that give rise to most of the overwintered moths the following spring. A determination must be made as to where and how many moths overwinter in various regions in the United States. We need to know how far and in what numbers the insect migrates. With such basic information, we will be in a better position to make a reasonable estimate of the feasibility of using the technique and of the costs likely to be involved in the suppression of this insect on a regional or national basis.

(b) Codling moth - Carpocapsa pomonella

Research by entomologists in Canada and in the United States has been under way for a number of years to develop the sterile-insect technique for control of this key pest of apples and pears. There is little need to go into detail in discussing this program, since published results are available. However, steady progress has been made in both countries and final demonstration tests may be all that is necessary to put the technique into practical operation.

(c) Pink bollworm - Pectinophora gossypiella

The pink bollworm has long been regarded as a likely candidate for practical application of the sterile-moth technique. As with most insect problems, the main goal of the technique will be to prevent the spread of populations and to eliminate low-level infestations after high established populations have been reduced by cultural, chemical and other means. The westward spread of the insect into Arizona, California and other irrigated cotton regions of the western United States is threatening economical cotton production in these areas.

Research by the cotton insect investigators of the Division's Brownsville, Texas, laboratory has shown that the pink bollworm can be sterilized by chemicals and by gamma radiation. Good progress has also been made on mass-rearing procedures, although the control of pathogenic diseases in the cultures is still a major problem in large-scale production. M. T. Ouye of the Brownsville staff demonstrated that caged populations could be greatly suppressed or eliminated by releasing a high ratio of sterile moths.

The present situation in California can serve as a good example of the potential role that sterile pink bollworms might play in preventing the spread of this insect.

The principal cotton growing area in California is in the San Joaquin Valley where about 200 000 acres are grown. In 1967 a few insects spread into the southern portion of the valley from infested cotton in other regions of the state. State and Federal regulatory agencies caught a few moths in sex pheromone traps, and a few infested bolls were found in the late autumn of 1967. On the basis of available information, it has been estimated that the total overwintered population of pink bollworms in the spring of 1968 will not exceed 3000-4000 in the lightly infested valley. Even though the successful use of sterile pink bollworms has not been demonstrated in field tests, it seemed desirable to recommend to regulatory officials that pink bollworms be reared to the maximum extent that current funds, facilities and technical knowledge would permit, and that the sterile moths be released in the infested part of the valley. It is hoped that this effort will prevent establishment of the insect and subsequent spread of the population into the entire valley. If the overwintered population does not exceed 5000 moths in an area of about 20 000 acres as estimated, the release of only one million sterile moths against the emerging overwintered pink bollworm moths would provide an average ratio of at least 200 sterile to 1 fertile moth in the infested area. Even if sterilized moths are substantially less competitive than normal moths, such a high ratio should prevent the usual increase in abundance. Continued releases of sterile moths throughout the season should in such an event prevent natural population build-up and spread.

The US Department of Agriculture and the California Department of Agriculture are engaged in the joint program to use sterile moths for release in the San Joaquin Valley. Intensive surveys will be conducted and moth releases made wherever infestations are found in cotton or where moths are caught in pheromone-baited traps.

The crash program to prevent the spread of the pink bollworm will be watched with great interest. In the meantime, research is continuing in an effort to demonstrate that sterile-moth releases are capable of

eliminating well established but low-level natural populations. If current efforts are successful, the logical step would be to reduce moth populations in known infested areas in the western region through a rigid cultural control program, supplemented by the use of chemicals if necessary, to achieve sufficiently low levels to permit the elimination of the insect by the release of sterile moths.

It is estimated that with current costs of rearing (about \$2 per 1000 moths) the release of sterile moths, if perfected for large-scale operations, would probably be more effective and economical than any other method of control when the natural population exists at a level of about 100 moths per acre. The release of 2500 sterile moths per acre per generation for five generations would provide an initial ratio of 25:1. The cost of moths for such a program would amount to about \$25.00 per acre. It is unlikely that an established population of this level could be eliminated by any other known means at the same cost. If the sterile moths exist at levels averaging only a few moths per acre, the method would become correspondingly more favourable in relation to other methods of control. If the natural population were 10 overwintered moths per acre, an initial release of 250 moths per acre would then provide a 25:1 ratio.

The population dynamics of the pink bollworm under different ecological conditions are likely to vary. However, field and cage studies indicate that a five-fold increase per generation is a realistic increase rate. A ratio of 25 reasonably competitive sterile moths to 1 fertile moth should in such an event be adequate to assure a downward trend in a natural population. Subsequent releases would then achieve progressively higher sterile-to-fertile ratios.

It might be pointed out that the pink bollworm in western irrigated cotton will probably have about five generations. If the starting population is as low as 10 moths per acre, the population could increase to economic-threshold numbers in one season. This is indicated by the hypothetical population model below:

Parent overwintered population	10
F ₁	50
F ₂	250
F ₃	1250
F ₄	6250

By the time the population reaches a level of 3125 males and 3125 females per acre, economic damage can be expected. Three thousand females would be capable of depositing about 300 000 eggs. If 25% of the eggs developed into larval infestations, this would provide an average of about one larva per boll in the late autumn before cotton is harvested. Such a rate of infestation would also provide a large potential overwintered pink bollworm population for the following season.

If it is not feasible to eradicate an insect population of this nature because of lack of isolation, control by the continuous release of sterile moths might be more effective, more desirable and more economical than by the use of current chemical control methods.

(d) Gypsy moth - Porthetria dispar

The gypsy moth is an important forest pest capable of defoliating and seriously damaging hardwood forests in the north-eastern part of the United States. It threatens to spread southward and westward into millions of acres of hardwood forests. Federal and State regulatory agencies have for many years attempted to prevent the spread of the pest from the New England region. The use of DDT provided a highly effective means of control. However, due to the residue problem, there is intense opposition to the continued use of DDT for this purpose.

The Plant Pest Control Division (Methods Improvement Laboratory) of the US Department of Agriculture has been investigating the possible use of sterile males to eliminate low-level gypsy moth populations in new areas of spread.

Research by Collier and Downey has shown that gypsy moths can be successfully sterilized with tepa without any adverse effects on mating competitiveness. Small-plot field tests have indicated that a ratio of 40:1 sterile-to-fertile males will suppress reproduction to a high degree. Moths radiologically sterilized show a high percentage of malformation of wings when pupae are exposed to 27 500 R. Tests by W. A. McDonald show about 99% sterilization of males when pupae are exposed to radiation doses ranging from 22 500 - 25 000 R. Lower doses (20 000 R) usually result in complete sterility of female gypsy moths but incomplete sterility of males. It is not known whether F₁ sterility occurs in this species.

Considerable progress has been made in the rearing of gypsy moths. However, it is apparent for this species as for many lepidopterous insects that the mass-production problem must be solved before the sterile-moth method can be used generally as a means of preventing spread. The control of virus and other pathogenic organisms in mass cultures is being investigated.

A pilot test was carried out in 1967 involving the rearing and release of about 30 000 sterile males in a test area in Pennsylvania and New York. Plans call for tests in 1968 involving the rearing and release of up to 100 000 sterile moths. These are still small-scale operations, but they do indicate that progress is being made.

It is apparent that for species such as the gypsy moth the number of insects that can be mass produced and used for insect control or eradication will be limited as compared with species such as diptera or some of the smaller lepidoptera. The circumstances under which sterile moths can be used to advantage will also be limited to situations where natural densities are low. However, relatively few moths, in terms of a few million per year, might be useful in preventing the spread of new infestations in several hundred thousands of acres, adjacent to known established infestations, that otherwise would have to be sprayed. The use of sterile males to supplement spraying of new isolated infestations could also permit the use of a minimum amount of sprays to accomplish eradication.

3.2. New developments in sterilization techniques for lepidopterous insects

D. T. North and H. M. Flint of the Metabolism and Radiation Research Laboratory, Agricultural Research Service, Fargo, North Dakota, have

shown during the past two years that sub-sterilizing doses, of either radiation or chemicals, can lead to a level of sterility in surviving F_1 progeny that is higher than the sterility level in the parent generation. Similar observations were made earlier on the codling moth by Canadian research workers. D. W. Walker of the Nuclear Research Center, Puerto Rico, has also obtained highly encouraging results on delayed sterility effects in the sugar-cane borer, *Diatraea saccharalis*, following the administration of sub-sterilizing doses of irradiation to parent moths.

In my opinion these findings represent a major advance in the sterility technique for controlling lepidopterous insect populations. One immediate advantage is that the low sterilization treatments should make it possible to release moths with a higher mating competitiveness than moths which receive a 100% sterilizing dose. However, there is an additional bio-mathematical advantage that could be even more important. The full benefit of the delayed sterility effect in increasing the efficiency of sterile moth releases cannot be fully appraised in this early stage of investigation. However, certain potential advantages can be postulated that are extremely encouraging. The figures below show the calculated theoretical population trend when a starting moth population of 1 000 moths of each sex is subjected to competition for one generation with 9 000 completely sterile males versus the trend of a similar population subjected to competition for one generation with 9 000 male moths that are 80% sterile. In the model it is assumed that progeny that develop from normal females mated to 80% sterile males will consist of 100% sterile males and 90% sterile females. A five-fold increase is assumed for normal matings.

Generation	Normal trend (5× increase) (all fertile matings)	Type of matings and population trend	
		Release of 9000 100% sterile males	Release of 9000 80% sterile males
1.	1 000 males 1000 females	100 fertile matings 900 100% sterile matings	100 fertile matings 900 80% sterile matings
2.	5000 males 5000 females	500 fertile males 500 fertile females	179 fertile matings 321 90% sterile matings 900 100% sterile matings
3.	25 000 males 25 000 females	2500 fertile males 2500 fertile females	1055 fertile males 1055 fertile females

The figures indicate a decided advantage in suppression of reproduction achieved by releasing 80% sterile males instead of 100% sterile males if the indicated F_1 sterility effect is achieved. If 100% sterile males were used, it would be theoretically necessary to release about 23 000 sterile males to achieve the same suppression effect achieved by releasing 9000 80% sterile males. If 80% sterile males were 50% more competitive in mating

than 100% sterile males, it would be necessary to release about 45 000 100% sterile males to have the same effect as 9000 80% sterile males.

It might be pointed out that a much higher level of population suppression would be achieved if released treated males were 100% fertile but progeny from their matings were 100% sterile in both sexes. In such a case only 250 moths of each sex would be expected in the 3rd generation instead of 2500 when 100% sterile moths are released. If 100% sterile moths are only half competitive, it would be necessary to release about 100 000 to have the same suppression effect as 9000 fully competitive moths that are fertile in the parent but sterile in the F₁ generation.

4. OTHER LEPIDOPTEROUS INSECTS

The sterility technique should eventually prove useful for suppressing or eliminating populations of a wide range of lepidopterous insects. In addition to the species discussed, research by the Entomology Research Division is under way on several important pests, including the tobacco budworm, H. virescens, the tobacco hornworm, Manduca sexta, the sugar-cane borer, D. saccharalis, the fall armyworm, Spodoptera frugiperda, the cabbage looper, Trichoplusia ni, and others. Suitable sterilization procedures and efficient methods of rearing the insects should be high priority research projects for the insects named. There is also an urgent need to determine how many insects occur in the natural population and the minimum range of distribution during the low period in the seasonal abundance. Some species such as the cabbage looper and the fall armyworm may be greatly restricted in their overwintering areas. We plan to undertake studies in the eastern half of the United States to determine the overwintering areas for the fall armyworm and the cabbage looper. These areas may be restricted to Florida and the warmer coastal regions of the south-east. If the overwintering areas are greatly restricted and if populations are greatly reduced, it may be possible to achieve complete suppression of these pests by sterile-male releases at only a fraction of the cost of insecticides later in the season when the insects have not only increased in abundance but have spread to areas ten times as large as that of the overwintering areas. The overwintering area and the abundance of Heliothis zea and H. virescens may also be greatly restricted.

Complete and continuous suppression may not be necessary for economic control of most lepidopterous species. The suppression of populations for one or two generations might be adequate to keep populations below economic-threshold levels for a crop-growing season.

The possibilities of suppressing such insects as Heliothis zea and the cabbage looper on a regional basis in other areas should also be investigated. This might be feasible, for example, in California. The agricultural region in this state is well isolated by mountains to the west and north. The southern area has much desert terrain with limited farming areas. A population density study might show that a few million dollars invested in the rearing and release of sterile moths, starting in the winter months, could control these major pests at costs representing only a fraction of current costs of control with insecticides plus losses that occur in spite of the use of insecticides. If, for example, the minimum density level of H. zea in the cultivated areas in California averaged about 1000 moths

per square mile per generation during the winter, the population at that time might not exceed 25 million. In such an event, the release of 250 million moths each month for about four months or 1 billion moths for a season might keep the insect suppressed below the economic density level. If moths can be reared and released for \$5 000 000 per billion, complete control might thus be achieved even during the first year at a cost less than the estimated \$13 million spent in California on control by chemical insecticides. Moreover, losses estimated to amount to about \$30 million per year could be saved.

4.1. Problems of insect rearing

Earlier in this paper, I mentioned a number of situations in which the sterile-insect release method could be useful for insect eradication or the continuous suppression of insect populations. I have placed primary emphasis in this paper on the potential role of sterile-insect releases for the suppression of lepidopterous insects on a regional basis. A number of the basic criteria that must be met appear highly favourable, including the importance of the species, low natural densities during low periods in the population cycle, and ability to sterilize the insects. It seems to me that the most important basic requirement that may pose the most formidable obstacle to the practical development of the sterile-insect release technique is the matter of mass rearing insects in suitable numbers and at reasonable cost. Several aspects need particular attention. The control of pathogenic organisms that develop in laboratory cultures is perhaps the most important obstacle that must be overcome. Major difficulties are being encountered in the mass rearing of such species as *Heliothis zea*, the tobacco budworm, *H. virescens*, the tobacco hornworm, pink bollworm, and the gypsy moth. It seems to me that there is need for a major research effort on the nature and cause of diseases in cultured lepidoptera and on ways to control the diseases involved. A second problem is the development of less costly ingredients in the nutritional media. It seems that no satisfactory substitute has been found for agar in the rearing medium. This item alone may represent 75% of the cost of the nutritional medium. A third problem is the matter of labour requirements in rearing the insects by present methods.

The inability to rear lepidopterous insects in large numbers and at reasonable costs is not only of importance in developing the sterile-insect release technique, but also in connection with the current efforts to produce and develop the use of pathogens for control and to produce and use parasites and predators for programmed releases to supplement the natural production of parasites and predators.

There are great opportunities for integrating the use of sterile insects and selective natural biological agents for the area suppression of lepidopterous insects. One of the basic requirements for this integration is successful mass production of the pest species to serve as a rearing medium for the natural biological control agents as well as to provide sufficient sterile insects.

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BIOLOGICAL INFORMATION NEEDED IN THE STERILE-MALE METHOD OF INSECT CONTROL

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Abstract

BIOLOGICAL INFORMATION NEEDED IN THE STERILE-MALE METHOD OF INSECT CONTROL. The necessity of accurate data in certain areas of ecology prior to application of the sterile-male technique is discussed. These data include population density, distribution, flight range and mating behaviour.

1. INTRODUCTION

Perhaps the most important requirement for successful use of the sterile male method of controlling insects is a thorough knowledge of the biology of the insect under consideration [1]. A certain amount of information must be obtained on the population density on a seasonal basis, and on distribution, flight range, mating places, mating behaviour, host preferences, etc. Failure in the development and evaluation of this new method of insect control can easily occur if adequate knowledge of the biology of an insect pest is not available.

2. POPULATION DENSITY

The first problem is to obtain a general idea of the numbers in which an insect is present in the area. The species may be so numerous that economical rearing of sufficient numbers of sterile males for release is unrealistic. In many instances it may be possible to reduce the population levels to make the release of sterile males feasible.

The approximate population of an insect species in an area must be known to determine the numbers of sterile males to be reared and released. The releases must be in excess of the native population. To establish information on the total numbers of a species over an area is not easy. Careful seasonal surveys with traps and other devices are needed. Both larval and adult surveys will possibly be necessary. Deducing meaningful population figures from trap data requires research of various kinds. Studies should reveal the sexual maturity of trapped insects, which is helpful in release schedules. Rearing and releasing tagged insects in a natural population will give good information on total numbers by applying mathematical formulae and studying the ratio of tagged to non-tagged insects recovered by hand collecting or by traps. Tagging insects for these studies may be done with paint or dye solution, pigmented dusts, radioisotopes and destructive mutants.

In a flight dispersion study of Culex pipiens fatigans Weid. in Rangoon, Burma [2], B. Grab of the World Health Organization Statistical Unit prepared estimates of the population size of the mosquitoes in the release area based on the collected specimens. He took into consideration the fact that approximately 20% of the native population as well as 20% of the released mosquitoes would die every day. He made daily estimates of the total population, but variability from day to day, due to the low numbers of recaptured specimens, suggested the use of a consolidated weighted estimate. The resulting final estimate of the number of C. fatigans living in the area was 62.5 million with 95% confidence limits of 42.5 million to 82.5 million. Grab presents statistical evidence to show that about 30% of the released mosquitoes have flown out of the study area, which would indicate that only 43.7 million C. fatigans inhabited the location.

Using the 62.5 million figure, one would find an average of about 968 000 mosquitoes per acre. This population appears to be too high to rear and release successfully a preponderance of sterile males for control of C. fatigans. A 90% reduction of the population by larviciding would leave 6 million to cope with by release of sterile males.

In the nineteen-thirties studies were initiated to obtain some idea of screw-worm fly populations in south-west Texas by securing data on numbers of livestock and of wild animals in Uvalde County (unpublished data). The number of screw-worm cases per thousand head of various classes of livestock was easily obtained by interviewing numerous ranchmen over a five-year period. However, very little information was available on numbers of deer, rabbits, opossums, raccoons and on the incidence of myiasis in the various species. Information was gradually obtained on the number of wild animals and the per cent of screw-worm infestations in different species [3].

Studies and estimates were made of the number of screw-worms maturing in each species of animal before gross infestation was lethal. A certain percentage of livestock harboring infestations was treated by the livestock-men and the worms were killed; other livestock were not treated and the worms matured. Studies had shown that about 85% of larvae dropping from infested wounds were destroyed by ants [4]. In general, the data indicated that the screw-worm fly was a relatively scarce insect. Even during periods of high abundance, populations probably did not exceed 4000-5000 per square mile rather than tens or hundreds of thousands as previously supposed. During periods of scarcity, natural populations diminished to fractions of the maximum numbers, possibly to 50 to 200 per square mile [5].

It should be emphasized that sterile males must be introduced into a control area in numbers greater than the insect exists in nature. The required ratio of sterile males to native males differs with different insects and may range from 5:1 up to 50:1 or more in initial releases. The higher the number of sterile males the greater is the competition with native males for the native females. The numbers released must be high enough to cause a degree of sterility that will overcome the population's ability to increase.

Seasonal studies of the insect population is important because most species have a low incidence at some period of the year. Identifying periods of scarcity of the insect is an important factor in the use of the

sterile-insect technique. Release of sterile males should start at or before the low incidence period.

If the population studies show that the size of an insect population in nature is too great for economically feasible rearing of the insects needed to produce a preponderance of sterile insects after release, efforts must be made to lower the native population with insecticides or other means. It must be emphasized again and again that low populations of insects are necessary for the sterile-male methods to succeed. Use of insecticides, sanitation measures and other methods to lower a population should always be considered and very likely employed before starting a release program. There are definite limitations and definite advantages to the sterile-insect release method. Unless these are thoroughly understood the role that sterile-insect releases can play in insect control cannot be realized. Most methods of insect population suppression, particularly the use of insecticides, are efficient in terms of the number of insects destroyed by a given effort when the natural population is high. However, when the population is low the method becomes inefficient in terms of actual numbers of insects destroyed. It requires the same amount of insecticide to kill 90% of 1000 insects as it does to kill 90% of 1000 000 insects. However, with the sterile-insect method, the release of 1 000 000 sterile insects would be 1000 times as efficient on a natural population of 1000 as on one of 1 000 000.

A recently published book, "Ecological Methods with Particular Reference to the Study of Insect Populations", by T. R. E. Southwood, Barnes and Noble, New York, N. Y., should be very useful to all who are giving consideration to the use of sterile-male methods. Among other items, the book treats sampling, measurement and dispersion and determination of absolute populations by marking techniques and sampling units of habitats.

3. DISTRIBUTION OF A SPECIES

In selecting a site for field trials or large-area eradication, study must be made to determine the degree of isolation and the probability of reinfestation of the plot or area. This requires surveys for species distribution.

Insects are not always evenly distributed in an area. Studies must also be made to determine concentration areas on a seasonal basis. A species may be concentrated in heavily shaded areas along streams or selected habitats, near host plants or in close proximity to human habitations at some time in its cycle. There are no doubt hundreds of particular ecological sites where vectors may concentrate for mating purposes, feeding or selection of favourable climate.

It has been found that with air releases of marked sterile melon flies, *Dacus cucurbitae* Coq., the insects quickly found certain host crop areas [6]. Fly densities in these locations exceeded those in other locations by as much as 15 times. These areas were probably favorite mating places, since many of the steriles were sexually immature. Concentration sites should be known so that sterile males can be released in high numbers in these places. For example: the Mediterranean fruit fly in Nicaragua is more or less concentrated in citrus groves from March to October, but

when the coffee ripens in October the fly spreads out over huge coffee-growing sections and infests the coffee berries. Accordingly, the citrus plantations should be hit hard with sterile-male releases from March to October in much greater numbers than the coffee plantations.

Studies must be continued after a release program has started to determine 'hot spots', i. e. areas where there are more native flies than released steriles. These 'hot spots' should, of course, receive special attention by the use of insecticides or a vastly increased release of sterile males. The ratio of marked released insects to native insects should be determined at regular intervals throughout the control area so that information is available at all times as to what is going on in the field.

4. FLIGHT RANGE

The distance insects will fly when distributed from aircraft or cars is important in determining swath widths of releases. A pattern of release must allow for even distribution within the flight range of the insect. Interpretation of flight-range studies for purposes of designing release patterns may not always be easy, since insects behave differently under different meteorological conditions and/or probably disperse according to food supply or age.

When tagged insects are released and recapture sites are set up in concentric circles, the numbers usually diminish progressively away from the release centre. This is probably to be expected with most non-migratory species. It was found in Rangoon, Burma [2], that 81% of the marked released *C. fatigans* were recaptured in houses within 0.34 mile. Only 5% were recaptured at 0.56 mile from the release point. On the basis of hand collecting in houses, both sexes were judged to be fairly evenly distributed over the area.

Released tagged screw-worm flies have been recaptured in liver-baited traps at a distance of 180 miles from the point of release. With wounded animals as oviposition sites, it was, however, found that released flies dropped along a straight line by an airplane were not effective very far from the flight lane. The effectiveness of the released flies decreased as a function of distance within 2-3 miles from the line of release.

Crowding of some insects in natural breeding places is known to influence greatly migration and flight range. Tropical fruit flies have moved from their point of emergence and have made sustained overwater flights of 12 to 40 miles. Oriental fruit flies from a single release site have spread over 100 square miles of surrounding mountain and coastal areas [7].

It is obvious that information on the flight of sterile insects is highly important and that our knowledge of the dispersion and flight range of any insect in all its aspects is meager indeed.

5. MATING BEHAVIOUR

For sterile-male control techniques, it is important to know when, where and under what conditions mating takes place. Do the insects need food of any kind before mating? If so, the insects should be fed before

release which causes extra difficulties and expense. Much thought and study went into this item in field trials with the screw-worm, tropical fruit flies and other insects.

Species differ in where and when they mate. Many species apparently do not mate immediately upon emergence but fly at least several hundred feet. No doubt some have a common meeting place where the sexes will be in close proximity to one another.

It was observed in Rangoon that C. fatigans emerging from tubs would rest on walls and then fly upwards 20-25 feet and take off over the tree tops. This suggests that released males should be distributed near breeding areas so that they could take part in these dissemination flights.

Information on all aspects of mating would assist in field trials of sterile-male techniques.

From the foregoing it might be concluded that 10 to 20 years of work is required before a field trial should be attempted. It is probable that research can never develop all the information needed for a highly efficient program. If one waits until all information is available, no field trials will ever result and interest will die. A great deal can be learned from properly conducted field trials even though they may be only partially successful. Actual field trials identify the problems that need to be solved. During initial field experiments, efforts should be made to gain all the information necessary for a successful operational program. This requires highly competent ecologists who study the area before, during and after trials.

In summary, it should be recognized that certain basic information on the biology and ecology of a species is needed before embarking on field trials to determine if the sterile male methods are practical for eradication of a particular species. Pilot test programs are essential in the development of the technique. These methods are new and require more ecological knowledge than does the use of insecticides, but they have many advantages over insecticides for eradication.

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POTENTIAL OF THE STERILE-MALE TECHNIQUE IN INTEGRATED INSECT CONTROL PROGRAMS

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Abstract

POTENTIAL OF THE STERILE-MALE TECHNIQUE IN INTEGRATED INSECT CONTROL PROGRAMS.

There are essentially three aspects which have to be considered in integrated control. First of all the approach should not be restricted to a given pest but should include the entire ecosystem, which entails all living organisms in their overall environment. Secondly, control measures should be applied taking into account mortality and suppressive influence of natural factors (biotic and abiotic) which could be exploited to the fullest extent possible. Thirdly, control procedures should have a minimum deleterious impact on the ecosystem. The potential of the sterile-male technique is discussed within these three aspects of integration and consideration is given to its possible side effects on natural control.

1. INTRODUCTION

The subject treated in this paper is not so simple as the title may indicate, firstly because of the confusion and differences of opinion regarding the scope of integrated control and, secondly, because the lack of practical examples of the use of the sterile-male technique in integrated control programs makes this a purely theoretical discussion. This brief text does not reflect what the title implies, in that emphasis is given to the concept of integration as understood today rather than to speculation on the potential impact of a technique within integrated control programs. The feeling is that once the concept is agreed upon, the potential of the sterile-male technique should be clear.

2. ECOLOGICAL IMPLICATIONS

The original title of this paper referred to "integrated insect control programs" but has been modified so as to avoid a restriction to certain Arthropods, since integrated control derives from basic principles of ecology and represents a global approach to a given ecosystem. This means that in the development of integrated control the pest or pest complex, which is a critical component of a given ecosystem, has to be considered within the overall conditioning environment, including diseases of economic importance, the numerous so-called indifferent botanical and zoological species, natural enemies (parasites, predators, entomopathogens), the chemical and physical elements, and man. Any other approach may lead to undesirable effects which are well known from the entomological and phytopathological literature of the last two decades.

From the ecological standpoint, a population of organisms exists as one of the interacting components of a more or less complex system [1, 2]. Organism populations may become dominant at a given time and in a given area and be pests because of their harm to man's goods. Any action against these pests intended to reduce their population is an action against the system as a whole and may have serious repercussions on other species of the environment. It is clear that the use of a pesticide, which is at present the most common means of killing pests, may disrupt the environment and also cause, in certain cases, more problems than it solves. The accent is generally on the use of the pesticide and not on the chemical itself which is a necessary evil in modern agriculture. So it may be, for example, nonsense to use certain fungicides preventively in orchards if they influence the population dynamics of Arthropod organisms to such an extent that these become major pests [3].

The problem of the disruption of the environment has been dramatized in the case of pesticides, but these are not the only possible causes. Nitrogenous fertilizers in orchards tend to increase the population of mites, whereas in rice fields they determine an augmentation of the susceptibility to infection leafblast (*Piricularia oryzae*) and other diseases, as well as to infestation by stem borers [4]. The introduction of a plant variety resistant to pathogens but susceptible to mites happened with strawberries in California [5]. The elimination of a weed which can be easily controlled can be followed by the invasion of another weed against which there are no means of control. On the same lines it has been suggested that the elimination of the screw-worm from the southern United States may lead to an increase in the populations of deer and jack rabbits and therefore to competition for food. Of course, it is not always possible to understand in advance all the complicated interactions of the components of the environment. The type of knowledge we have about agricultural ecosystems is at best most unsatisfactory, and it is therefore necessary to gain more experience from ecological investigations. A knowledge of the ecosystem permits the assessment of the mortality factors operating on organism populations and sometimes the identification of those which permit a species to achieve pest status. There are cases where entomophagous species are key factors, as was recently reported from northern Chile [6], where the Mediterranean fruit fly reduction campaign by the use of pesticides resulted in an alarming increase in the damage caused by citrus scales and aphids. Entomophagous species had to be reintroduced to reduce the new pests to the original, economically insignificant level. There was a similar occurrence during the last decade in North Africa, where the simple replacement of white oils by organophosphates in citrus pest control has permitted indifferent species to achieve pest status through the destruction of their natural enemies. Similar examples have often been mentioned in relation to pesticidal treatments and show that in very many cases the natural enemies are able to exert a pressure which is sufficient to maintain a species in an indifferent or tolerable status.

Besides natural enemies, cultural practices may also be key factors. According to current practice, the rice crop is followed in Thailand by the cultivation of different vegetables (such as onions, beans, etc.). During the rice-growing season, which lasts from about June to December, leafhopper species of the genus *Nephotettix* are sometimes able to build up important populations before October and may have to be reduced by chemi-

cal. To increase production in the best irrigated zones of the country, there is a tendency to introduce a second rice crop replacing vegetables and, in doing so, to establish in selected areas a monoculture throughout the year. Nephotettix species, which transmit the dwarf disease virus, as well as stem borers and other pests, are then able to mass reproduce on the second rice crop and invade the main rice crop from its beginning, thus obliging numerous chemical interventions which definitely disrupt the whole ecosystem.

The assessment of factors responsible for the variation of pest abundance should lead to their possible manipulation, thus keeping them from causing economic damage. One example which is now often mentioned in entomological literature concerns the grape leafhopper in California [7]. The eggs of the leafhopper are parasitized by a Mymarid, Anagrus epos Girault, which, unlike its host, cannot overwinter in vineyards unless it breeds during the winter on another leafhopper infesting wild and commercial blackberries. The expansion of vineyards has simplified the ecosystem at the expense of blackberries, and the parasite has not been able to follow the grape leafhopper which has become a pest. The re-introduction of infested blackberries in vineyards has been made with a view to re-establishing the original condition.

So much for the necessity of a global approach in integrated control.

3. ECONOMIC IMPLICATIONS

The second principle concerns the economic injury levels. Whether or not an organism is regarded as a pest depends more on the amount of harm that man can tolerate than on the amount actually caused by the organism. The amount of harm at a given time depends on the pest population density and is therefore defined in terms of density levels. The economic injury level is attained when the organism population has reached such a density that it may cause economically important damage. Some people recognize a threshold of tolerance which precedes the threshold of injury and is a kind of alarm indicating that it may be necessary to intervene and stop the pest from continuing to cause damage. "It may be necessary" but it is not always so. The economic injury level has a different significance according to pest, crop, time and space, and the economic aspects involved. The density at which Oryctes rhinoceros L. starts to cause intolerable economic damage in coconut plantations is about 20 or 25 adults per hectare, whereas millions of citrus scales over the same surface may be needed to cause similarly great damage in citrus groves. The importance of the citrus scales depends on the market situation of a given country. In exporting countries economic injury levels are very low, whereas in countries with predominant local consumption the levels are much higher. The olive moth attacks olive tree flowers but not every flower which is destroyed represents damage, which only begins when the fruit-carrying capacity of the tree is lowered. The economic injury level is therefore higher in abundantly flowering varieties than in low flowering varieties.

The economic importance of a species also varies according to time. An aphid population in an orchard shortly before migration to another host plant can be tolerated, although it has reached the normally recognized injury level. All this means that it is time to abandon empirical methods

of pest control and that the need for intervention has to be considered within a complex of factors, ecological or otherwise, which in the long run are always of an economic nature.

Ideally, if a species has attained an economic injury level, a highly selective control method should be applied. Today, the most selective method we have is biological. Other methods have a broad spectrum action and have therefore wider repercussions on the other species of the complex. If selective means cannot be applied, either because they are non-economical or do not exist, the available ones can be used in the best possible selective way. This is always done if consideration is given to the known components of the ecosystem. However, the selectivity of available chemicals through modifications of dosages, formulations, time and methods of application is not exploited as it should be. For instance, Tanada demonstrated in 1967 that application of small and sub-lethal doses of DDT to larvae of the gypsy moth (Lymantria dispar L.) or of the fall web worm (Hyphantria cunea Drury) apparently activates the viral and bacterial diseases in these insects.

One of the merits of integrated control has been the introduction of the concept of the economic injury level and the recognition of the needs for suitable sampling techniques which also give the possibility of predicting population trends. Integrated control procedures emphasize, therefore, the need for managing pests in such a way that they are maintained at a sub-economic level, i. e. at a level at which they do not have a pest status or, in other words, at which they remain potential pests. Pest management implies the continued existence of potentially noxious species below the tolerable level of abundance. It is therefore very important to know the significance that economic injury levels can have according to time and marketing conditions.

4. TECHNICAL IMPLICATIONS

Pest control is an economic problem which has to be considered from two different angles, i. e. the benefit in the immediate future (accrued quantity and quality of the yield), which is obtained through the application of the most appropriate control mean against a pest, and benefit over a number of years (during the whole life of a perennial crop or the succession of an annual crop), which is obtained by applying the most suitable control means in respect to the whole environment. The first point is generally a consequence of the second and the second point is a compromise with the first. In managing pests at sub-economic-threshold levels, natural control factors affecting organism populations have to be primarily considered and control means have to be compatible with them as well as with each other. Among these factors the most important are natural enemies, as they regulate populations on a permanent basis. Natural enemies already exist and the main care should be to render them more efficient through suitable manipulation of the environment. Biotic control agents do not always act satisfactorily, but they are always important, particularly in respect to the very numerous so-called indifferent species which in many cases contribute to the stability of the Arthropod population as a whole. It has been calculated that about 50% of the animals living in Central European orchards is represented by indifferent species [8]. At a given moment biotic regulating mechanisms may fail and the population of a potential pest may rise above the level of tolerance. A potential pest may

even become a pest without changing anything but the economic injury level, when this is lowered. In these cases, commercial control is achieved only by intervening to reduce populations below the tolerable level. In an integrated approach this should be done while keeping in mind the immediate results together with the long-term action of the intervention. The sterile-male technique can be regarded here as any other measure applied against a certain component of the ecosystem, i. e. a given pest. The technique has fundamentally the same limitations as chemical control, i. e. if eradication is not achieved, the application of the technique has to be renewed [1]. Therefore, as a control practice aimed at reducing pest populations, the procedure is the same as for other control techniques. There are, of course, several known advantages over chemical control. In addition, the inoculation in the environment of the pest which cannot develop beyond a certain stage could provide in certain cases the necessary support for the increase of parasite and predator populations [9-11]. Considerations are different if it is applied to achieve eradication, as this is in antithesis to integrated control [5]. Eradication provides, of course, the ultimate solution to the problem of noxious species, but, as far as is known, eradication can reasonably be attempted only under exceptional circumstances [2], which do not prevail for most agricultural and forest pests [5]. Eradication means the complete deletion of a component of the ecosystem and it is fully justified in the case of recently introduced pests. Otherwise it may have repercussions on the other interacting components, either through the elimination of an important host for natural enemies of other pests or through the elimination of competition for food or space with other pests. In the Sudanosahelian zone of West Africa, for instance, it has already been noted that keeping grain-eating birds of the genus Quelea under control has influenced the increase in number of the golden sparrow, Auripasser luteus Licht, which has always been a species of secondary importance. This is just one simple case where the eradication of a species which is apparently only regulated by the available food and water could lead to another problem of the same economic importance. It appears, therefore, even in the case of eradication, that many other aspects have to be evaluated besides the practical feasibility.

Before concluding, it might be worth mentioning that integrated control or pest management is not a simple superimposition or juxtaposition of methods of control. The reduction of a pest population by chemical or biological means and the following control or the eradication by a biogenetic technique cannot be called pest management if the target species is not considered within the whole environment. Integrated control means integration with the existing natural mortality factors and may therefore be achieved with the application of one single method, i. e. with chemicals or with the sterile-male technique. To date, the integrated control concept has been applied only in desperate cases such as cotton or orchards, but efforts are now being made to conceive integrated control for problems which have not yet been dramatized by the excessive use of pesticides.

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ACTIVITIES OF THE UNITED STATES ATOMIC ENERGY COMMISSION RELATED TO RADIATION TECHNIQUES USED IN CONTROL OF INSECTS

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Abstract

ACTIVITIES OF THE UNITED STATES ATOMIC ENERGY COMMISSION RELATED TO RADIATION TECHNIQUES USED IN CONTROL OF INSECTS. The activities of the US Atomic Energy Commission (USAEC) in relation to the sterile-male technique for insect control are listed. As an example, the joint efforts of the USAEC with the Instituto Interamericano de Ciencias Agrícolas (ICA), the Organismo Internacional Regional de Sanidad Agropecuaria (OIRSA) and the IAEA are discussed. The co-operative activities with Puerto Rico and Peru are also mentioned. Work supported by the USAEC at different universities in the United States of America is briefly described.

The US Atomic Energy Commission carries on various activities which have a bearing on problems associated with the sterile-male technique for the control of insect pests. The Commission has no direct responsibility for large-scale applications of these techniques, yet it makes contributions in other ways. Because of the demonstrated and potential success of the technique, its exploitation is most important. However, exploitation of a technique is not always possible without background research. It is in this research area that the Commission's principal role is visualized. The research supported by the USAEC covers a broad spectrum, from projects whose objectives are to answer immediate questions of applications of the sterile-male technique to other projects concerned with basic studies and with no obvious immediate application to specific problems of insect control.

The USAEC supports such research efforts to help provide the essential information that must precede the establishment of a control programme involving sterile-male techniques. At present, support is being given to research work on such topics as radiation biology of insect pests, development of diets and techniques for mass rearing and the population dynamics of natural populations of specific pests. In a number of instances these research projects complement those being carried out by the US Department of Agriculture and certain international agencies.

One example of this activity is the co-operative effort, which has been underway for several years, of investigators at the Instituto Interamericano de Ciencias Agrícolas (IICA) at Turrialba, Costa Rica, supported by the USAEC and the Organismo Internacional Regional de Sanidad Agropecuaria (OIRSA) and, later, the IAEA. The Mediterranean fruit fly (medfly) problem in Central America has been studied for several years. The feasibility studies on the use of the radiation sterilization technique against the medfly in Central America were first started in 1961. The early co-operative

studies focused on the biology, rearing techniques and responses of the medfly to radiation. The sterilizing dose was determined to be approximately 10 krad. In order to minimize loss of vigour and mating ability it was found that the best time to radiate the flies was between the seventh and ninth day of the pupal stage. Cage experiments were performed to determine the flooding ratio of sterile to normal flies necessary to reduce fertility to a critical level. To determine the dispersion of the irradiated flies tests were run in 1963 on the peninsula of Puntarenas in Costa Rica with sterilized and ^{32}P tagged flies. In the test the distance covered by released flies was less than 1500 m. These experiments are simply an illustration of the co-operative efforts to solve this problem that have preceded the larger scale feasibility studies supported by UNDP funds. This co-operative effort is still in effect. Currently Dr. K. Katiyar of IICA is attempting to induce, identify and raise a suitable medfly mutant in numbers adequate to be used in tracing the dispersion of released flies in the natural population.

In addition to his studies on medfly, Dr. Katiyar has done considerable work on the Coffee leaf miner Leucoptera coffeella, Guer., which he reported in December 1967 at the IAEA Symposium on Use of Isotopes and Radiation in Entomology. Preceding the work on the Coffee leaf miner the USAEC supported work at the Turrialba Center on the tropical warble fly Dermatobia hominis, Linn. Jr. Unfortunately the problem of mass rearing of this insect was a refractory one and success in these investigations was limited. However considerable information on the biology, sterilizing doses (12.5 krad for males, 10 krad for females) and other features of the insect was accumulated.

In Puerto Rico, Dr. David Walker is engaged in studies that necessarily must precede an induced sterility control programme for the sugar cane borer Diatraea saccharalis. The problem of developing an inexpensive diet is perhaps the most formidable obstacle yet to be overcome. The radiation dose for sterilization has been determined (35 krad males, 30 krad females). Walker noted, as have others working with Lepidopterans, the occurrence of sterility in generations descending from adults exposed to sub-sterilizing doses (8 krad in this case). The US Department of Agriculture is also involved in co-operative work on a number of studies of the sugar cane borer.

Recently the USAEC has begun support of an investigation to provide scientific background for using the sterile-male technique in controlling Anastrepha fraterculus, the South American fruitfly. These investigations are now underway at the La Molina Agricultural Experiment Station in Peru, and are described elsewhere in this publication.¹

The possibility of taking advantage of radiation-induced chromosomal translocations in controlling insect populations is at present under investigation at the University of Notre Dame. Work on Aedes aegypti is supported by the USAEC.²

In addition to the research contracts so far mentioned, the USAEC assists in other ways. For example, radiation sources are, on occasion, made available for support of this kind of work. A ^{137}Cs irradiator was

¹ SIMON F., J.E., "Present stage of research into the eradication of the Mediterranean and South American fruit flies and the cotton stainer in Peru by the sterile-male technique", these Proceedings.

² RAI, K.S., "Status of the sterile-male technique for mosquito control", these Proceedings.

loaned to the Government of Peru to help with work on medfly and South American fruitfly at La Molina. An irradiator is scheduled for loan to Chile to be used principally for work on food irradiation, but entomologists there plan to use the source for insect sterilization experiments as well. In the United States of America workers at Louisiana State University have taken advantage of the presence of an AEC mobile ^{137}Cs irradiator to continue work on the sweet potato weevil, Cylas formicarius elegantulus; by radiating infested sweet potatoes with 18 krad the larvae were sterilized. Recently a field test was run under the direction of Dr. Dale Newson who used the large food irradiator to produce sterile males. The sterile males were released in a ratio of nine sterile to one normal which resulted in a significant reduction in the weevil population in the test fields.

Perhaps the greatest contribution of the USAEC to the furtherance of the sterile-male technique in the control of insects may come from more indirect support. What I refer to are a number of projects which are supported by the USAEC which are of a more basic nature. The information and concepts generated by these projects could in the long run have a very profound influence on population control techniques, just as Muller's work has had up to now. I would now like to mention a few areas which may contribute to improved techniques of population control.

Clearly there is a great paucity of knowledge with respect to the dispersion and interaction of populations in the wild. Dr. Bruce Wallace of Cornell University is studying the mode of dispersion of different lines of Drosophila melanogaster placed in the field carrying different easily identifiable genetic markers. The flies were released by allowing them to hatch in open vials. The results to date suggest that dispersion is not great and the amount of inbreeding appears to be higher than was expected. If these results prove to be correct and are extended to other insect species the implication is that the release techniques for population control must provide very extensive distribution of sterile males since dispersion may be limited.

Other Drosophila population studies are being carried on by Dr. Elliot Spiess of the University of Illinois in which he is investigating the mating advantage of males of certain genetic constitution in a given natural population. The effects of temperature, nutrition and other environmental variables on mating propensity of flies of different genetic constitution is also under study. The bearing on sterile-male releases is obvious, for if the genetic constitution of the released sterile flies could be manipulated so that they have a competitive advantage over "wild type" flies, control might be more effective.

Still other studies are underway in which natural populations, insects and other animals are being investigated with the aim of formulating models which describe events in nature on the basis of available data. The models which are to be tested with experiments can lead to predications of how component forces such as selection, which influence the constitution of natural populations, act. While this kind of approach to population dynamics is still relatively undeveloped it offers high potential for placing population manipulation on a more rational basis.

Another important research activity supported by USAEC deals with radiation effects on mating systems of insects. At the University of Wisconsin Dr. S. Abrahamson is investigating the entire gamut of radiation-induced alterations of genetic materials. Using appropriate stocks of

Drosophila melanogaster each chromosome of the genome is being examined genetically for visible and lethal mutants as well as detrimental and sterility factors. In addition cytological studies are in progress to identify radiation-induced chromosomal changes such as translocations, deletions, etc. This study is unusual in that it is aimed at determining a total picture of radiation damage rather than identification of some specific type of lesion. Work is also being carried on at Oak Ridge National Laboratory by Dr. R. C. von Borstel on assessing the genome of Habrobracon for dominant lethality, recessive lethality and translocations following treatment with radiation or chemical mutagens. Other investigators in the USAEC programme are concentrating their attention on more specific radiation-induced genetic effects in Drosophila.

Mention should be made here that a variety of other insects have been studied at one time or another with respect to radiation effects, but the basic problems have for the most part utilized Drosophila. The reasons for this are of course because of the wealth of genetic knowledge available, the ease of handling, the few large chromosomes in the genome which can be examined cytologically and perhaps because of the considerable activity of other scientists in the field using the same organism. It is not without considerable basis that the transfer of many of these results to other insects is more than a hope.

One study carried on by Dr. D. L. Lindsley of the University of California at San Diego is aimed at determining the genetic control of gametogenesis in Drosophila. The approach is to identify different genetic loci which affect different stages of the overall gametogenic process with emphasis on spermatogenesis and meiosis. Mutants are being sought which are blocked at different points in the process. Once identified the mutants will be genetically localized and the nature of the lesion studied. Such questions are being asked as to whether several loci affect a specific step of the process, how such loci are distributed in the genome, whether a particular genetic locus acts on both sexes, what is the mutability of the respective loci and what is the frequency of such mutant alleles in the wild population. Another effort along somewhat different lines but also aimed at understanding spermatogenesis is being undertaken by Dr. Dean Parker of the University of California, Riverside. His work deals with investigating the function of the Y chromosome in spermiogenesis. Information from these kinds of experiments might well provide the basis for new strategy in inducing sterility.

I would like to mention one other line of work now underway at Georgetown University by Dr. R. C. Baumiller. This has to do with a study of the synergistic induction of mutations in Drosophila as a result of the interaction of virus infection and radiation. Flies which are infected with sigma virus show twice as many mutations with the same radiation dose as do non-infected flies. At present information on enhanced dominant lethal and recessive lethal mutations is being obtained. Conceivably, in cases where sterilizing doses do impair the insect so that it is not competitive with the wild types then a lower sterilizing dose might be achieved by viral infection.

I have tried to provide an impression of the USAEC program which bears on problems of the use of the sterile-male technique in population control. Obviously this has been a sampling and admittedly a superficial one, but I hope that it has conveyed the approaches and thinking that

represent the USAEC program. The sterile-male technique is one of the most accessible applications of nuclear energy for developing countries. However, we would be concerned if the technique were to be employed indiscriminately by workers who have not been adequately trained or have not the appropriate facilities and support to make the program work effectively.

The success of the technique to date underscores its importance and value, especially in these times when concern about food supplies and insecticide residues is growing.

It is apparent that much research could and should be done to provide a better theoretical background for the application of the technique. We think that the technique has a very bright future both in the developed and developing countries.

PROBLEMS IN LARGE-SCALE STERILE-MALE TECHNIQUE PROGRAMS IN DEVELOPING COUNTRIES

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Abstract

PROBLEMS IN LARGE-SCALE STERILE-MALE TECHNIQUE PROGRAMS IN DEVELOPING COUNTRIES. Experience acquired in a co-operative project which involves several international organizations plus individual governments has demonstrated that difficulties associated with supply, logistics, communication and personnel are some of the basic problems likely to be encountered by a sterile-insect release program when undertaken in developing regions.

An awareness of some of the distressing burdens under which a newly developing nation struggles will perhaps permit a better understanding of the problems confronting a sterile-insect release program initiated in such a country.

The severity of these problems will vary with the level of development and degree of self-sufficiency attained by the country. Characteristically its economy, stemming from a predominantly agrarian base, is dependent on one or two chief export products. As their prices tend to fluctuate sharply on the world market a stable income cannot be assured. Extensive natural resources are lacking. Some heavy industry may be established but more often these enterprises are absent, and manufacturing generally is in the early stages. Highway or rail systems are rudimentary. Telecommunications and commerce between urban centres and the hinterland are poor. Its low productive capacity, scarcity of opportunity and frequent inflationary crises condemn a large part of its bulging population, particularly the illiterate and unprepared, to live on the edge of abject want. As a high illiteracy rate generally prevails, most of the individuals who would constitute the labour force of the project - apart from the technical counterpart personnel - possess little or no formal education, and specially acquired skills among them are uncommon.

Before a feasibility study or eradication campaign is initiated, certain preconditions are essential if the ultimate goal of the program is to be reached in the most effective manner possible.

Thorough knowledge of the insect pests' behaviour and physiological responses to environmental conditions existing in the test area is a prime prerequisite in planning for release operations. Reliable information regarding distribution, potential areas of infestation, possible alternative or native hosts, seasonal population levels and resulting crop damage should be available. If not, it would be highly advisable to assign a team of qualified personnel to the area so that at least one year's data be obtained before the program begins.

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Logistics problems can be minimized by situating the laboratory as near the work site as practical. If aerial operations are planned, ground transportation difficulties could be reduced by locating the laboratory close to an airfield. Proximity to urban centres is important for certain supplies, and for a suitable labour force which, during the initial phases, will undoubtedly have a high turn-over rate.

The physical lay-out of the laboratory must be suitable for insect handling procedures. Far greater efficiency results by constructing a building specific to the requirements rather than attempting to adapt an available structure. In an eradication program it is necessary, of course, that the laboratory be designed to prevent insect escape. Space should be ample to meet not only immediate needs but also those resulting from possible future expansion. Not to be neglected are provisions for air conditioning which encompass heating, cooling, and humidifying or dehumidifying equipment. Sufficient electric power, lighting, water and drainage systems are other important considerations.

Articles manufactured in developing countries are largely utilitarian in nature and reflect the immediate needs of the popular classes. Minor items of equipment taken for granted in any ordinarily furnished laboratory such as forceps, glass tubing, filter paper or even rubber stoppers generally are not available on the local market. Therefore, all laboratory supplies and instruments must be procured from the outside as well as equipment associated with insect rearing and handling. Scientific instruments that are damaged or require maintenance must be sent to the manufacturer as possibilities for their local repair are extremely limited or non-existent. It would be well to use instruments as simple in design as possible which nevertheless will perform the necessary function, and to have sufficient replacement parts on hand. It may be desirable to have duplicates of the more essential apparatus.

Some areas may not have dependable electricity services. Power may be cut unexpectedly for considerable periods. Without a stand-by unit to supply current for essential tasks difficulties could develop.

What can industrially underdeveloped countries offer which may be utilized in a sterile release program? Depending on the geographical location and climatic conditions, such material as sugar cane bagasse, refined sugar, wheat bran or wheat germ (all used in larval diets) may be found. If there is a timber industry material for cages and rearing cabinets would be comparatively cheap as well as providing a source for sawdust, often used as a pupation medium. Wood excelsior also can be produced by means of relatively simple machinery. If there is a cotton processing plant cotton wicks and twine can be obtained.

Paper bags and cardboard products may be made locally even though their manufacturing depends on imported material. It might also be possible to establish a simple plastics industry which could supply sheeting, bags and trays used in various operations.

A well-co-ordinated program is a virtual impossibility without reliable communications. Although communication systems throughout developing regions will vary from country to country, in general they are deficient. Complete telephone or telegraph coverage within all areas of these countries is in all probability lacking, and the efficiency of existing networks may be sub-standard because of inadequate servicing and maintenance.

When considerable distances are involved between the rearing facility and the test area, or the two lie in separate countries, the problems are magnified. Base operations must be in immediate contact with field personnel who will inform on present needs and current sterile-native insect relationships. If aeroplanes are used adverse weather conditions in the drop zone must be reported quickly. Relying on the mails to convey important field records is hazardous. Too often vital data are delayed or lost because of an indifferent postal service. To circumvent these obstacles it may be well to follow the example of many institutions which operate in areas with poor communications by installing two-way radio equipment. At times when atmospheric conditions disrupt reception between stations, there may be other agencies or amateur operators to relay urgent messages.

Air-to-ground communications are especially useful in aerial release activities. Information on surface winds, bag drift, bag openings and accuracy of placement along flight tracks or in localized "hot spots" can be readily conveyed by portable transistorized sets.

Logistics is another important factor in a sterile-insect release program that should be given primary consideration before such an operation is implemented. Various factors will dictate the manner and stage of development in which the sterile insects are to be transported and disseminated over the infected zone as well as the type of equipment required. If the area to be treated is relatively small, easily accessible and situated at no great distance over good roads from the rearing plant, an air conditioned truck may suffice. Rail transport may also be possible, and if schedules permit, night shipment should be used to avoid overheating the pupae.

For covering rugged terrain or sites further removed from the rearing facility, air services are needed. For certain types of releases, a large number of pupae can be carried in small single- or twin-engined aircraft. For larger operations involving packaged adults these types may not be practical because of their restricted cargo capacity. The Douglas DC-3, or C-47 as designated by the military, is universally used as a cargo and passenger carrier. Its flight characteristics, carrying capacity and proven reliability combine to make this a generally acceptable type for aerial dispensing of packaged insects. Terrain and weather conditions may combine to create situations hazardous to fixed wing aircraft. Severe turbulence may prohibit their flying at low levels and high altitude releases may be impracticable. In such instances helicopters which are less affected by turbulent weather can be used advantageously. Even though available, however, they present formidable difficulties with their high operating costs and constant maintenance requirements.

What of the availability of aircraft in the emerging nations? Surprisingly enough, in many developing countries air travel is the only practical means to reach remote areas. Consequently small flying companies engaged in air taxi service and cargo transport are not uncommon. If an air force exists within the host country, arrangements may be made whereby the use of aircraft along with flight crews can be obtained gratis, or at a nominal cost. Perhaps through civil action activities, a plane may be assigned to the sterile release project. This type of operation is quite common in Latin American countries. Carried out by the military its primary purpose is to better the social and economic welfare of the people

by becoming directly involved in various community enterprises, particularly those in rural areas.

If exploratory work is contemplated within a particular country, the size, location and manner of insect distribution throughout the experimental site will be determined primarily by the facilities available to the project. Other factors should not be neglected. A critical study of the geographical features of the proposed site should be made. In planning for aerial releases, it may be found that the nature of the terrain or prevailing weather conditions in certain regions present serious problems for effective air distribution of sterile insects. Careful examination of available meteorological data or consultation with local pilots familiar with the test area before beginning the experiment will help guarantee that the project will proceed as efficiently as possible. Even then, a feature that has been overlooked or an unexpected occurrence could jeopardize the study. Once in northern Panama, for instance, a river swollen by torrential downpours swept away a highway bridge linking the isolated test site with the outside. Fortunately, by means of a nearby footbridge and a vehicle providentially situated within the area the sterile fly releases were able to continue. Again, in both test zones in Panama and Nicaragua extended periods of uncertain flying conditions exist at certain times of the year. Weather is highly variable from day to day or even within the same day. Flexibility of operations both in regard to sterile-insect handling and aircraft availability are essential if the effects of adverse conditions on distribution are to be minimized. Alternative dispensing systems should be pre-scheduled in case releases are held up because of bad flying weather. It may be possible for the plane to land near the test area and the packaged flies to be trucked in for ground liberation.

Political customs as practised in some countries could possibly prove troublesome for the work program. In certain instances when the reigning party is defeated many positions extending throughout all levels in the government departments are filled by members of the new regime. Subsequent loss of trained and experienced counterpart personnel and disruption of project timetables may result.

Obviously, the outcome of a sterile release program would be uncertain if the project were undertaken in a country with a recent history of repeated political or civil upheavals. Throughout periods of social unrest any services or facilities provided by the host government would undoubtedly be suspended and certain restraints placed on civilian movement. Such turmoil occurring at a critical time or of prolonged duration could prevent the successful conclusion of the program.

The efficacy of a program in which numerous organizations participate may be impaired by internal discord arising as a result of conflicting interests or varying degrees of involvement. This type of co-operative endeavour, apart from the personnel problems it creates, requires an inordinate amount of co-ordination and should be avoided whenever possible. If the project can be implemented only by means of a joint undertaking, a central authority having complete control over all functions is absolutely essential.

The executing agency drawing on the broad and varied background experience of its experts and consultants must exercise its prerogative to define and assign precise areas of responsibility to each member organization. Before operations begin a mutually acceptable arrangement should

be made to ensure that each group fulfil its designated tasks. Reasonable suggestions concerning the program certainly should be encouraged and considered but it must be understood that overall policy and direction will be administered by the executing agency.

Comments thus far have centred on some of the concrete problems and situations likely to be encountered in a large-scale sterile-insect release program. But what of the more intangible human element, particularly the quality and attitudes of the workers through whose efforts the operation is actually carried out? Difficulties of a technical nature are usually overcome with relative ease. Once the problem is identified, it simply becomes a matter of searching for and applying the appropriate remedial action.

If only human relationships could be so easily defined. Complex enough even among peoples sharing a similar background, they become further complicated if expert and counterpart personnel originate from widely divergent cultures. Yet to establish and perpetuate an effective and harmonious working atmosphere among the project personnel is without doubt one of the most important requirements to ensure a smoothly functioning and ultimately successful program.

An important aspect which may be hard to assess accurately beforehand is the professional competence of the counterpart technical personnel assigned to the project. An entomological background is, of course, basic. It would be highly desirable if these workers possessed a good understanding of the underlying principles of sterile-insect-release methods and had received practical training in at least some of the essential laboratory and field operations.

In this respect the expert should proceed with forbearance and understanding in his working relationship with counterpart personnel. Unless the co-operating agency is fortunate in having well-trained and experienced persons a wide technical knowledge gap is likely to exist. Yet it is imperative that this chasm be bridged. The expertise and experience of the expert must be imparted to his counterpart if a functional program is to be realized. The manner in which this is accomplished is often nearly as important as the knowledge itself. Knowing the nature and idiosyncracies of the people undoubtedly would aid the expert in developing closer communication ties with his co-workers which in turn would favour a more responsive effort on their part. On the other hand, workers who prove themselves to be irresponsible, lazy or non-receptive to training should be removed promptly. Not to do so invites continual operational difficulties and serious problems with worker morale.

It is imperative that expression and the free interchange of ideas should not be restricted because of language barriers. In the interest of fostering rapport it would be desirable for the expert to possess a good command of the host country's language. If the counterpart is not knowledgeable in the expert's tongue then a common language in which both are proficient is a necessity.

Different attitudes, values and customs, incomprehensible perhaps to the uninitiated expert in a foreign country, may leave him feeling puzzled and frustrated. An indifferent, undisciplined approach towards work or a lack of a sense of urgency may characterize the general attitude of large numbers in certain developing nations. It is unfortunate also that some of the more educated persons in these countries hold the belief that menial tasks and physical labour are unworthy of their elevated station.

How the expert confronts and resolves the manifestations arising from these potential pitfalls to the program's well-being in the face of the exigencies demanded by living material will depend greatly on his own degree of insight and understanding of human nature, and his flexibility and sense of dedication.

DEVELOPMENT OF RESEARCH IN STERILIZATION TECHNIQUES FOR AGRICULTURAL INSECT PESTS IN THE USSR

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Abstract

DEVELOPMENT OF RESEARCH IN STERILIZATION TECHNIQUES FOR AGRICULTURAL INSECT PESTS IN THE USSR. A list of insects is presented on which the effect of chemo- and radiation sterilization is studied. Some specific data on chemosterilization are given for Carpocapsa pomonella Linnaeus. Results of several experiments using gamma-radiation to sterilize Acanthoscelides obtectus Say are presented.

Major progress in the development of sterilization techniques as a means of controlling insects harmful to agricultural plants has spurred on research in many countries. In this respect a large part has been played by the International Atomic Energy Agency.

Symposia held by the IAEA on the use of isotopes and radiation in entomology in Bombay, Athens and Vienna, together with panels on the practical application of sterilization techniques, have brought to light the principal and most promising trends in this field of research. The publications issued by the IAEA contain valuable information that can serve as a guide for specialists working on this topical problem. This is of particular importance in the light of the fact that the research in progress in many countries has much in common as regards its aims and objectives.

Over the last few years the Soviet Union has considerably stepped up research on the application of sterilization techniques. Studies have been conducted on two levels: the development of, first, a technique for sterilizing insects using chemical sterilants, and, second, a technique based on the sterilizing effect of gamma-radiation.

Chemical sterilization studies are being carried out on a number of agricultural insect pests: the mallow moth, Pectinophora malvella HB; the corn earworm or scarce bordered straw moth, Chloridea obsoleta F.; the cutworm or turnip moth, Agrotis segetum Schiff; the dark sword grass moth, Agrotis ypsilon Rott; the beet army worm or small mottled willow moth, Laphygma exigua HB; the codling moth, Carpocapsa pomonella L.; the Colorado beetle, Leptinotarsa decemlineata Say; the 28-spotted ladybird, Epilachna vigintioctomaculata M.; the beet pest, Bothynoderes punctiventris Germ; and the melon fly, Muiopardalis pardalina Big.

Alkylating compounds are used as sterilants, and studies have shown that the most effective sterilants are the ethylenimine derivatives: Tiotef (triethylenethiophosphoramidate), Tet (tretamine), and Apholate.

These compounds have been used in various concentrations and are either applied in the form of a solution to the abdomen of the moth, or are fed to the moths in a sucrose solution. It has thereby been possible to

determine the optimum concentrations of sterilant solutions required to ensure a high percentage of sterilization in the insects without any appreciable decline in their biological activity and competitiveness compared with non-sterilized specimens. For example, in the case of the codling moth, Carpocapsa pomonella L., 100% sterilization of the eggs was obtained by feeding males and females with a 0.1% Apholate solution, 0.08% Tet and 0.08-0.1% Tiotef.

When the males alone were fed with a 0.1% Tiotef solution, 94.6% sterility of the eggs was obtained.

At present we are working to discover new chemosterilants, to determine their optimum concentrations in solution, and to find techniques for sterilizing different species of insects. Furthermore, we are experimenting in the practical application of chemosterilization techniques in the field. The most promising method, as is now known, is the use of chemosterilants coupled with different kinds of attractants exhibiting selective action.

Research is in progress on chemical attractants and we are also testing natural and synthetic attractants. In addition methods are being developed for using chemosterilants and physical attractants together. The attraction exerted by light sources of certain wavelengths is also being used for this purpose [1-8].

Study of the sterilizing effect of gamma-radiation on insects is being conducted on a large scale. A major part of it relates to the theoretical side, particularly the cytogenic problems, such as the effect of radiation on spermatogenesis and oogenesis, and the production of lethal mutations [9-10]. Furthermore, for practical application of the radiation sterilization technique, we have organized studies aimed at determining the sterilizing action of radiation as a function of the dose.

These studies have been carried out on a variety of insect pests that damage crops of economic importance, namely the mallow moth, Pectinophora malvella HB, the corn earworm or scarce bordered straw moth, Chloridea obsoleta F., and the small mottled willow moth or beet army worm (cotton) Laphygma exigua HB; the mangold fly, Pegomya hiosciami Panz, and the beet pest, Bothynoderes punctiventris Germ (beet plants); the dried-bean beetle, Acanthoscelides obtectus Say, and pea beetle, Bruchus pisorum L. (leguminous plants); and the melon fly, Muiopardalis pardalina Big, the codling moth, Carpocapsa pomonella L., the apple moth, Hyponomeuta malinellus Zell, the oriental peach moth, Zaspeyresia molesta Busck, and Phylloxera vastatrix Planch, etc. (fruit and berry crops).

The studies have enabled us to determine the optimum sterilizing doses as a function of phase of development, age and environmental conditions [11-16].

Practical application of the sterilization technique necessitates breeding the insects in artificial conditions and rearing them on artificial nutrient media.

However, certain technical difficulties involved in obtaining large quantities of insects (poor rearing techniques, the comparatively high cost of nutrient media, inadequate automation of artificial breeding systems and the need to invest capital in the construction of special insectaria) make it difficult to reap the full advantages that the method offers. In order to select insect pests which could be controlled by the radiation sterilization

technique at minimum cost, we made a comparative analysis of the biological features of a variety of species.

Detailed analysis shows that at the present stage of development the sterilization technique is best suited to leguminous plant pests (the dried-bean beetle, *Acanthoscelides obtectus* Say, and the pea beetle, *Bruchus pisorum* L.). In this case there is no need to rear the insects under artificial conditions, since very large numbers of them are brought into the granaries with the harvest in the autumn. They can be sterilized by means of portable gamma-ray sterilizers. The remainder of the insects left in the field can be eradicated by releasing those in the granaries after their sterilization. The number of sterilized insects released from the granaries will be considerably greater than the population left in the field.

As a result of mating sterilized specimens with those that have overwintered in the field, the new generation will be considerably smaller in number. Subsequent releases could reduce the dried-bean beetle population to zero. For direct control of the dried-bean beetle by sterilization, we have been carrying out studies aimed at determining the optimum sterilization doses, the ratios between sterilized and non-sterilized insects, and the effect of radiation doses on the competitiveness of irradiated insects compared with normal ones. In these studies the reduction in the hatch of the new generation as opposed to the control has been used as the sterility index.

Figure 1 shows the effect of the irradiation dose on the hatch of the new generation. As can be seen, for a dose of 12 krad this hatch approaches zero. Consequently, a dose between 12 and 15 krad (12 krad + 20%) should be considered as the sterilizing dose for the dried-bean beetle, *Acanthoscelides obtectus* Say.

In the next series of experiments males irradiated with a 12-krad dose were placed beside non-sterilized males and females in the proportion of 5:1:1, 10:1:1 and 20:1:1 (Fig. 2). As can be seen from the graph, the curve asymmetrically approaches zero as the ratio increases. At 20:1:1 the hatch for the new generation drops to 3.3%, i. e. by 96.7%.

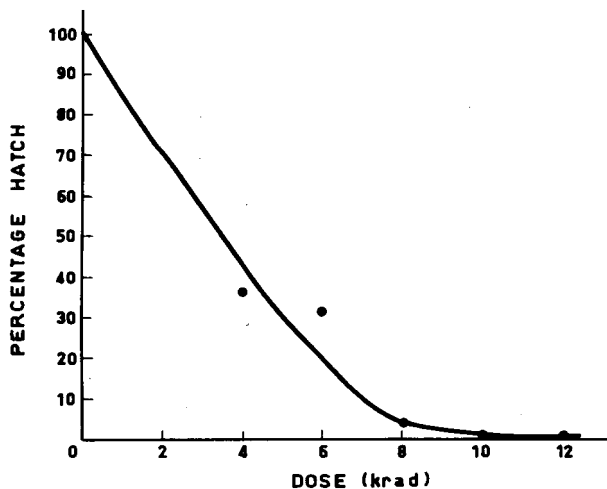


FIG. 1. Effect of radiation dose on the new generation hatch.

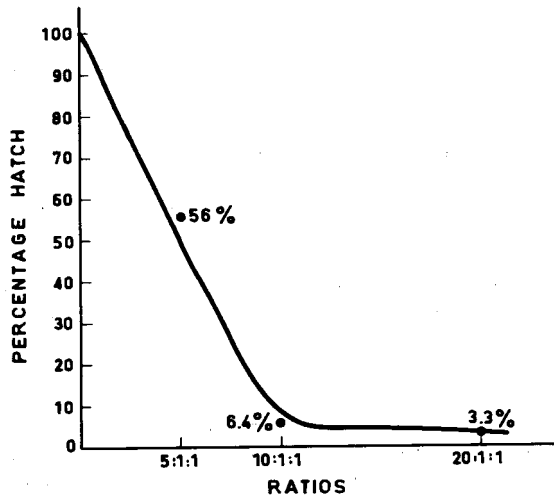


FIG.2. Results of males irradiated with 12-krad dose placed beside non-sterilized males and females in various ratios.

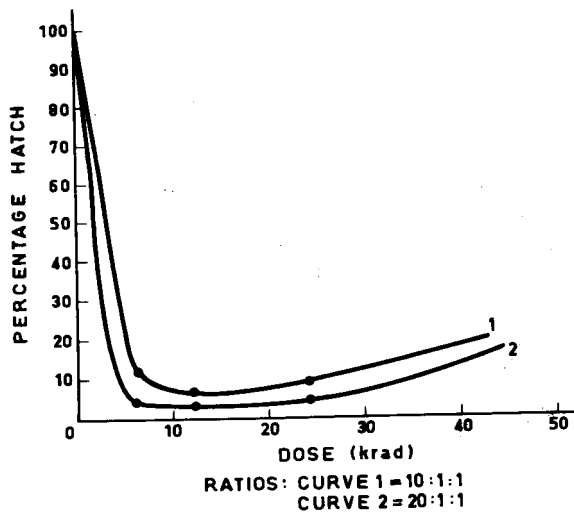


FIG.3. Effect of dose on competitiveness of sterilized males.

To ascertain the sterilizing dose more accurately and clarify the effect of the dose on competitiveness of sterilized males, we conducted a series of experiments with two of the previous ratios (10:1:1 and 20:1:1) but with different radiation doses (Fig.3). As the curves show, the hatch for the new generation falls sharply, approaching zero at doses between 10 and 20 krad. As the dose is further increased, the percentage again rises. This fact should be regarded as due to a decrease in the competitiveness of the sterilized beetles.

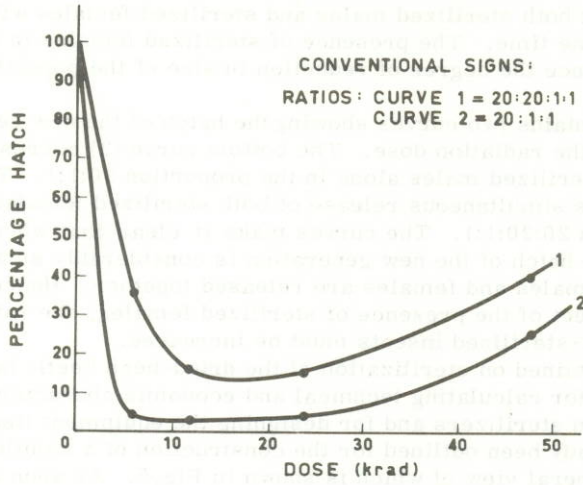


FIG. 4. Hatch of the new generation as a function of the radiation dose.

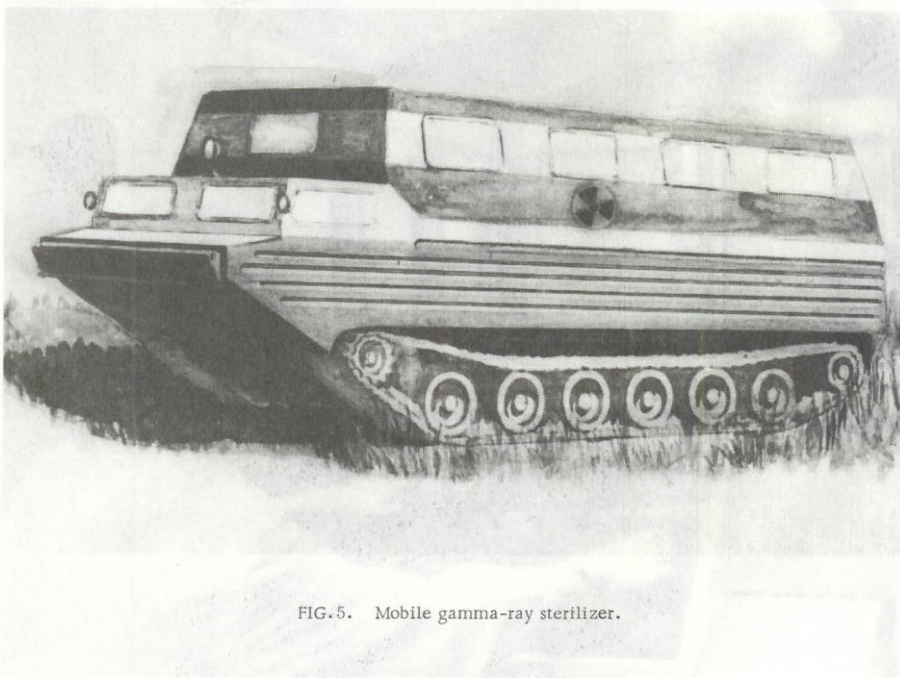


FIG. 5. Mobile gamma-ray sterilizer.

During the practical application of the radiation sterilization technique it is not possible to release sterilized males alone. It should therefore be kept in mind that both sterilized males and sterilized females will be released at the same time. The presence of sterilized females in the population will influence the degree of reduction in size of the population in the new generation.

Figure 4 contains two curves showing the hatch of the new generation as a function of the radiation dose. The bottom curve (2) corresponds to the release of sterilized males alone in the proportion 20:1:1. The top curve represents simultaneous release of both sterilized females and males in the proportion 20:20:1:1. The curves make it clear that when only males are released the hatch of the new generation is considerably smaller than when sterilized males and females are released together. Hence, in order to lessen the effect of the presence of sterilized females, the ratios of sterilized to non-sterilized insects must be increased.

The data obtained on sterilization of the dried-bean beetle have been used as a basis for calculating technical and economic characteristics of gamma-radiation sterilizers and for designing the equipment itself [17-19]. Plans have already been outlined for the construction of a mobile gamma-ray sterilizer, a general view of which is shown in Fig. 5. As soon as it has been built, the sterilization technique will be tried out under field conditions in an attempt to control the dried-bean and pea beetles. This sterilizer will be used in the granaries to sterilize insects brought in with the harvest.

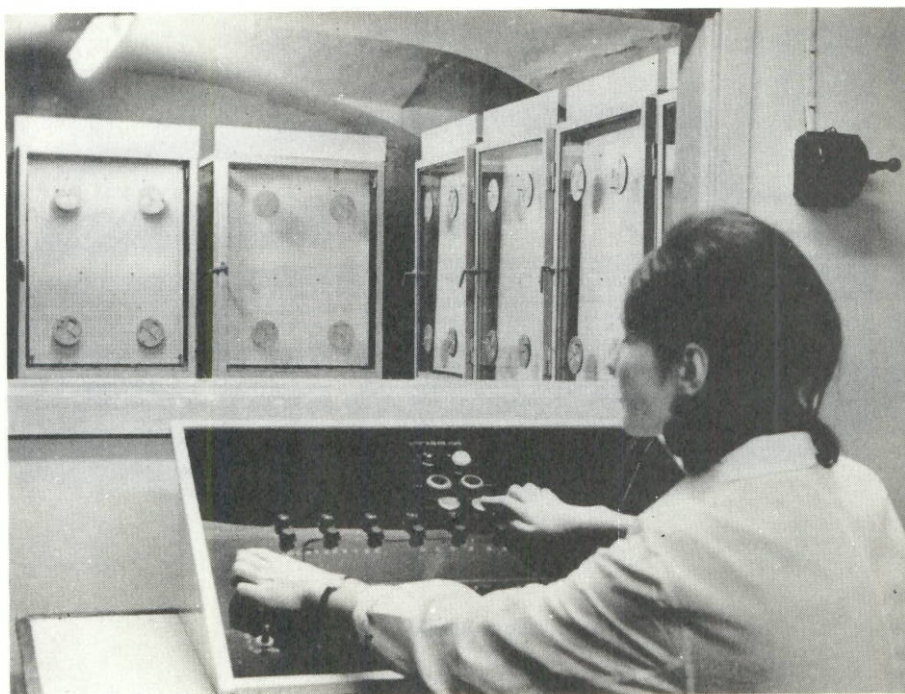


FIG. 6. Automated line for rearing *Trichogramma*.

Over the last few years, intensive development of practical research on biophysical, biological and microbiological control techniques has not only necessitated the development of nutrient media and methods of rearing insects, but also created the need for the construction of equipment enabling us to automate rearing systems for both harmful and useful insects. In view of this, research is currently being conducted on the development of mass-rearing techniques under artificial conditions. A particularly important part of this research is concerned with the principles on which the rearing of insect pests can be automated, with allowance for their specific biological features and the optimum conditions required for the insects to develop throughout all phases from egg to imago. These principles can be applied both in the sphere of chemical and radiation sterilization as well as in the rearing of insects used in biological and microbiological control, i. e., predaceous insects, parasites and viruses [20].

In Fig. 6 we show an automated line for rearing Trichogramma, and at the present time other versions of it are being worked out for mass rearing other insects, among them the codling moth, Carpocapsa pomonella L., on windfallen apples and on semi-synthetic media, and the melon fly, Muiopardalis pardalina Big, on natural food.

Current Soviet research on the sterilization of insect pests shows how important this method is in plant protection. At the present time we are laying great stress on the sterilization technique because of its potential use on a large scale in the control of agricultural insect pests.

It is because of its tremendous possibilities that we hope that in the near future, with the assistance of the IAEA, the technique will be widely employed for purposes of practical pest control in the developing countries.

Even now we can utilize the experience gained by a large number of countries in dealing with a series of pests, among them the codling moth, Carpocapsa pomonella L., the dried-bean beetle, Acanthoscelides obtectus Say, and fruit flies, Dacus dorsalis Neudel, and others.

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STERILE-MALE TECHNIQUE FOR CONTROL OR ERADICATION OF THE BOLL WEEVIL, Anthonomus grandis Boh.

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Abstract

STERILE-MALE TECHNIQUE FOR CONTROL OR ERADICATION OF THE BOLL WEEVIL, Anthonomus grandis Boh. Results of several field experiments to study the sterile-male technique for eradicating the boll weevil, Anthonomus grandis Boh., are reported. The weevils were sterilized by dipping the adults in a solution of apholate. Although eradication was not achieved in any tests, definite population suppression was obtained, indicating that the sterile-male technique is applicable for boll weevil eradication. One experiment utilizing gamma-radiation for sterilization is described.

The boll weevil, (Anthonomus grandis Boheman), is the most important cotton insect pest in the United States of America. Most, if not all, of the problems associated with development of the sterile-male technique for eradication of an insect species have been encountered in research to develop the technique for this insect. I shall discuss some of the experiments for eradication of the boll weevil that have been conducted and some of the problems that were encountered.

One of the earlier tests, in 1962, was conducted in Plaquemines Parish, Louisiana, approximately 100 km south of the city of New Orleans. The test cotton field contained 2.4 ha and was compared with a check field of 0.4 ha, 48 km distant. The nearest commercial cotton was at least 80 km distant.

We released 10 gravid females in each field. In the test field all 10 females were released in a 0.4-ha portion of the field. In the next five days we searched for the released females. Eight established themselves very near each release site; one moved 17 rows and the other 77 rows from the release site. Our method of detection consisted of looking at every square in the field for oviposition punctures. Detection of very low level populations is an important problem now as it was then. Because squares were plentiful, the released females moved very little after establishing themselves. The number and timing of the sterile-male releases were based on certain theoretical calculations involving the number of F_1 offspring that we might expect, the developmental period, peak emergence, and other factors. We decided to strive for a constant 20:1 ratio of released sterile males to normal males developing in the field. The males were sterilized by dipping them twice, 24 h apart, for 15 s in a 2% apholate solution. They were released once each week. To offset mortality that might follow handling, shipping, and toxicity of the chemosterilant we dipped approximately twice the number of males we actually released. The calculations and releases are summarized in Table I. We prevented reproduction

TABLE I. ASSUMED F_1 EMERGENCE FROM 10 GRAVID BOLL WEEVIL FEMALES AND THEORETICAL NUMBER OF STERILE MALES REQUIRED TO MAINTAIN A CONSTANT RATIO OF 20:1 OF STERILE: F_1 MALES AND ACTUAL NUMBER OF STERILE MALES RELEASED IN THE LOUISIANA EXPERIMENT. THE 10 GRAVID FEMALES WERE PLACED IN THE TEST PLOT ON JULY 26.

Date	Assumed σ or ϕ emergence		Sterile σ releases			
			Theoretical		Actual	
	No.	Cumulative total	No.	Cumulative total	No.	Cumulative total
Aug. 1	0	-	-	-	200	200
8	5	5	100	100	700	900
14	60	65	1200	1300	2100	3000
21	70	135	1400	2700	3000	6000
28	61	196	1220	3920	1400	7400
Sep. 4	4	200	80	4000	750	8150
12	0				600	8750
19	0				100	8850

TABLE II. OVIPOSITION PUNCTURES AND EGG HATCH IN AN EXPERIMENTAL EFFORT TO ERADICATE AN ARTIFICIAL INFESTATION OF THE BOLL WEEVIL IN PLOTS IN LOUISIANA.

Date	Test plot		Check plot	
	Punctures at release site (%)	Hatch of eggs (%)	Punctures at release site (%)	Hatch of eggs (%)
Aug. 1-2	7	-	From 1 to 40	-
15	16	0		70
28-29	36	0		100
Sep. 5	14	0		70
12	9	0		-
24	0.9	0		-
Nov. 15	0 (all plants	-		-
21	0 examined)	-		-

of the population of boll weevils in this test (Table II). Details of other calculations, based on the observed number of eggs laid by the original 10 gravid females, indicated that we actually had a ratio of no less than 47:1 of sterile: normal males but very likely the ratio was nearer to 395:1.

We conducted two other release tests in 1962. In these tests the ratio of sterile:normal males was kept constant at 20:1 based on the number of original virgin females or males that were released. We failed to prevent population build-up in these tests. In one test we had shipping difficulties and could not maintain the desired release schedule in the test plot. In both tests we believe that the ratio was actually somewhat less than 20:1 because of the deleterious effects of the chemosterilant.

Our most ambitious field experiment up to 1968 was an attempt to eradicate a natural field population of weevils in a partially isolated area of the cottonbelt in 1964. The males were sterilized in the same manner as in the previous experiments, two 15-s dips, 24 h apart, in a 2% apholate solution. Figure 1 shows the experimental set-up in Baldwin County, east of Mobile, Alabama, where we attempted to eradicate the boll weevil with a combination of applications of insecticides and sterile-male releases. The number of letters in each circle indicates the number of fields at that location. All the circled fields below a line running from Robertsdale west were treated at weekly intervals eight times with methyl parathion in the autumn of 1963 to reduce the overwintered population to as low a level as possible. The weevil population was estimated to be about 30 per acre on each of five weekly counts towards the end of the treatment period. No hibernating

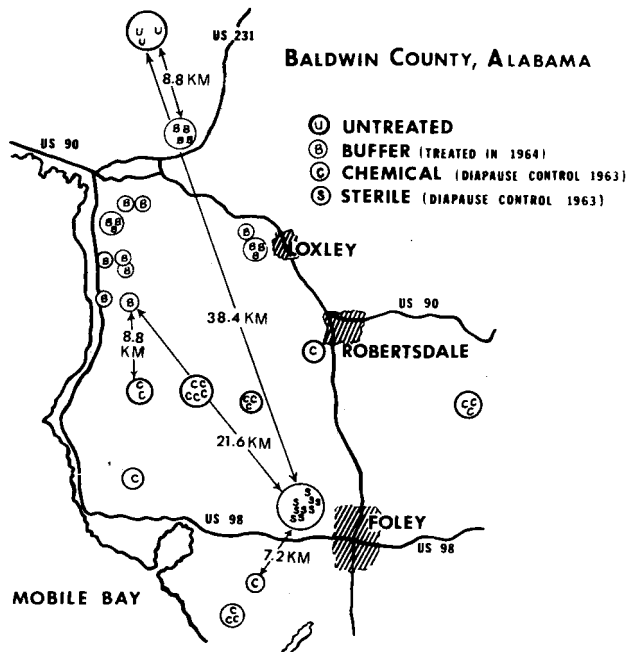


FIG. 1. Map showing location of fields in the combination insecticide-sterile-male release experiment.

weevils in the treated zone and 400 per hectare in the untreated buffer zone were found in the examination of limited numbers of spring woods trash samples. Five boll weevils were found in 1964 on 3500 linear metres of seedling cotton inspected in the buffer zone. None were found on 4000 linear metres of seedling cotton inspected in the chemical control zone.

Early in 1964 greenhouse-grown, squaring cotton plants grown in pots were placed in seven fields of the 1963 treated zone and at two locations in the untreated buffer zone. Results are shown in Table III. Although weevils were not found, punctured squares were found on trap plants in one location in the treated zone. Towards the end of May, cotton in the buffer zone fields was as attractive as the trap plants accounting for the fewer numbers trapped on May 18 and 25.

TABLE III. NUMBER OF BOLL WEEVILS FOUND ON TRAP PLANTS, FRUITING COTTON PLANTS GROWN IN POTS AND PLACED IN FIELDS, EARLY IN 1964, IN EXPERIMENT IN BALDWIN COUNTY, ALABAMA

Date	Treated zone	Untreated (Buffer)
May 5	0	16
7	0	22
11	0	13
18	0	5
25	0	1

In 1964 we released apholate-dipped males in the nine S-encircled fields shown in Fig. 1. We treated with insecticides the remainder of the test acreage intensely. Nine fields contained a total of 6.5 ha in the sterile zone, 15 fields a total of 48.6 ha in the chemical control zone, and 34 fields a total of 46.5 ha in the buffer zone.

The sterile-male release area was almost surrounded by insecticide-treated fields with the nearest field 7.2 km distant and the nearest untreated cotton 38.4 km distant. This is poor isolation so far as the boll weevil is concerned. Buffer zone fields were not treated with insecticides in 1963 but they were treated in 1964 after the square infestation level reached 10% in each field. The fields were treated for the rest of the growing season and into the diapausing population control period. The fields were treated to minimize migration into the insecticide and sterile-male release zones.

In 1964 the insecticide control zone fields were treated seven times with azinphosmethyl-DDT at approximately five-day intervals. Applications were begun in each field when the first boll weevil or punctured square was found. Beginning in the last week of May each of the nine fields in the sterile-male zone was examined one or more times weekly. Before plants began to fruit, every plant in the 6.5 ha was examined. After plants began to fruit, every plant on every row was examined. Towards the end of the growing season it was possible to examine only 20% of the plants in this zone. We began releases of sterile-male boll weevils in each field when

the first punctured square was found. In three fields the releases began on 17 June, or two days after the first punctured squares were found. In these fields the infestation seemed to be increasing too greatly, so we used applications of insecticides between releases of sterile males to reduce numbers. We made 11 releases of sterile males between June 17 and August 26 on a weekly schedule. A total of 134 800 sterile-male boll weevils were released for an overall average of approximately 19 700 per hectare. Allowing for post-dip mortality of males and separation of females from males before dipping required 750 000 boll weevils reared in the laboratory for the experiment.

The numbers of squares with oviposition punctures per hectare are shown in Table IV. Only 4 of the 15 counts that were made, and the seasonal averages, are shown. The fields that received insecticides to stop population build-up are fields 1, 2 and 3. The best and the worst of the six remaining fields from the standpoint of oviposition in the sterile-male zone were fields 4 and 5 respectively. Although a fair number of eggs was laid, the numbers laid is not the whole story. In Fig. 2 we show the seasonal average of viable eggs in the buffer check at the top, in the three fields that received insecticides with sterile-male releases (broken line), and in the six fields receiving sterile-male releases (bottom solid line). The arrow indicates the last date sterile males were released. The seasonal average of inviable eggs in the sterile-male release plots was 67% compared with 4% in the buffer check. Even this is not the whole story. All the squares with oviposition punctures do not necessarily contain an egg or larva. In the buffer zone 90% of all oviposition punctured squares contained eggs or larvae compared with 62% in the sterile zone. The sterile eggs in some squares apparently had disintegrated so that the squares containing them were classified as not containing an egg or larva.

End of season data obtained in each zone is given in Tables V and VI. In Table V stages of weevils per hectare refer to larvae, pupae and adults. Population levels were considerably lower in the sterile-male release zone than in the insecticide-treated or buffer area. In the two ground trash

TABLE IV. NUMBER OF OVIPOSITION-PUNCTURED SQUARES PER HECTARE IN STERILE-MALE RELEASE FIELDS IN BALDWIN COUNTY, ALABAMA. ELEVEN RELEASES BETWEEN 17 JUNE AND 26 AUGUST 1964

Date	Sterile release fields No.				
	1 ^a	2 ^b	3 ^b	4	5
15/6	59	128	133	0	0
14/7	872	2705	4537	47	1946
17/8	178	17	4167	148	341
15/9	190	44	1588	25	0
Seasonal aver.	291	637	2608	67	417

^a Insecticide treated 23/6, 29/7, 4/8, 13/8 and 17/8.

^b Insecticide treated 23/6, 4/8, 13/8 and 17/8.

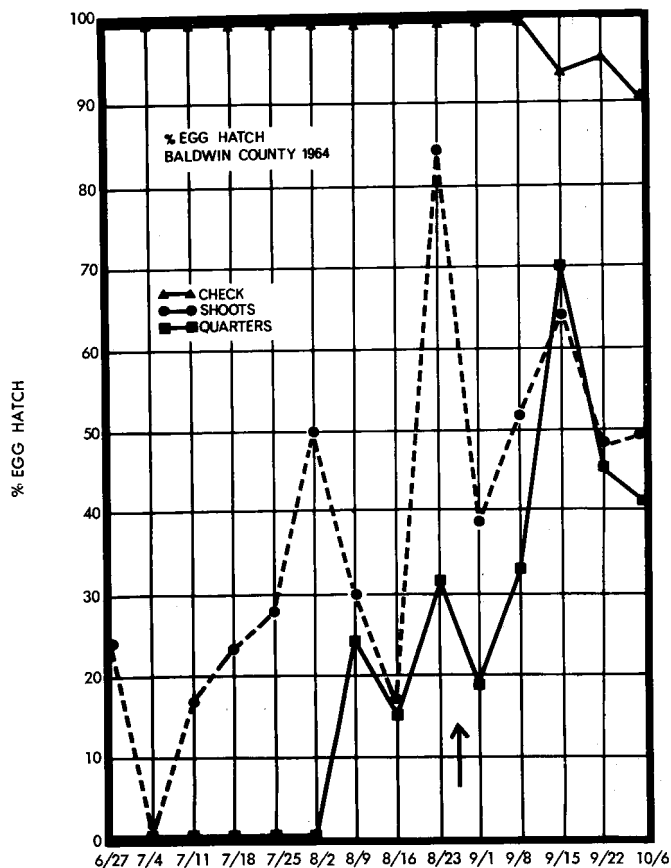


FIG. 2. Seasonal average of egg hatch in the Baldwin County, Alabama, boll weevil eradication experiment. Shoots represents the three fields that had applications of insecticides with release of sterile males. Quarters represents the six fields receiving only sterile males during 1964. The arrow indicates the last day of sterile-male releases.

examinations fruit was collected from numerous 33 metre subsamples, drill to drill from the ground; the collected fruit was dissected to obtain the per hectare figure. Total plant involved checking all parts of the plants for larvae, pupae and adults in the same number of linear metres. Shagging plants represented numbers of adults collected by shaking the plants while they were held in a bag. Woods trash represented the number of adults collected from hibernation sites. Only data from fields that had not received insecticide applications in 1965 are shown in Table VI. The effect of sterile-male releases apparently carried over into the subsequent season.

Why wasn't the boll weevil eradicated? First, we did not obtain a high enough degree of sterility with our chemosterilant. We ran quality control tests on a part of each shipment of treated males. When we mated the treated males to untreated virgin females the percentage of hatch of the eggs laid by the females ranged from 0 to 12 with a mean of 4.2. This

TABLE V. END-OF-THE-SEASON RECORDS OF STAGES OF BOLL WEEVILS OR ADULTS PER HECTARE IN THE BALDWIN COUNTY, ALABAMA, EXPERIMENT, 1964

Type record	Date	No. of weevils or weevil stages per hectare in zone:		
		Buffer	Insecticide	Sterile
Ground trash	19/8	2050	27	37
Ground trash	24/9	-	121	32
Total plant	9/10	1321	551	94
Shagging plants ^a	17/11	385	687	121
Woods trash ^a	17/12	3107	1435	0

^a Adults only.

TABLE VI. ADULTS OR STAGES OF WEEVILS PER HECTARE IN 1965 IN FIELD IN WHICH STERILE-MALE RELEASE EXPERIMENT WAS CONDUCTED IN BALDWIN COUNTY, ALABAMA, IN 1964

Type record	Date	Zone		
		Buffer	Chemical	Sterile
Woods trash ^a	March	479	0	0
Trap crop	May	59	15	2
On field	June 15	9 097	783	0
plants and	June 30	20 019	3905	42
in shed fruit	July 28	26 836	14 524	3423
	Aug. 11	33 387	14 341	1588

^a Adults only.

means that regardless of the number of sterile males we released to overflood the field population, we could not expect a greater average ratio than 23:1 of sterile:fertile eggs. In addition, the treatment of males with apholate reduced their competitiveness in mating. Another contributing factor to our failure may have been the lack of sufficient isolation to prevent influx of migrant boll weevils. Another factor was due to regaining of fertility in males that survived for two to three weeks after being treated with apholate. The last and perhaps most important factor was that we failed to reduce the native population to low enough levels with the autumn insecticide program to reduce diapausing populations to make the sterile-male release program effective.

In the autumn of 1967 we released boll weevils sterilized with gamma-irradiation in two small fields along the Rio Grande River near Presidio,

Texas. These fields had been included in a program to control reproducing-diapausing populations for several years previously. The weevils we released were exposed to 9600 rad in a ^{60}Co source and were flown from our laboratory via commercial aeroplanes to Fort Stockton, transported to Presidio by car and released, primarily, by hand in the fields. We attempted releases of weevils from aeroplanes by dropping them in gypsy moth cartons designed to open as they fell towards the ground or as they hit the ground. The distribution of weevils released in this manner was very poor. Thereafter we made the releases by hand. We made eight releases of gamma-irradiated weevils of mixed sex at the rate of approximately 2500 per hectare per week. Throughout the release period we collected samples of eggs and observed them for hatch. Only 21 of 75 eggs collected in one field hatched. The 21 that hatched were collected from a very small portion of one field. In the other field none of 26 eggs collected hatched. Shortly after we made our eighth release migrant boll weevils from a field 3 km distant moved into our fields and forced us to terminate the test.

This test emphatically illustrated the need for early detection of an incipient infestation of the boll weevil. The infested small part of the field was first discovered when we had made about one-half of our releases. We then overflowed this part of the field with the equivalent of 5000 gamma-irradiated weevils per hectare. If we had detected the infested part of the field sooner we very likely would have done better with our sterile-male releases than the egg hatch records indicated. The greatest problem associated with gamma-irradiated weevils is that there does not appear to be a distinct line of separation between sterilizing and lethal doses. The males are competitive sexually for only about five days after irradiation. In our procedure it took one day to sterilize, package, ship and distribute the weevils. In addition, it takes a day of feeding on squares for the released males to compete in attractiveness to females with native males. Thus we only had three to four days of effective mating following each release of sterile males.

In summary, the most important problem to be overcome in developing the sterile-male release technique for eradicating the boll weevil is to find a method of sterilizing the weevil that does not adversely affect mating, competitiveness and longevity. Other problems concern development of methods for detecting very low level populations and for distributing sterilized weevils when they are released. Another problem is the need for a cheap method for separating the sexes. Minor problems are handling, and shipping sterilized insects, and the possibility of crop damage when both sexes of boll weevils are released.

Indications are that problems associated with mass rearing will soon be solved. Reduction of native populations before release of sterile males no longer is a problem because this can be done with applications of insecticides programmed against the last reproducing generation and diapausing populations in the preceding late summer and autumn.

SIGNIFICANCE OF THE STERILE-MALE TECHNIQUE IN PEST MANAGEMENT OF THE WHITE GRUB (Melolontha vulgaris F.)

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Abstract

SIGNIFICANCE OF THE STERILE-MALE TECHNIQUE IN PEST MANAGEMENT OF THE WHITE GRUB (Melolontha vulgaris F.). The known facts on biology and behaviour of the cockchafer (Melolontha vulgaris F.) and the conventional control methods are reviewed in relation to the possibility of applying the sterile-male technique to this insect pest. The long development cycle and the aggregation of population in areas which may be delimited and sampled for population estimates facilitates long-term prognosis of the damage to be expected. Actual and potential control methods are critically evaluated in order to integrate pest management with methods not merely reducing numbers but also lowering the reproduction rate. Dynamics of cockchafer populations under favourable and unfavourable conditions are described and the consequences of conventional control and regulation methods are demonstrated. With the aid of simplified hypothetical models long-term effects of the sterile-male technique are compared with those of chemical control. It is concluded that the sterile-male technique would contribute decisively to long-term population regulation. As a unique and efficient method it should therefore be integrated into management of this insect pest, and could be recommended under conditions favourable to the development of cockchafers where rapid resurgence of population after conventional treatments have to be expected as well as under ecologically unfavourable conditions, where conventional methods are not feasible because of topographical difficulties or because of high costs.

1. BIOLOGY OF THE COCKCHAFER (Melolontha vulgaris F.)

1.1. Developmental cycle

In most regions of Switzerland where the cockchafer is as a pest, the developmental cycle requires three years for most of the population. The flight period of the adults lasts only a few weeks every three years. In the intervening years only a few individuals may be observed at the same locality. There are, however, a few instances known where considerable flights occur in two successive years.

Larval development involves three stages with the first moult occurring in the autumn of the flight year, the second during early summer of the following year and the third moult during late summer of the second year after flight. Metamorphosis is completed during late summer or early autumn of the second year.

Adults hibernate in the soil near their exuviae at a depth of 20 to 30 cm in most cases. In the spring of the third year beetles are ready to emerge and to take to their wings sometime after 20 April.

Damage of economic importance is caused by the feeding of the white grubs, mainly starting with the second and continuing into the third stage.

They feed on roots of various agricultural crops, herbs and woody plants. Adults feed predominantly along the edges of woods on trees with deciduous foliage.

Females mate and oviposit several times (at most three batches). Although the potential full complement after three ovipositions could be 72 eggs the average number that may be expected under natural conditions probably is much lower, about 20 per female.

All adults die in June or July of the flight year. There are therefore no surviving adults from one generation to the next.

1.2. Behaviour of adults during the flight period

1.2.1. Emergence of beetles

Cockchafer are characterized by some behavioural peculiarities which make them particularly suitable for studying and applying the sterile-male technique. Although the life cycle of the same generation spans several years, flight of individuals of the same population is synchronized to occur simultaneously during a few weeks as soon as the young foliage of the host trees appears. Males emerge before females and may be caught in light traps in bigger numbers than females.

1.2.2. Aggregation of adults

During their primary flight, which is crepuscular, cockchafers follow determined lines of flight. By hypsotactical orientation they are led to the highest skyline on their horizon which in most cases are hillsides covered with forests [1].

1.2.3. Aggregation of white grubs

After maturation feeding and copulation their orientation reverts to the opposite: females head for oviposition in the fields. The same sites, if not necessarily the same plots from where the adults emerged, serve as breeding grounds for their offsprings.

This behaviour results in isolated populations with their own territories, between which there is no exchange unless the adults suffer from food shortage. However, as long as population density is low, which would be one of the necessary requirements to apply the sterile-male technique or other autocidal methods, this behavioural isolation is valid. Even in an open landscape without topographical barriers such as mountains or lakes, populations are fenced in their territories.

Based on this behavioural isolation of cockchafers infestation zones may be delimited. Within these areas population density may be estimated and the size of population predicted. Neighbouring infestation zones may be treated independently, at different times or with different methods and intensities. During the application of the sterile-male technique one infested zone may serve as a bank, from where cockchafers are obtained and, after irradiation, released in a neighbouring zone where the population is to be eradicated.

2. ACTUAL AND POTENTIAL CONTROL METHODS

2.1. Reduction of adult population

The aim of reducing the number of adults is to prevent oviposition and the build-up of white grub populations.

2.1.1. Collection of adults

In several Swiss Cantons cockchafer have been collected for many decades if not for more than a century. In several Cantons collection was obligatory as soon as widespread damage of white grub was evident, e.g. when population density was high. Results in reducing white grub damage on crops by this method are doubtful. Of even more questionable character is the influence on reduction of population density lasting more than one generation. In a few Cantons quantities of collected beetles were recorded over many cycles. This material would be perhaps interesting evidence for statistical evaluation.

2.1.2. Chemical control of adults

Since 1948 several control operations on a large scale have been attempted to control or eradicate cockchafers by treating the woods and also dispersed host trees with insecticides. Compounds based on lindane proved to be the most effective and were therefore the most frequently used insecticides. These treatments on a large scale of several hundreds or even thousands of hectares during a short period of maturation feeding created for the organizing agency many problems of a technical and biological nature concerned with residues, and frequently roused public opinion. Very close co-operation among a well-trained technical and biological staff has to be emphasized. Results of these treatments as regards crop protection may be satisfactory whereas the influence on population dynamics remains highly controversial. As regards insecticide residues and undesirable side effects on the environment, treatments of wood in the short period of flight have to be compared with application of soil insecticides to control white grubs. We consider the former as the lesser of two evils.

2.2. Protection of crops from oviposition

Preferences during oviposition is strongly influenced by topographical features and the nature of crops.

Non-preferred crops are protected from oviposition and from white grub damage. Crops grown on non-preferred sites as well as non-preferred crops are protected from oviposition and hence from white grub damage. Several practices prevent or reduce adult oviposition, for example irrigation and drainage, fertilization, mowing after flight, soil management and growing of cover crops.

2.3. Reduction of white grub population

Methods mentioned below are suitable for controlling white grubs in single plots. They result at best in a reduction of a limited and localized segment of a cockchafer population.

Different and more or less efficient control methods may be applied to particular plots depending on the tolerance level to white grub damage of the crops to be protected.

Such control methods are:

1. Cultural methods such as crop rotation, soil management, grazing of grassland, irrigation and planting of resistant varieties.
2. Chemical methods, treating the soil with chlorinated hydrocarbons (Lindane, Aldrine, Heptachlor), but this practice is limited for well-known reasons, and carbonates as well as organophosphates are considered as potential replacements.
3. Reduction of reproduction.

2.3.1. Radiation

Research on the application of radiation to sterilize cockchafer in order to eradicate white grubs is limited to a few species of Melolontha vulgaris F. [2-5] and Amphimallon majalis R. [6]. With the first species the lower level of sterilizing dose lies at about 3 krad for X-rays for both the Swiss as well as for the Hungarian cockchafer population. Apparently the same dosage level applies to gamma-rays [5]. Longevity and male competitiveness are not affected at this dosage level.

2.3.2. Chemosterilants

Melolontha melolontha L. served Landa for testing of chemosterilants in his laboratory. So far as we know chemosterilants have not been assayed in field experiments.

2.3.3. Other methods of genetic control

Possible methods which should be considered are cytopharmic incompatibility, hybrid sterility, translocations, inversions and deleterious genes. None of these possibilities have been tried with Melolontha species. It appears that cytopharmic incompatibility and the use of translocations should have priority.

3. POPULATION ESTIMATES

In order to be efficient genetic control methods depend on reliable population estimates of the target species. In contrast to the more conventional control methods where abundance of a harmful species frequently may be assessed in general or relative terms which sometimes may even be based on damage assessment on infested crops, genetic control methods depend on population counts or estimates that are as precise as possible. This requirement has to be stressed not only to ensure a sufficient level of released naturally or artificially burdened individuals on the one hand but also to measure and evaluate the effect of the release on the natural population on the other hand.

The different possibilities of population estimates, observations on flight activities, prognosis for the adult and larval stage, together with the appropriate methods and deadlines, are summarized in Table I.

TABLE I. POSSIBILITIES OF PROGNOSIS FOR THE OCCURRENCE OF COCKCHAFFERS AND WHITE GRUBS

Stage	Methods	Deadline
Adult	Mapping of infestation zone	Years before flight
	Estimation of population density	Autumn before flight
	Prediction of start of flight period by the temperature sum	Begins with 1 March of flight year
White grub	Observation of flight intensity in infestation zone	Spring of flight year
	Mapping damage on host trees	15 June of flight year
	Sampling diggings in grassland	September of flight year

3.1. Territories of cockchafer populations

For several reasons populations of cockchafer (*Melolontha vulgaris* F.) lend themselves particularly well to carrying out population estimates. The long developmental cycle of three years leaves enough time and offers many opportunities to estimate in turn adult or larval populations before and after treatment. As previously mentioned, populations of the cockchafer are segregated through behavioural isolation. In any infested area each separate population territory may be delimited and mapped as soon as maximal defoliation of host trees appears. The territories concerned may be measured as to size and surface of different crops most likely to harbour considerable segments of the population in the particular area.

3.2. Estimation of adult population

Soil sampling for adults is effected in autumn or spring before the flight starts. Sampling units are of 0.25 m² of surface area down to a depth of 20-40 cm. About 10 plots of grassland (natural meadows or old lays of grass and legumes) of 0.4 to 0.6 ha are chosen in each area. In each plot 16 random 0.25 m² sampling units are averaged. The number and sex of beetles is recorded separately for each plot.

3.3. Estimation of white grub population

The same procedure as outlined above is repeated during the late summer and autumn of the flight year. The same number of sampling units are dug in the same plots in consecutive surveys. For identification purposes the plots are numbered and drawn on a sketch plan to the scale of 1 : 5000 or 1 : 10 000 and in addition on a 1 : 25 000 scale survey map for the whole region.

3.4. Observation of flight activity

Points for observation of flight activity are chosen on exposed angles, preferably on the western border of woods overlooking the territory considered. Records are taken of meteorological conditions, of numbers of flying beetles at five-minute intervals and of the direction of their flight to or from the wood.

3.5. Assessing damage on preferred food trees

At weekly intervals, beginning on 20 April, exposed angles of the woods adjacent to the territory considered as well as those of the neighbouring woods are inspected for damage by cockchafers. The following tree species may be considered as preferred by cockchafers: Quercus robur L., Fagus silvaticus L., Acer campestre L., Juglans regia L., Prunus cerasus L., P. domestica L., Populus tremula L. and Larix decidua L.

The final inspection tour should be completed before 15 June. Care should be taken not to confound defoliation caused by other species, e.g. Tortrix viridana L., on oak with damage done by cockchafers.

4. POPULATION DYNAMICS IN COCKCHAFERS

4.1. Parameters used to describe population dynamics

The counts of cockchafers and white grubs respectively described above serve for the estimation of:

- (a) the population density of cockchafers before flight, their sex ratio and their distribution over the area;
- (b) the population density of white grubs after the flight period and their distribution over the area;
- (c) the rate of reproduction after the flight period, obtained by dividing the number of white grubs counted in a given plot or area by the number of cockchafers in the same plot or area before the flight period;
- (d) the mortality in the three years between successive white grub or cockchafer counts.

4.2. Reproduction rate in cockchafers

Although the anatomy of their ovaries would allow female cockchafers to produce three batches with a total of 72 eggs, it is realistic to assume a much lower reproduction rate.

For practical reasons routine sampling after the flight period is carried through in August and September of the flight year when white grubs have hatched and grown to a size which allows them to be found more easily in the sod. Then white grubs have either attained full-grown first larval stage or they are already in their second stage.

Net-reproduction rate (R) is expressed as follows:

$$R = \frac{N_W}{N_A}$$

where N_W = Number of white grubs per square metre and
 N_A = Number of cockchafers per square metre.

4.3. Mortality in white grubs – survival rate of adults

During the period between sampling for white grubs in the autumn of the flight year and sampling for adults in the spring of the following flight year

any reduction of population is regarded as due to "larval mortality", although metamorphosis and overwintering of adults is also embraced in that period.

Percentage mortality is expressed as follows:

$$\% M = \frac{N_W - N_A}{N_W} 100$$

Survival rate (\ddot{U}) is the complement to Mortality: $100 - M$ or is directly obtained from surviving adults:

$$\% \ddot{U} = \frac{N_A}{N_W} 100$$

4.4. Dynamics under different ecological conditions

Dynamics of insect populations have for many years been subject to intensive studies in many insect species and also have led to much controversy. Populations of cockchafer, owing to their slow development of one generation in three years, require patience from the observer but offer the advantage of a slow motion movie. We had the privilege to start population studies on that species in 1950 in three different regions of the Swiss Cantons Berne, Lucerne and Thurgau and to follow gradation under natural conditions over several cycles. In the following paragraphs we report results obtained in one of these regions in Canton Lucerne.

Our survey includes four different areas in a valley called "Luzerner Seetal", each area measuring about 30 ha. Two areas are situated near Aesch and Gelfingen at the bottom of this valley whereas the other two occupy terraces near Sulz and Schongau on the upper slope of a hill range called Lindenberg.

The terrain stretches across the western slope of this hill range with altitudes ranging from 450 to 812 m above sea level. Extended woods top this hill range, and strips of woods line the water-courses draining the slope.

Intensive general farming is possible in the whole area with fruit trees, grass, cereals, potatoes, sugar beet, rape and vegetables cultivated on most of the arable surface. Milk production provides the main source of farm income.

The climate is influenced by two lakes and the Föhn, which frequently lengthens the vegetation period in spring and autumn.

At the bottom of the valley there is a vineyard. In the grassland farmers take normally five to six cuts yearly.

On the top of the hill range the climate is much harsher.

To control cockchafer insecticidal treatments were undertaken in 1951, 1954 and 1957 and, after an interruption covering two flight periods, again in 1966. These treatments affected one to two surveyed areas, the untreated served as control (Table II).

4.4.1. Dynamics under ecologically favourable conditions

The two areas situated in the bottom of the valley near Aesch and Gelfingen apparently are favourable to the development of cockchafer populations. This is evident from the higher rate of reproduction (Table III),

TABLE II. INSECTICIDAL TREATMENTS FOR COCKCHAFFER CONTROL

Treated areas	Topographical situation	Flight periods			
		1951	1954	1957	1966
Aesch	Bottom of valley	+	+	+	+
Schongau	Top terrace	+	+	-	-
Gelfingen	Bottom of valley	-	-	-	+
Sulz	Top terrace	-	-	-	-

TABLE III. REPRODUCTION RATE 1954-66 (Luzerner Seetal)

Flight period	Area	Topographical situation				Average
		Bottom of valley		Hilltop		
		Aesch	Gelfingen	Sulz	Schongau	
1954		9.1 ^a	7.7	2.0	3.0	5.4
1957		0.97 ^a	4.7	0.20	0.25	1.5
1960		25.2	6.0	0.13	0	7.8
1963		9.7	6.6	-	-	8.1
1966		1.15 ^a	1.2 ^a	2.5	0.1	1.2
Average		9.2	5.2	1.2	0.8	4.1

^a Area with insecticidal treatment for cockchafer control before estimate of white grub population.

where in spite of frequent insecticidal treatment this parameter is above average, whereas in the two areas on the hilltop reproduction is much lower. Mortality is lower than average in the bottom areas and higher than average in the hilltop areas. From close inspection of ecological conditions we find that in the two areas in the bottom of the valley not only is climate moderated by two lakes and protection from northern winds is better but also soils are richer in humus content. This is brought about by intensive fertilizing with liquid manure. Through this manure the composition of grassland associations is drastically changed because graminaceous plants are replaced by herbs which in general are preferred by white grubs. Moreover farm management favours white grubs by zero-grazing. Mechanical destruction of white grubs in pastures is therefore avoided. Because of high milk prices farm management in this region avoids breaking up grass to arable land. Mechanical destruction of white grubs through plough and harrow and other implements efficient in killing soil insects is not carried out. This composite action of several factors beneficial to white grub populations explains the higher densities of white grubs (Table IV), higher cockchafer counts (Table V), higher rate of reproduction (Table III) and lower mortality (Table VI).

4.4.2. Population dynamics under ecologically unfavourable conditions

The two areas of Sulz and Schongau on the terraces near the hilltop offer less favourable climatic conditions. They are more exposed to winds from all directions including northerlies. The small lakes in the bottom

TABLE IV. WHITE GRUB POPULATION 1951-66 (Luzerner Seetal)

Area	Situation	Flight year					
		1951	1954	1957	1960	1963	1966
(white grubs per m ²)							
Aesch	Bottom of valley	33.1 ^a	20.9 ^a	3.7 ^a	10.1	34.9	6.1 ^a
Gelfingen	Bottom of valley	34.6	19.2	29.3	12.7	25.6	7.8 ^a
Schongau	Hilltop	24.1 ^a	4.8 ^a	0.05	0	0.2	0.03
Sulz	Hilltop	27.8	12.8	0.1	0.02	0.25	0.25

^a Area with insecticidal treatments for cockchafer control before estimate of white grub population.

TABLE V. ADULT POPULATION 1954-66 (Luzerner Seetal)

Area	Situation	Flight year				
		1954	1957	1960	1963	1966
(Cockchafers per m ²)						
Aesch	Bottom of valley	2.3 ^a	3.8 ^a	0.4	3.6	5.3 ^a
Gelfingen	Bottom of valley	2.5	6.3	2.1	3.9	6.3 ^a
Schongau	Hilltop	1.6 ^a	0.2 ^a	0	-	0.3
Sulz	Hilltop	6.4	0.5	0.15	-	0.1

^a Area with insecticidal treatment for cockchafer control after adult population estimate.

TABLE VI. PERCENTAGE MORTALITY OF WHITE GRUBS 1951 - 66 (Luzerner Seetal)

Cycle of development	Topographical situation					Average
	Bottom of valley			Hilltop		
	Area	Aesch	Gelfingen	Sulz	Schongau	
1951-54		92	91	77	94	89
1954-57		88	66	93	96	86
1957-60		90	95	92	100	94
1960-63		64	69	-	-	67
1963-66		80	73	-	67	77
Average		83	79	87	89	84
		81		88		

of the valley do not exert any influence over this distance and difference in altitude. Farming is less intensive and particularly in the area near Sulz the surface of arable land is proportionately greater. Pastureland with grazing throughout the whole vegetation period makes up a higher portion of grassland because of less traffic at that altitude. Because of steep gradients the plots are less accessible for transporting and spreading stable manure. Soil is poorer in humus content, and heavier textured.

This in turn makes drainage more difficult although in addition precipitation is higher at this altitude. Grassland associations are richer in graminaceous plants which are not preferred by white grubs. This composite action of several unfavourable factors explains lower densities of white grubs (Table IV), lower cockchafer populations (Table V), lower rate of reproduction (Table III) and higher mortality (Table VI).

5. POPULATION REGULATION BY CHEMICAL CONTROL OF ADULTS

The same parameters used to describe population dynamics in cockchafer populations were applied to measuring the efficiency of chemical control of adults. As may be seen from population density of white grubs (Table IV) in treated areas near Aesch and Schongau the first treatment of 1951 did not reduce the white grub infestation compared with the untreated areas, the second attempt succeeded in reducing it in only one area near Schongau and only the third attempt finally reduced it also in the area near Aesch.

One might expect that a reduction in the population density of the white grub could also lessen the power and efficiency of mortality factors. It is interesting to note from the figures in Table VI on mortality in white grubs that no such reduction could be observed. Chemical control as it was carried through with the insecticides used and with the technical means available did not affect natural mortality in white grubs. Another criterion to watch is the reproduction rate. On the average the reproduction rate lies between 4-5 with the exception of the area near Aesch which had 9-10 on the one hand and 0.8-1.2 in the areas on the hilltop. It is apparent that chemical control in the area with favourable ecological conditions for the cockchafer population caused a compensation or even an overcompensation (note the reproduction rate of 25 in Aesch in 1960). This rapid resurgence of population as soon as chemical control ceases necessitates frequently repeated treatments. This is not desirable from many points of view – balance of nature, risk of residues, toxication of livestock, bees, fish and wildlife.

5.1. Thinning out versus extinction of a population

It is logical to assume that by chemical control of adults in an environment offering favourable conditions, the few survivors or their offsprings are freed from the burden of intraspecific competition and other density-dependent factors detrimental to the species. The few survivors of the next generation are likely to be more vigorous because of longer life-span, higher fertility, and higher cold and disease resistance.

Thinning out a cockchafer population by merely reducing the number of adults, as it was practised by collecting adults or, in a more efficient way, by means of chemical control, is not sufficient to reduce a rapidly resurging population under ecologically favourable conditions over many generations, much less to eradicate it permanently.

In such a situation the only alternative would be to reduce fertility of the few survivors and their offsprings genetically. Reduction of fertility in cockchafers could be achieved by different means, for instance by resistant or antibiotic host plants. Neither replanting of forests with trees

resistant to adults nor growing of agricultural crops which uniformly would consist of varieties resistant to white grubs would be practicable. A quicker way to achieve results would be to utilize sterile-male methods.

5.2. The minimal density or extinction level of a cockchafer population

The cardinal problem in population dynamics is to know or, even better, to be able to predict turning points of gradation. In most cases applied entomologists are interested in knowing the upper turning-point when a gradation reverts from progression into regression. Another critical moment in gradation occurs when density approaches the extinction level. Below this threshold population will soon completely disappear, above this level, population is likely to continue or to enter progression again in case of a periodic gradation. We tried to determine this point for cockchafer populations as follows (see Fig. 1).

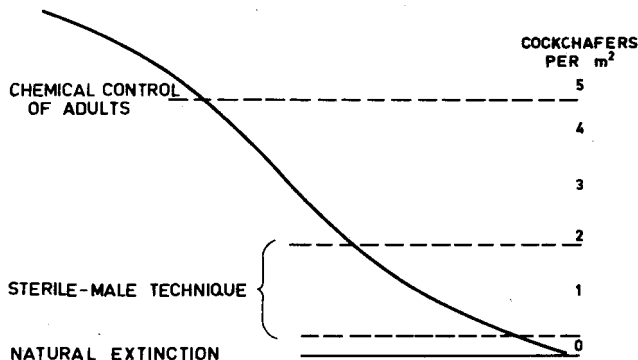


FIG. 1. Critical levels of cockchafer populations within which the sterile-male technique would contribute decisively to long-term population regulation.

Below the extinction level mating chances may be too slim or predation too heavy for population increase. To maintain mating chances and to escape predation cockchafers rely on their classical tactic of synchronizing flight during one short period during their three years' developmental cycle. Then the few survivors of the whole population which during larval stage were dispersed — or which statistically were even "overdispersed" — over hundreds of hectares are now directed to and concentrated on a few hundred metres of borders of woods with host trees providing food and mating places at the same time and locality.

Precursors flying a year ahead as well as stragglers trying their chance one year later are running an incomparably greater risk of failing to mate or of being predated upon and therefore they are likely to vanish completely from the scene. However, if a considerable number of either vanguards or rearguards happen to succeed in trespassing across this threshold they will establish a second or rival flight year.

If this rival flight meets favourable conditions more frequently than the old cycle, it will flourish, and the old cycle eventually disappears. Such transitions back and forth from one flight cycle to another has been

experienced over extended parts of the Canton Zurich in the first decades of the last century and again at the beginning of this century.

In the region considered (Luzerner Seetal) the bulk of the cockchafer population flies with the Bernese cycle (1966-69, etc.). However, there is a clear difference in the composition of the populations in the two areas at the bottom of the valley on the one side and the two on the hilltop on the other side. In the former with favourable conditions the main flight is preceded by a small segment of vanguards, occasionally using two years only to complete the developmental cycle, whereas on the hilltop with unfavourable conditions the main flight is accompanied by a number of stragglers, using four years for development.

If the main flight were eradicated by natural or by man-made catastrophe either the vanguard or the rearguard would have to take over. Depending on which would encounter better conditions more frequently, either one of them eventually could build up a new cockchafer population flying with another cycle.

It is interesting to follow these accompanying flight cycles in order to establish the minimal density or extinction level of a cockchafer population. From our experience we estimate that such a level would have to be fixed at a fraction of 1 cockchafer per m^2 .

It is also important to know such extinction levels for each cockchafer population where we are to judge the feasibility of applying the sterile-male technique.

6. CONCLUSIONS

From the known facts on biology and behaviour of the cockchafer (*Melolontha vulgaris* F.) and from recent studies on population dynamics of this species under favourable and less favourable conditions as well as from critical evaluation of conventional control and regulation methods it is concluded that sterile-male methods would contribute decisively to long-term population regulation. Therefore, management of this historic insect pest could be integrated in a unique and efficient way.

The conventional control methods consist of:

- (i) Reducing numbers of adults to prevent oviposition and keeping white grub density below tolerance level;
- (ii) Diverting flying adults to preferred oviposition sites and thereby attracting them from and protecting susceptible crops from white grub damage;
- (iii) Controlling by means of cultural methods or by soil treatments with insecticides already established white grub populations in the early stages of larval development, before they cause crop losses, could be implemented with the sterile-male technique.

This is recommended under following conditions:

- (i) Where cockchafer populations are favoured by ecological conditions in such a way that through increased reproduction rate in the generations following treatments loss in numbers are compensated or even overcompensated, resulting in rapid resurgence;
- (ii) In regions where conventional methods are not feasible for technical or financial reasons as in topographically difficult areas or extensively cultivated valleys in the alps and fore-alps.

Therefore, it is proposed to:

- (i) Locate rapidly resurging populations;
- (ii) Repress the reproduction rate by dysgenic methods as for instance by charging populations with dominant lethal mutations or other unfavourable heritable traits.

ACKNOWLEDGEMENTS

This research project is supported by a special grant from the Division of Agriculture of the Federal Department of Public Economy, Berne.

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PRESENT STATUS AND POTENTIAL USE OF THE STERILE-MALE TECHNIQUE FOR CONTROL OF RICE STEM BORERS

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Abstract

PRESENT STATUS AND POTENTIAL USE OF THE STERILE-MALE TECHNIQUE FOR CONTROL OF RICE STEM BORERS. After discussion of some biological and control aspects of the Asiatic rice stem borer, *Chilo suppressalis* Walker, radiation experiments are described. Some general conclusions are arrived at for the use of the sterile-male technique on the rice stem borer.

The Asiatic rice stem borer, *Chilo suppressalis* Walker, is one of the most destructive insect pests of the rice plant in Korea. It is distributed throughout Asia exclusive of the farthest north. Chang [1] reported that the annual loss from the insect was 14% and the infested areas were increasing with the introduction of intensive cultural practices.

This insect overwinters as old larvae in rice straw or stubble. The spring moths from the overwintering larvae begin to emerge early in May with the peak flight in early June. The damage from the first brood larvae results in decreasing the number of tillers in the growing plant, but it is not serious compared with that of the second brood larvae.

The summer moths begin to emerge in the last third of July with the peak in the middle of August. The damage from the second brood larvae results in half-shooted heads, poor kernels with poorly matured grain, and white head, depending on the time of actual feeding. The loss from the second brood larvae is serious and substantial.

The control of the rice stem borer has been largely by means of insecticides; dipterex, r-dol, sumithion, EPN, diazinon, dimecron have been the common insecticides for the control of this insect.

I have studied with some co-workers radiation effects on the biology of the rice stem borer, and some results are presented; the potential use of the sterile-male technique will also be discussed briefly here.

The pupae from overwintering larvae, which were collected from the field in early spring, were irradiated with gamma-rays, doses of 0, 2, 2.5, 3, 4, 5, 7, 10 krad when they were 0 to two days old.

The pupal mortalities increased considerably at doses higher than 5 krad with some sexual differences. Although there was some inconsistency in the results, probably because of the unusual condition of the glass dishes where the moths had emerged, the median lethal doses seemed to be about 14 krad for the female and about 10 krad for the male.

Some abnormal moths were also found at higher doses. The longevity of the emerged moths was not affected except for a small effect found among the group irradiated at the dose of 10 krad.

TABLE I. EFFECTS OF GAMMA-RAY IRRADIATION ON THE FECUNDITY OF THE STEM BORER [2]

Dose (krad)	Male treatment (TM × NF)		Female treatment (TF × NM)	
	No. of eggs/female	Large egg masses (%)	No. of eggs/female	Large egg masses (%)
0.0	130.25	10.7		
2.0	96.17	12.1	75.91	26.3
2.5	74.60	5.9	72.50	6.3
3.0	72.00	14.9	47.25	0
4.0	102.19	8.1	90.22	0
5.0	50.88	3.1	44.67	9.1
7.0	55.00	0.0	36.00	0
10.0	44.00	4.1	61.00	0

TABLE II. EFFECTS OF GAMMA-RAY IRRADIATION ON THE HATCHABILITY OF RICE STEM BORER

Dose (krad)	Hatchability (%)	
	Male treatment	Female treatment
0.0	62.56	
2.0	36.14	21.51
2.5	8.33	16.79
3.0	2.79	5.82
4.0	19.71	3.86
5.0	0.00	1.49
7.0	0.00	0.00
10.0	0.00	0.00

The fecundity was examined for the various mating pairs by confining them in a glass tube which was lined with paraffin paper on which the eggs were laid, supplied with water by means of wet cotton. Since it is known that the viability of the egg has some relation to the size of the egg mass in rice stem borer, the fecundity was examined in terms of total number of eggs per female as well as the proportions of large egg masses to the total number of egg masses.

The average number of eggs per female decreased at the higher doses and rates of reduction were greater with the treated female than treated male. The results are shown in Table I.

The greater decrease in fecundity with female treatment might have resulted from direct effects of the irradiation on the germ cell. The

decrease in fecundity with male treatment at high doses seemed to be related to the decrease in the vigour of the male, and subsequent incompleteness of matings.

The percentage of the large egg masses also decreased at higher dosages with the same sexual differences in the number of eggs.

The viability of the eggs decreased at the higher dosages as shown in Table II. It was considered that the average per cent of the hatched eggs in this experiment would be somewhat less than normal because of the small mating glass tube. The sterilizing dose was 8 krad for females and 6 krad for the males. These are reasonably lower than the median lethal doses.

From these rather preliminary and laboratory scale experiments, the radiation-induced sterile males could be used for control of the rice stem borer; radiation decreases the fecundity of the female and viability of the eggs without any serious effects on the vitality of the adult moth. The effects on the longevity of the moths seem not to be serious because most of the mating occurs in the day after emergence and oviposition is completed within four days after the moths emerge.

The most serious problem connected with the use of the sterile-male technique in the control of the rice stem borer seems to be economic, because of the low price of the rice, and the high cost of the technique.

The light-trap data show that the density of the first generation moths is considerably lower than that of the second generation. The average number of moths caught by the light trap in summer (moths from the first generation larvae) was only 21% of the total number of the trapped moths. Moreover, the flight periods were 49 days for the summer moths compared with 71 days for the spring ones.

Together with the serious damage and somewhat greater difficulties associated with the second generation larvae, the shorter flight period and lower density of the first generation moths suggest that the sterile-male technique could be used more effectively in summer than in spring.

Considerable work has been done on the rearing of the rice stem borer on an artificial medium and on rice sprouts. The main difficulties associated with the mass rearing are handling costs in both media and reduction of vitality in successive generations for the artificial medium. Some work is under way in my laboratory to solve the former problem by using replaceable screens.

In conclusion, the following general problems are important in connection with the use of the sterile-male technique in the control of the rice stem borer.

- (a) Development of economical rearing methods, which would not affect the vigour of the moth.
- (b) Development of a comprehensive method for evaluation of the larval density in late June to determine the dispersal ratios of the irradiated pupae.
- (c) Development of comprehensive collecting methods for larvae or pupae for the irradiation.
- (d) Development of dispersal methods for the irradiated larvae or pupae.
- (e) Integration of the chemical control and sterile-male technique.

- (f) Further ecological studies of this insect: ecotypes, prediction of the moth emergence and behaviour of the moth.
- (g) Further studies of the radiation effects on the biology of the insect: total control of reproduction, including the lethal mutation in post-embryonic development, mating competition, and other possible effects of radiation.

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STERILE-MALE TECHNIQUE STUDIES IN HUNGARY

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Abstract

STERILE-MALE TECHNIQUE STUDIES IN HUNGARY. Preliminary experiments have been carried out by the Hungarian Research Institute for Plant Protection on various insect pests. Cockchafer (Melolontha melolontha L.) males were irradiated at different doses of gamma- and X-rays and were tested in laboratory experiments. Mass releases of sterilized males in 1966 and 1967 to obtain experience in collecting, mass irradiating, shipping, marking and releasing methods as well as to make observations on dispersion, were undertaken. Males and females of the bean weevil (Acanthoscelides obtectus Say), treated with gamma-radiation, were tested for sterility and the males for competitiveness in the laboratory.

The well-known advantages of the sterile-male technique compared with the use of conventional insecticides motivated the beginning of studies on this method in Hungary.

The first task was to draw up a list of insect pests to have priority in these studies taking into consideration the biology, the possibility of mass-rearing or mass-collection, the economic importance, etc., of the most common pests. The following groups of pests were formed:

Species on which studies had already begun:
Cockchafer (Melolontha melolontha Linnaeus)
Bean weevil (Acanthoscelides obtectus Say)
Codling moth (Carpocapsa pomonella Linnaeus)
Plum fruit moth (Grapholitha funebrana Tr.)
Corn borer (Ostrinia nubilalis Hübner)

Species to be studied in the near future:
Other fruit-damaging microlepidopterous species
Some microlepidopterous pests of stored products
Cabbage maggot (Hylemya brassicae Bouché)
Onion maggot (Hylemya antiqua Meigen)
Cherry fruit fly (Rhagoletis cerasi Linnaeus)

Species which will probably be studied later:
Fallwebworm (Hyphantria cunea Drury)
Some noctuid moths

1. COCKCHAFER STUDIES

The first extensive experiments were carried out on the cockchafer (Melolontha melolontha Linnaeus). Basing our program on the results of Horber's pioneering experiments [1] in which X-rays were used for sterilization, we first determined the sterilizing dose for the Hungarian cockchafer population and compared the sterilizing effect of X-rays and

gamma-radiation on males. The methods applied and the results of the laboratory experiments briefly outlined below have been published in detail by Jermy and Nagy [2].

Using doses of 0.75, 1.5 and 3.0 krad we found that 3 krad produced almost complete sterility. As was to be expected, there was no difference in the sterilizing effect of X-rays (therapeutic X-ray unit, type TUR T 200, operated at 120 kV and 20 mA, dose-rate 8.58 krad/min, 30 cm distance, 5 Al filter, temperature 20-22°C) and gamma-radiation (^{60}Co source, 2.85 krad/h, temperature 12°C).

The competitiveness of males exposed to 3 krad of gamma-radiation was tested in laboratory cages with the following combinations of SM : NM : NF - 0 : 20 : 10, 10 : 10 : 10, 18 : 2 : 10 and 20 : 0 : 10, in three replicates each. The comparison of the percentage viability of eggs laid in the cages showed that there was no significant difference in the competitiveness of irradiated and untreated males under the conditions of the experiment.

We also compared the longevity of irradiated and non-irradiated males when kept together with females. The above-mentioned doses of X- and gamma-radiation had no marked effect on longevity. In some replicates the irradiated males lived longer than the non-irradiated. This could not be due to reduced sexual activity, since the copulation frequency was the same in the two groups of males.

Intensive locomotive activity of the cockchafers during irradiation has been observed even at 12°C. After ending the irradiation the activity ceased at that temperature within a few minutes.

The aim of field experiments carried out in 1966 and 1967 was to gain experience in collection, storage, transport, cooling, irradiation, marking and releasing manipulations as well as to study dispersion of released beetles.

In 1966 a total of 53 010 males were collected from trees at the beginning of the flight period in several parts of Hungary. The easiest method of transport was to place the cockchafers with hay in flat cardboard boxes or small sacks which were then placed in bigger boxes with heat-insulated walls. Several smaller cans or plastic sacks filled with crushed ice were arranged for cooling purposes among the flat boxes and sacks containing the beetles.

The males were irradiated in a panoramic gamma-source (^{60}Co) and were marked with a fast-drying paint spray. The mass releases took place on 23 April, 28 April and 3 May, 1966, in a 250-m long forest belt of 3- to 4-m high trees (mostly poplar) in an agricultural district near Mosonmagyaróvár, Western Hungary. Shortly after the mass releases marked beetles were found at distances of more than 1 km. This extensive dispersion was probably caused by the high temperature and the prevailing wind.

Soil samples taken in the following autumn showed a reduction of the white grub population in the area round the experimental plot, compared with most other parts of the area. However, a similar reduction was observed in some non-treated parts too, so the effect of the sterile males released was not proved.

It also should be mentioned that high mortality rates were observed both in irradiated and non-irradiated cockchafers during the experiments in 1966. These were probably caused by the comparatively lengthy collection, transport and storage. The whole procedure was much improved in

1967 when 2400 cockchafer, both males and females, were released for dispersion studies in the same forest belt. Practically no mortality was observed during the experiments, and the dispersion of the adults was also very limited, since no marked specimens were found farther than 50 m from the release point. This might be due partly to the low temperatures during release, but partly also to the shorter and gentler manipulations.

The following conclusions can be drawn from the above experiments:

(i) The possibility of collecting large numbers of cockchafers and the competitiveness of radiation-sterilized males enables the sterile-male technique to be used against this pest.

(ii) Nevertheless, the mass collection and packing of the beetles is labour-consuming and expensive. A suitable mechanization of these procedures would considerably reduce the costs.

(iii) The use of the sterile-male technique seems to be practical only in areas where gamma-sources are available in which large numbers can be irradiated quickly, since the whole procedure of collection, transport, irradiation and release should not take longer than one to two days.

2. BEAN WEEVIL STUDIES

The second species on which more detailed studies were carried out was the bean weevil (Acanthoscelides obtectus Say). This species occurs in a few isolated areas of Hungary, and its population density seems to be quite low at the beginning of the infestation. Thus the ecological conditions in this case appear to be favourable for the sterile-male technique. Continuous mass-rearing is also very simple and easy.

The experiments, which are still continuing, showed that exposure of adults to 10 krad of gamma-radiation (^{60}Co source, dose-rate 35 krad/h, temperature 10-12°C) before emergence from the beans caused practically complete sterility in both sexes.

Competitiveness of males irradiated at 10 krad was studied in the laboratory. For this purpose 5 NM, 5 SM and 5 NF or 10 NM and 5 NF of the same age were put in 100 ml bottles filled with beans. After a few weeks, when the adults died off, the percentage of non-viable eggs was determined. In 23 replicates non-viability ranged from 17.3% to 97.0% with an average of 59.5%, whereas in the control experiments (10 replicates) these values ranged from 0.9% to 5.5% with an average of 3.0%. Since the calculated percentage of non-viability was 50%, the irradiated males were fully competitive.

The competitiveness of males hatching from the beans at 23°C within eight days after irradiation did not vary. After that time, however, a sudden drop in competitiveness was observed so that the viability of eggs became equal to that in the control.

Further experiments on competitiveness in field cages, studies on population density and migration as well as mass release experiments are planned for 1969. Taking into consideration the biological properties of the bean weevil and the results obtained so far it is most probable that the sterile-male technique will be suitable for the control of this pest in Hungary.

3. CODLING MOTH STUDIES

The codling moth (Carpocapsa pomonella Linnaeus) is another species on which it is expected this technique can be used within a comparatively short

time, thanks to the extended studies made in Canada [3] and in the United States of America [4, 5].

Preliminary experiments have been made in Hungary on trapping males by virgin females, and on rearing the larvae on small apples and on artificial diets. We have recently begun mass-rearing experiments using apples and we plan to do the first migration studies as well as competitiveness experiments in field cages in the summer of 1968.

The following facts make the sterile-male technique promising for the codling moth in Hungary:

- (i) The population density is very low in the commercial orchards because of intensive insecticide treatments.
- (ii) Recently planted large commercial orchards are available in which the establishment of the pest could be prevented by releasing a comparatively small number of sterilized moths every year at the period of migration.

However, we are aware that the use of the sterile-male technique against the codling moth is only one part of a selective control program to be developed for fruit orchards. We are therefore going to study the possibilities of developing a complex of selective control methods directed against these chief pests which have been recently controlled together with the codling moth.

4. PLUM FRUIT MOTH STUDIES

Studies have also begun on the plum fruit moth (Grapholitha funebrana Tr.). Sáringer et al. [6] have carried out preliminary experiments on the dispersion of ^{32}P -marked males, trapping them with virgin females. Irradiation experiments with newly emerged males resulted in some sterility even at 20 krad of gamma-radiation (^{60}Co source, dose-rate 40 krad/h, temperature 16-18°C). This dose did not affect longevity. Research is going on to develop a practical mass rearing method.

Research on the sterile-male technique against the plum fruit moth is justified also by the fact that this is practically the only pest in Hungary which requires the regular use of insecticides in commercial plum orchards.

5. CORN BORER STUDIES

Experiments carried out with the corn borer (Ostrinia nubilalis Hübner) have resulted so far in a very simple semi-synthetic diet for mass rearing. However, the practicability of the sterile-male technique in the case of this pest is very questionable in Hungary because of the large populations present in nature and the long distances the adults migrate.

6. CONCLUSION

The development of the sterile-male technique — as shown above — is still in the early stages only in Hungary. We hope, however, that it will become an important part of a larger complex of selective pest control measures which should replace, at least partly, the general use of conventional insecticides in the next decade.

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EXPERIMENTS ON MEDITERRANEAN FRUIT FLY CONTROL WITH THE STERILE-MALE TECHNIQUE

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Abstract

EXPERIMENTS ON MEDITERRANEAN FRUIT FLY CONTROL WITH THE STERILE-MALE TECHNIQUE. A summary of preliminary experiments to evaluate the control or eradication of the Mediterranean fruit fly, *Ceratitis capitata* Wied., by the sterile-male technique is discussed. Methods of shipping and releasing sterile medflies as well as a preliminary medfly population suppression experiment are described. The suppression experiment, conducted on the island of Capri, Italy, resulted in data which indicate that the sterile-male technique shows promise for controlling or eradicating the medfly.

INTRODUCTION

The principles involved in the application of the sterile-male technique for insect control are straightforward and simple. However, in practice the method has many pitfalls. Unless all factors that influence rearing, irradiation, packaging, transport, releasing and evaluation have been investigated in small-scale field pilot experiments, no eradication program on a larger scale is justified.

In 1966 a Panel on Radiation, Radioisotopes and Rearing Methods in the Control of Insect Pests, organized by the Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture, recommended that an area be located for a Mediterranean fruit fly, *Ceratitis capitata* Wied., eradication experiment using the sterile-male technique. Further, it was recommended that an island in the Mediterranean basin be chosen where acceptable isolation and climatic conditions would be assured. The Joint FAO/IAEA Division became involved in this, and within several months contacts were made with the Italian Ministry of Agriculture and the Italian Atomic Energy Commission (CNEN). These organizations suggested several test areas for such an experiment.

Except in Israel, no laboratory existed in the Mediterranean basin or Europe in early 1967 to mass produce and irradiate medflies in sufficient numbers for such an experiment. Therefore, a co-ordinated program was set up. The Israel Atomic Energy Commission agreed to furnish at least 2 to 4 million irradiated medfly pupae (males plus females) each week. The Israel part of the program was under the direction of Dr. Rachel Galun. In Italy, the Ministry of Agriculture would supply the test sites, background

information including survey of host trees and trainees for the program; CNEN would provide professional entomologists and technical help as required. CNEN also would supply all funds and personnel necessary for that part of the project carried out in Italy. The Joint FAO/IAEA Division would plan and co-ordinate the program and provide professional supervision as required. Later in the program the Seibersdorf laboratory of the IAEA would supply a portion of the sterile medflies.

In the spring of 1967 the situation with regard to the use of the sterile-male technique for medfly eradication or control was as follows:

- (1) Adequate mass-rearing techniques had been developed [1].
- (2) Laboratory experiments had shown that irradiation of pupae with about 7000 rad just before adult emergence resulted in sterile males and females [2].
- (3) Previous field experiments in Hawaii [3] and Central America [4] had indicated that the sterile-male method was effective against the medfly. Eradication, however, had not been demonstrated, primarily because of lack of isolation.

The specific objectives of this research were: (1) to locate a suitable experimental site which included maximum natural isolation, yearly history of medfly attack and a variety of cultivated host species; (2) to work out procedures for an eradication attempt, including shipping, releasing and evaluation; (3) to evaluate longevity and general behaviour of laboratory-reared flies under field conditions; and (4) if possible conduct an actual medfly eradication or control experiment.

METHODS AND MATERIALS

Experimental area

The Italian Ministry of Agriculture offered as experimental sites the islands of Capri, Ischia and Procida. These islands, located in the Bay of Naples, were the most convenient islands to Rome, Headquarters of CNEN, having a yearly history of medfly infestation. Of the three islands Capri was selected as the best release site for various reasons, including isolation from the mainland (9 km), small size (10.3 km² with about 3.5 km² under cultivation), and the presence of a variety of host trees including peach, apricot, citrus and figs. The island had some disadvantages from the point of view of a ground release program, such as heavily terraced areas, many smallholdings surrounded by high walls and very few roads. Almost all trapping, fruit sampling and releasing was done on foot. With the exception of grapes and lemons no commercial fruit culture exists on Capri.

The island of Capri is traversed along its short axis by a mountain ridge. This ridge divides the island into two separate geographical areas Anacapri (upper) and Capri (lower) and forms a natural barrier to the movement of Mediterranean fruit fly populations, especially between the Capri and Anacapri areas (Figs 1 and 2). Procida was used as the check island.

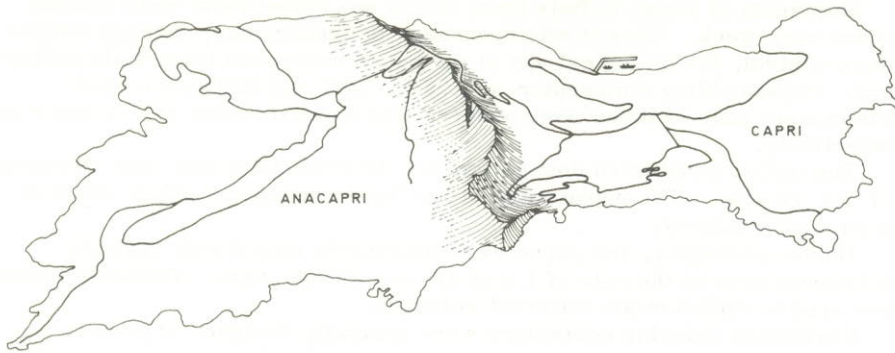


FIG.1. Map of island of Capri.



FIG.2. Photograph showing part of Capri.

Experimental insects

Pupae were produced by the Israel Atomic Energy Commission at the Entomology Department of the Biological Research Institute, Ness Ziona, and shipped weekly to Italy from 19 April to 5 September 1967. Pupal shipments from the Seibersdorf laboratory of the IAEA were made weekly from 1 July to 15 October. Production methods followed those developed by Nadel [2] and Nadel and Peleg [1] and varied between 2 and 4 million pupae weekly.

Shipments of pupae to Italy from Israel and Seibersdorf were limited to once each week. Thus it was necessary to synchronize, through temperature control, the biological age of the pupae recovered from daily collections. Pupal holding temperatures of 20°C, 25°C and 28°C were used. Development time at these temperatures was approximately 16, 11 and 9 days respectively.

The initial irradiation dosage was 6 ± 12 krad; later this was increased to 7.5 ± 12 krad. The pupae were in the "blue eye" development stage at the time of treatment.

Before packaging, the pupae were thoroughly mixed with daylight fluorescent dyes at the rate of 1 g of dye per 20 000 pupae. Different colours were used to differentiate different releases.

Cardboard shipping containers were specially designed to protect the pupae against mechanical injury and overheating in transit. Four shallow trays, each holding 25 000 colour-dyed pupae, were placed in a shallow cardboard box having a cloth top to permit aeration and dispersal of metabolic heat (Fig. 3). A shipping unit consisted of a light-weight wooden frame containing eight of these boxes stacked together, with spacers between each box to increase aeration. Each shipping unit contained 800 000 pupae. Flies which might emerge in transit could not escape from the containers.

Logistics

The pupae from Israel and afterwards from Austria, already coloured and gamma irradiated with 7.5 krad, were shipped weekly to the Rome airport and immediately sent to Capri by the CNEN. Customs and quaran-



FIG. 3. Shipping container for medfly pupae.

tine clearance caused some delays of certain shipments, particularly when commercial airlines did not meet their schedules. One shipment was completely lost by the airline.

Packaging and holding

Upon arrival at the Capri laboratory the pupae were immediately transferred to individual white paper bags (60 × 40 cm) containing sugar-coated excelsior to provide food and resting places for the emerging flies. Each bag contained 25 000 pupae, i. e. equal to the number of pupae contained in one shallow cardboard tray in the shipping container. The bags were closed with a length of thin wire.

The bags containing pupae were hung for two to three days in a darkened temperature-controlled room (25°C - 27°C) during which time the adults emerged. The flies were released in the field when most of them had emerged.

Release

The 100-200 bags of flies were usually transported by car or motor scooter to five central release locations. From this point it was necessary to proceed on foot to the release stations (Fig. 4). In the first weeks of the program the bags were hung on branches of host trees and slit open. In warm weather most of the healthy flies soon left the bag. As the season



FIG. 4. Photograph showing paper bags used for release of sterile flies and typical enclosed garden area where releases were made.

progressed ants became important predators and it was necessary to shake the flies out of the bags. The bags were then hung in the trees as markers to indicate where releases had been made. Releases started on 19 April and were discontinued on 15 October 1967. However, during September and October releases of sterile flies were limited to the Anacapri part of the island of Capri. A total of about 60 million pupae were utilized in this sterile insect release experiment.

Two experimental releases were made using a four-place helicopter supplied by the Italian Ministry of Finance. Release was accomplished by holding the individual bags outside the helicopter and tearing them open. With a load of about 50 bags each trip 150 bags could be released in about one hour.

Experiments to evaluate pupal releases also were conducted. Release containers were made from pressed cardboard inserts of egg shipping containers. These were hung by wires in trees and protected from rain by a plastic cover.

Evaluation

Trimedlure baited traps were used to establish field longevity of released sterile flies, movement of released flies under local conditions, a guide to relative medfly populations, and as a means of estimating ratios of sterile-to-wild flies. The traps used were constructed of plastic and contained a small polyethylene bottle to hold the attractant and insecticide (95% trimedlure and 5% Vapona¹). Traps were usually put in place 24 h before each release of sterile flies and taken down immediately before release the following day. The captured flies were inspected for colour marking. From 30 to 50 traps were operated each week.

RESULTS

The procedures described above for shipping sterile medflies (as pupae) from Tel-Aviv or Vienna to Rome were satisfactory. The most critical points in the shipping procedures were: (1) to use a shipping container with maximum ventilation and to place the pupae in each container so that they are no more than 1 cm deep to prevent overheating from metabolic heat; and (2) to arrange with customs officials for fast processing of each shipment so as not to expose the pupae to high temperatures and rough handling.

The ground release method described above was satisfactory, even though it required 50 to 90 man-hours weekly. However, the ground release made it possible to confine releases to host areas only.

The aerial release experiments using a helicopter resulted in a uniform distribution of the released flies on the island. Furthermore, the release time with a helicopter was about one hour per week. Based on these limited experiments, it is believed that a helicopter is ideal for releasing sterile medflies.

¹ 50% DDVP.

The preliminary experiments with releasing the sterile flies as pupae in the field indicated that this method was unsatisfactory in the spring or autumn because the cool night and morning temperatures (8°C-15°C) resulted in many crippled adults emerging. Predators also were a problem.

In a limited number of trapping experiments, it was found that the effective distance the released flies would move in six days, from a point release, was 150 m, under the conditions of the test. On the basis of trapping, it was found that the released medflies lived for one week but very few were trapped two weeks after release.

It was observed on several occasions that the released sterile medflies congregated on the ripest fruit in the vicinity of the release. This indicated that the laboratory-reared flies retained the physiological mechanism for selecting optimum oviposition sites.

One of the questions frequently asked about the sterile-male technique is the possibility of damage caused by the released insects. In the case of the medfly, the sterile females will sting fruit but very rarely lay any eggs since the ability to produce eggs has been destroyed by the radiation treatment. On 11 July 159 ripe peaches in the immediate vicinity of repeated releases of sterile medflies were examined. A total of 37 peaches (23.3%) were stung; no eggs were found. Although the effect of stings by sterile females may cause slight damage to host fruit, it is not believed to be significant.

At the beginning of this series of experiments it was decided to attempt a medfly suppression test in conjunction with the other work planned. It was realized that the probability of success was not very great because of lack of ecological data such as estimates of normal populations and specific host preference of the medfly at various times of the year, shipping and releasing techniques that had not been proved successful, and inexperienced personnel.

Fruit infestation data obtained from May through December (Table I) shows a negligible medfly infestation on Capri. The check island of Procida had an appreciable medfly infestation in various host fruits from August until sampling was concluded in December. It should be emphasized that only ripe fruit, either on the tree or on the ground, was inspected.

Weekly trapping data on Capri during this period indicated ratios of marked-to-unmarked medflies of 40:1 to 50:1. Examination of sterile marked flies showed an average of only 98% of the released flies were marked with the dyes. Thus, the highest ratio of sterile (marked) to wild (unmarked) flies that could be trapped was 49:1. This apparent ratio would be obtained even though no wild flies were present. Therefore, evaluation of the suppression phase of the experiment was done by fruit inspection.

It is very likely that Capri would have had a medfly infestation had not the sterile flies been released. The cold wet spring and very late ripening of host fruit in the entire Naples area resulted in a much later and lower medfly attack than normal. However, there was a medfly infestation in August on the nearby island of Procida as well as on the island of Ischia.

To summarize, releases of the sterile medflies on the island of Capri from 19 April until the end of August prevented a medfly infestation. From 1 September until 15 October releases of sterile medflies on the Anacapri part of Capri continued to prevent a medfly infestation. On the nearby check island of Procida, medfly infestations increased extensively from August until fruit sampling ceased in December. Also, in 1968, both Capri and Procida were heavily infested with medflies.

TABLE I. RESULTS OF FRUIT INSPECTION FOR MEDFLY INFESTATION, 1967

Month	Percentage medfly infested fruit ^a				
	Peach	Fig	Orange and tangerine	Persimmon	Cactus
	<u>Capri</u> ^b				
May	0(1400)	-	-	-	-
Jun	0(3400)	-	-	-	-
Jul	0(5000) ^c	-	-	-	-
Aug	0(5600)	0(4500)	-	-	-
Sep	0.5(1600)	0(2000)	-	-	0(1000)
Oct	0.6(500)	-	-	0(500)	0(1500)
Nov	-	-	1.0(500)	0(200)	-
Dec	-	-	0(600)	-	-
	<u>Procida</u>				
Aug	20(500)	5(600)	-	-	-
Sep	75(1500)	40(1700)	5(1000)	-	10(800)
Oct	85(1000)	-	7.5(1500)	2.0(1000)	-
Nov	-	-	40(3000)	5.0(2000)	-
Dec	-	-	55(4000)	-	-

^a Numbers in parentheses are numbers of fruits examined.

^b From 1 Sep through Dec data are from Anacapri area of Capri.

^c One larva found.

It would appear from the results of this suppression experiment and the previous medfly sterile-male technique experiments [3, 4] that the next logical step in the development of this technique is a large-scale field experiment. The purpose of such an experiment would be to perfect automated mass-rearing methods, develop adequate aerial release techniques, streamline evaluation procedures and obtain realistic cost figures.

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STATUS OF THE STERILE-MALE TECHNIQUE FOR MOSQUITO CONTROL *

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Abstract

STATUS OF THE STERILE-MALE TECHNIQUE FOR MOSQUITO CONTROL. The present status of research to use the sterile-male technique for eradication of mosquitoes is reviewed. Included are descriptions of experiments in which use is made of radiation and chemically induced sterilization. Also, genetic incompatibility as a means of eradication is discussed.

The successful eradication of the screw-worm fly from the island of Curaçao and the southeastern United States of America through the release of males sterilized by gamma-radiation [1] has stimulated great interest in the possibility of extending this technique for the control of several other noxious species of insects. On the whole, the general principles on which this technique is based are too well-known to merit any detailed discussion here. In short, it consists of inducing dominant lethal mutations in male gametes by radiation or chemosterilants, and overwhelming the natural populations with such sterilized males. The doses used are intended to induce maximum dominant lethality in the sperm and minimum undesirable somatic effects. Thus, this technique is generally effective if sterilization procedures do not affect the mating ability and competitiveness of males.

In recent years, besides the screw-worm fly, the sterile-male technique has been applied with success to several insect species, e. g. Dacus tryoni – Queensland fruit fly in New South Wales, Australia [2], Dacus cucurbitae – melon fly, in Rota, Mariana Islands [3], and Carpocapsa pomonella – codling moth in Canada [4]. In addition, the olive fly (Dacus oleae), boll weevils (Anthonomus grandis), the Mediterranean fruit fly (Ceratitis capitata), tsetse fly (Glossina sp.) and several other insect species are already being used or considered in programs of sterile-male releases in various countries.

FIELD TRIALS WITH MOSQUITOES

In the case of mosquitoes, this technique has been tried with Anopheles quadrimaculatus [5], Aedes aegypti [6] and Culex fatigans [7]. The feasibility of using a direct chemosterilant application to suppress an isolated, desert population of Culex tarsalis has also been investigated [8]. Measured in terms of reductions of natural populations, none of these trials

* AEC Document No. COO-38-613. This work received support from US Atomic Energy Commission Contract (11-1)-38 with the Radiation Laboratory, University of Notre Dame.

were successful. However, the possible causes of these unsuccessful attempts with mosquitoes are rather instructive. In the case of Anopheles quadrimaculatus, the failure of the field experiment using this technique may have been due to behaviour differences between the native females and the sterilized males which were obtained from stocks having a long history of laboratory colonization. Laboratory and field experiments conducted after the unsuccessful field trial in this species have demonstrated that "the laboratory strain reared in captivity for 25 years or longer and through perhaps 200 or more generations, did not readily compete with normal wild males in mating with wild females" [1]. Furthermore, Knipling has emphasized that "this example of failure in the application of the sterile-male release method cannot be ascribed to a defective principle but rather to the release of a strain inferior to the wild one from the standpoint of competitiveness in the field".

In the case of the Aedes aegypti field trial, males were sterilized by irradiation of the pupae with doses ranging from 11 000-18 000 rad. This treatment has been shown to reduce the vigour and mating competitiveness of males [9]. Work in our laboratory has shown that a dose of 8000 rad administered to adult males was sufficient to induce complete sterility [10]. Thus, through the use of either optimal radiation doses or chemosterilants, it may be possible to attain utilizable sexual sterility in Aedes aegypti and other mosquitoes.

In the case of the Culex fatigans field trial in India, the experiment was discontinued because of objections from the villagers at the site after release of 24 000 sterile males over a period of 35 d. Nevertheless, a reduction of 6% in hatchability of egg rafts in this experiment compared with the controls indicated that matings between the sterile males released and native females did take place. If the releases had continued, the results may have been more definitive. Similarly, limited results following three applications of apholate over a one-month period to an isolated population of Culex tarsalis in California indicated that "the treatments were exerting an influence on the mosquito population" [8].

RECENT FAVOURABLE DEVELOPMENTS

The so-called failures with mosquitoes therefore may not reflect on the basic applicability of this technique for mosquito control. On the contrary, several important characteristics of a number of important mosquito species seem particularly suited for the use of the sterile-male technique for their control. Furthermore there have been some recent developments which indicate that genetic manipulation of mosquito populations is practicable. The following are some examples of these developments and characteristics:

(1) Laven [11] has reported "eradication" of Culex pipiens fatigans through releases of incompatible males in Okpo, an isolated village near Rangoon, Burma. The field trial was undertaken under World Health Organization (WHO) sponsorship and complete control of Culex pipiens fatigans population was brought about in about three months or five to six generations. This successful field experiment indicates that if properly executed, mosquitoes are amenable to genetic control.

(2) Brown [12] has reported the development of traps to which male mosquitoes could be attracted either through light or specific baits. This provides a means for autochemosterilization and represents an important advance. Using a battery-operated CDC trap fitted with u.v. light, Culex fatigans adults were drawn into a chamber treated with tepa. The escaping adults showed about 87-93% sterility. If large numbers of adult mosquitoes can thus be sterilized and dispersed in their native habitats, several problems would be solved simultaneously. Furthermore, autochemosterilization of females along with males would provide an additional advantage. Nevertheless, additional research is needed to ensure that adults thus treated will not carry chemosterilant residues on their bodies and thus become hazardous.

(3) White [13] has reported chemosterilization by thiotepa of Aedes aegypti through pupal treatment. A wide safety margin exists between sterilizing and toxic dose levels with this procedure. With treatments at either pupal or adult stages, undesirable somatic effects resulting in reduced vigour and male competitiveness can almost certainly be prevented. In fact, increased competitive ability of males sterilized by dusting of adults with apholate has been reported [14]. However, releases of adults sterilized by dusting may be extremely hazardous.

(4) Since the male mosquitoes in general emerge before females, previously it was often feared that emerging females may be inseminated by their own sibs as they emerge from their breeding sites. This fear was compounded by the demonstration that multiple inseminations do not take place in mosquitoes and that the sperm from the first mating are used throughout the reproductive life of a female [15]. However, Lea [16] and Gwadz and Craig [17] have shown that Aedes aegypti females are not inseminated unless they are about two days old. The exact duration of this period depends upon the environment and the strain used. If delayed female sexual receptivity is characteristic of mosquitoes in general, the possibility of the application of the sterile-male technique for mosquito control is considerably enhanced.

(5) Several mosquito species that transmit important human diseases occasionally occur as localized, highly isolated populations. Good examples are provided by Aedes aegypti breeding in rice-growing villages which are surrounded by large, uninhabited, barren areas in countries like Thailand or small island-like situations with Culex fatigans populations surrounded by large bodies of clear water as in Ceylon [18]. The density of these populations can be greatly reduced by traditional methods of chemical control and by elimination of artificial breeding sites. After these populations are thus suppressed, inundation with sterilized males may be entirely feasible in experimental trials.

(6) Based on an evaluation of the possible causes responsible for several unsuccessful attempts with this technique, it has been concluded that induction of 100% sterility, which may often adversely affect male competitiveness, is not essential. Thus, treatments which will induce 95-99% sterility may prove more effective in achieving control.

(7) Economical mass production techniques have already been developed for certain species of mosquitoes [19]. Facilities to produce 2 million Aedes aegypti weekly currently exist. In field tests with this species Morlan et al. [6] released 4 777 000 sterile males in 43 weeks. In similar experiments with Anopheles quadrimaculatus, 433 600 males were sterilized in about 14 months [5].

Besides the above, it may be mentioned that several additional requirements for the successful application of the sterile-male technique listed by Lindquist [20], Knipling [21] and in Ref. [22] may be applicable to mosquitoes as well. Furthermore, extensive backlog of basic information has been collected in mosquitoes concerning the biology and detailed mechanisms of radiation and chemical sterilization [23-27].

ASPECTS ON WHICH ADDITIONAL INFORMATION IS NEEDED

On the other hand, before the sterile-male technique can be actually applied to mosquito control, there are certain difficulties which must be overcome. Some of these have been mentioned by Schoof [28] and Smith [29]. In general, these difficulties stem from the fact that there is a paucity of reliable information dealing with several important aspects of mosquito populations. What is needed, therefore, is much additional work dealing with the ecology and dynamics of field populations particularly in those areas where pilot field releases may be contemplated. Although fragmentary data are available on a number of mosquito species, more information is needed in several areas [18]. Of these, the following may be particularly emphasized.

Flight range and adult dispersal

The flight habits and range of mosquitoes, particularly of released males, are of the utmost importance in any control program. In general our knowledge of these parameters is meagre. In experiments conducted in Rangoon, Burma, it was observed that 81% of the marked released Culex fatigans were recaptured at 0.56 miles from the release point [30]. In Aedes aegypti, this range has been reviewed by Schoof [28] and on the average may not exceed a few hundred feet although the maximum distance travelled may vary from 330 feet to more than 1.5 miles. On the whole, it appears that mosquitoes do not travel far from the spot where they are released. As pointed out by Schoof [28], the limited dispersal of mosquitoes "creates a disadvantage as to the possible use of a sterile-male technique". However, it may be possible to overcome this by seeding sterile adults or pupae at relatively short space and time intervals. The ease with which the permanent breeding sites of species like Aedes aegypti and Culex fatigans can be mapped (and temporary ones destroyed) should prove useful in this regard. Furthermore, results obtained by Laven [11] demonstrate that in spite of limited adult dispersal, genetic control methods can be successfully applied to mosquito control.

Population density

There are few studies which are more important for the success of the sterile-male approach than a knowledge of the absolute numbers of an insect

species per unit area in a given habitat, its increase per generation and the factors responsible for the fluctuations of these numbers. The total number of males to be sterilized and released would depend upon the availability of reliable estimates of the numbers already present in a natural population. As pointed out by Lindquist [30], "sterile males must be introduced in a control area in numbers greater than they exist. The number of sterile males to native males required differ with different insects and may range from 5 to 1 up to 50 to 1 in initial releases. The greater the number of sterile males, the greater the competition with native males for the native females. The numbers released must be high enough to cause a degree of sterility that will overcome the population's ability to increase". Thus a knowledge about absolute numbers of natural populations at experimental sites is most crucial. Yet, there are few dependable methods which can be used to make accurate estimates. Consequently, additional research on this subject is urgently needed.

Mating behaviour

Since the success of any genetic control method is based on the ability of the males to transmit their genetic material to field females, it is crucial to know when, where and under what conditions matings take place. Unfortunately, this is another area in which we know relatively little, and there is need for more work. Furthermore, as already mentioned, sterilization with mutagens, particularly radiation, often results in reduced male sexual activity possibly following induced somatic damage. This has been shown with several species. Research should be encouraged on methods not only of overcoming but enhancing male competitiveness by genetic or other methods. Introduction of heterosis may be particularly helpful in this regard. In addition to the above, research on mass production procedures of those species where eggs cannot be stored is also needed.

It may be pointed out that in most of the above-mentioned areas, research activity is already increasing. The World Health Organization has set up several field Units during the last few years in different parts of the world, e.g. in Rangoon, Burma, and Bangkok, Thailand. Invaluable contributions to our understanding of the biology of several mosquito species have been made at these Units. Several additional Units are contemplated in the near future.

PROPOSED FIELD TRIALS

To re-evaluate the possibility of using the sterile-male technique for mosquito control, the following field trials are contemplated.

Ceylon

A feasibility study for the control of Culex fatigans in Ceylon through the use of this technique was undertaken under the sponsorship of the International Atomic Energy Agency and the Government of Ceylon [18]. The conclusions of this study were that (i) a valuable backlog of information on the distribution, abundance and several other ecological parameters was

available in Ceylon, (ii) the ecological aspects of certain isolated areas of infestation were highly favourable and (iii) field experiments involving sterile-male releases were feasible if and when certain prerequisites were met by the Government of Ceylon. These prerequisites included expansion of personnel and facilities, and collection of additional laboratory and field data with sterilized males of local strains of Culex fatigans. A World Health Organization Co-ordination Group on Genetic Control of Insects of Public Health Importance (1967) concurred with the above recommendations. A joint field trial under IAEA and WHO sponsorship is contemplated, and Dr. Erdman (IAEA) and Dr. Pal (WHO) visited Ceylon during March 1968 to plan additional details.

India

The World Health Organization has formulated plans to establish a field unit in India to investigate the feasibility of genetic control of Culex fatigans and Aedes aegypti. The initial program calls for six years of research beginning in 1969 and a budget of \$2 000 000 furnished by US counterpart funds. The emphasis during the first three or four years will be on collecting ecological data dealing with adult dispersal, natural population densities, sexual behaviour, relative efficiency of normal and released males and on development of economical methods for mass production. During the final two years of the project, operational studies of the feasibility of certain promising genetic methods of control including the sterile-male technique will be undertaken in large trial areas.

ALTERNATIVE STERILITY MECHANISMS

In addition to the traditional sterile-male approach, it may be possible to use the following two genetic systems which result in either complete or high levels of male sterility for controlling natural populations. Since both radiation and chemosterilants may reduce mating competitiveness and vigour in sterilized individuals, techniques using naturally occurring sterility mechanisms may be more promising.

Hybrid sterility

The members of the Anopheles gambiae complex which transmit malaria in most of the continent of Africa consist of at least five sibling species. Crosses between any two of these five species result in hybrid male sterility though the degree of this differs with different species. Crosses involving species A and B males and females of Anopheles melas, Anopheles meras or species C produce not only completely sterile males but few females in the progeny. Furthermore, because of their hybrid nature, the sterile males show increased longevity and competitive mating ability [31]. This method may therefore provide several important advantages over mutagen-induced sterility. Laboratory experiments with these hybrid males have proved very encouraging. Search for a suitable site in Africa is currently underway to test this method under field conditions.

Chromosomal sterility

Certain types of chromosomal rearrangement may result in varying degrees of sterility [32]. Of these, reciprocal translocations have received

considerable attention during the last two years as possible tools for genetic control purposes. In mosquitoes, a radiation-induced translocation between chromosomes I and II of *Aedes aegypti* is of particular interest [33]. Lines heterozygous for this sex-linked translocation have been established. Because the radiation-induced breakage of chromosome I occurred very near the male-determining allele (\bar{M}) of the sex-locus, this translocation breeds true in the male progeny, i. e. it is transmitted to all the sons produced by males bearing this translocation. Furthermore, up to approximately 80% of the eggs from normal females inseminated by translocated males fail to hatch. Thus the existence of this aberration offers possibilities for its use in *Aedes aegypti* control. The release of partially sterile males, which can be bred in the laboratory and which transmit this sterility to the offspring, presents a possible method whereby a self-propagating sterility mechanism can be introduced into the population. Furthermore, several undesirable effects on male performance which often follow mutagen-induced sterility may be avoided by the use of this method, for no treatment will have been given to males in the generation in which they are released. In fact, by crossing the translocation heterozygotes with diverse genetic backgrounds (particularly with females from regions where a release may be contemplated), heterosis can be incorporated in the males to be released. Laboratory trials utilizing this translocation are already underway and small-scale field experiments are contemplated.

CONCLUSIONS

Although earlier results have been negative, the sterile-male technique could prove very useful in controlling mosquito populations. Properly executed experimental field trials on a small scale are needed and should be undertaken in the near future. The groundwork must be prepared with extreme care and precision, and additional data on the biology of those populations where ultimately field trials might be contemplated must be collected and evaluated before actual releases. The selection of a proper site for field evaluation is of the utmost importance and, if possible, island-like experimental sites should be located.

Finally, to achieve its maximum potential this technique should be used only as an adjunct to traditional methods of mosquito control.

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The technical assistance of Miss Carole Destefano is gratefully acknowledged.

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PRESENT STAGE OF RESEARCH INTO THE ERADICATION OF THE MEDITERRANEAN AND SOUTH AMERICAN FRUIT FLIES AND THE COTTON STAINER IN PERU BY THE STERILE-MALE TECHNIQUE

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Abstract

PRESENT STAGE OF RESEARCH INTO THE ERADICATION OF THE MEDITERRANEAN AND SOUTH AMERICAN FRUIT FLIES AND THE COTTON STAINER IN PERU BY THE STERILE-MALE TECHNIQUE. Laboratory studies at the Entomology Department of the La Molina Experimental Station in Lima, Peru, were undertaken on the following insect species: Cotton stainer, Dysdercus peruvianus G., the South American fruit fly, Anastrepha fraterculus Wied., and the Mediterranean fruit fly, Ceratitidis capitata Wied. Some data on irradiation and field work are also included.

Peru presents ideal conditions of isolation for the development of the sterile-male technique since its natural coastal region is formed by nearly 50 valleys, isolated from one another, with the Pacific Ocean lying to the west, the Andes (5000-7000 m above sea level) to the east, and desert areas between 2 and 50 km to the north and south, criss-crossed in places by ridges of hills 500 - 1200 m in height. In addition, rain and electric storms are unknown in this region.

For purposes of convenience in presentation, this work is divided into three parts:

1. Study of the cotton stainer, Dysdercus peruvianus G.
2. Study of the South American fruit fly, Anastrepha fraterculus Wied.
3. Study of the Mediterranean fruit fly, Ceratitidis capitata Wied.

1. THE COTTON STAINER, Dysdercus peruvianus G.

Since 1930 the Entomology Department at the La Molina Agricultural Experimental Station has been rearing Dysdercus in wide-mouthed bottles in a room kept at a temperature of 27°C and 75-80% r. h. Each day a fresh supply of cotton seed and young shoots of the cotton plant are put into the bottles, which contain between 150 and 200 adult insects in the proportion of three females to two males.

The eggs are collected daily and transferred to petri dishes, each containing a small cotton leaf, also changed each day. After five days, the eggs hatch and the nymphs emerge. They pass through stages I, II and III while still in the dishes, and are then transferred to the bottles for adults for stages IV and V. The complete cycle lasts 35 days, adults living from 35 to 53 days. The reproduction ratio may reach 75:1.

In 1966 a semi-automatic rearing system was developed in the same laboratories [1]. The system consists of 16 cages, 1.20 m × 0.60 m × 0.60 m in size, 15 of which have four walls, a floor made of wood, and a plastic gauze top with fifteen-strand mesh per square inch; these are known as the nymph cages. The remaining cage has four wooden walls and the same kind of top, but the floor of the cage is made of galvanized wire gauze with a nine-strand mesh per square inch. This cage is placed on top of each of the other fifteen for two days each month.

The upper cage contains 2000 adults and a supply of food (crushed cotton seed and water and/or cotton shoots). The eggs drop to the lower cage, which also contains crushed cotton seed and shoots. About 10 000 nymphs hatch and after reaching the third instar they are transferred to the cages for adults or are used for biological tests or for irradiation.

1.1. Irradiation

Research aimed at sterilizing this insect has been carried out in Lima [2] and in La Molina [1]; good results have been obtained by irradiating adults and nymphs in the fifth instar with 10 000 rad.

Irradiation reduces the adult life span but does not affect the insects' ability to mate.

Abnormal weather conditions up to now (May 1968) have made it impossible to carry out any field work.

2. THE SOUTH AMERICAN FRUIT FLY, Anastrepha fraterculus Wied.

Fruit flies have been known in Peru since the beginning of this century; before that time, no records were kept since there were no agricultural colleges.

Between 1930 and 1940 attempts were made to control the pest by mechanical techniques such as wrapping the fruit in bags and refrigerating collected fruit to avoid larval development. Later on, with the advent of organic insecticides, 0.5% DDT, and still later 0.4% Dipterex, plus 0.4% hydrolyzed protein [3], proved an effective means of control. Over the last five years investigators including Ramos F. [4] have worked on chemical control of the fly, but have restricted their study to the bait spray technique, using a mixture of 0.4% hydrolyzed protein and an insecticide, since it was proved between 1963 and 1967 that 0.4% Dipterex, 0.2% Lebaycid 50 CE, 0.075-0.1% Diazinon 60 CE, 0.4% Perfekthion (Dimethoate) 50 CE, 0.2% Gusathion 20 CE, 0.6% Malathion 50 CE, 0.2-0.5% Anthon CE 25%, are all effective in controlling the fruit fly more or less equally.

2.1. Mass rearing of Anastrepha fraterculus Wied.

In May 1965 the Entomological Department began project 1.60.10.15 entitled "Control of the fruit fly", developed earlier and submitted for approval at the end of 1964.

This project is aimed at applying the sterile-male technique for the eradication of the fruit fly along the Peruvian coast since this region is composed of isolated valleys suitable for the purpose.

The project began with attempts at mass rearing of the fruit fly by a technique developed in Mexico based on studies made in Hawaii [5]. The insects were reared in wooden cages with plastic gauze walls in a room kept at a temperature of 27°C and 50% r.h. Ten domes made of waxed cloth were placed over the top of the cages on two perforated wooden strips and the eggs were deposited on the cloth. After washing them off, the eggs were collected on a small piece of muslin, which was then left in a petri dish for two days. At the end of this period the eggs hatched and the nymphs were reared on the following diet made up to a pH of 4.5:

Water	2.89 ml
Sodium benzoate	0.28 g
HCl	2.14 ml
Yeast	17.86 g
Chopped carrot	25.00 g
Powdered carrot	23.75 g
Tegosept (p-hydroxybenzoate)	0.36 g

The nymphs remained in the dishes until their final larval stage, at which time they were transferred to moist sand where they pupated. Twelve days later the adults emerged and ten days later they began laying eggs; thus, the egg-to-egg cycle was completed in 38 days. It proved possible to rear five generations in 1965, but the final population was only about 10 000 flies.

In 1966 the breeding was transferred to a laboratory specially constructed for the purpose but unfortunately it does not have the adequate temperature and humidity conditions.

Four oviposition surfaces were tried - waxed cloth domes, waxed cloth sheets, perforated polyethylene bottles and dacron-cotton fabric. In the first two cases normal egg depositits were obtained, but no eggs were deposited in the bottles. On the fabric the deposit was low and there was a high percentage of non-viable eggs.

The adults thrived well on a mixture of 300 g of hydrolyzed protein M, 400 g of sugar, and water.

The following diets were tried out for the larvae:

	<u>a</u>	<u>b</u>
Powdered carrot	100 g	-
Fresh carrot	-	4000 g (3 net kg)
Yeast	25 g	120 g
Tegosept (p-hydroxybenzoate)	-	3 g
Sodium benzoate	1 g	1.8 g
HCl	4 ml	18 ml
Water	650 ml	-

Diets consisting of sugar-cane bagasse, wheat germ, yeast and sugar were also tested; at first they were successful, but abnormal conditions in the laboratory, in particular lack of humidity, produced a high mortality rate among the pupae, and the adult population, which reached a total of 125 000, was reduced to a few hundred by infestation of mites.

The average cycle for 1966 was: egg 3, larvae 10, pupae 14, and adult life span 10 days.

TABLE I. DIETS FOR LARVAE OF *Anastrepha fraterculus* Wied.

	Vienna	Hawaii	IROPAD (Turrialba)	USA (Mexico)	IROPAD (S. José)	La Molina
Water	80.80	84.36	88.00	80.35	65.40	79.20
Sodium benzoate	0.16	0.093	0.24	0.077	0.13	0.14
HCl	0.84	0.39	0.80	0.595	0.66	0.70
Fermented molasses	5.00	3.98	2.86	5.00	11.75	5.66
Powdered carrot	13.20	11.18	8.10	14.00		14.15
Nipagin (methyl-p-hydroxybenzoate)					0.13	0.125
Sugar					13.70	
Bagasse					8.20	
pH	3.9	3.6	3.5	3.5	3.8	3.8

In 1967 studies were continued abandoning the large cages and adopting smaller-size cages of 0.45 m × 0.45 m × 0.45 m fitted with three gauze walls, one glass wall and two waxed cloth domes at the top. Towards the end of the year, the method of supplying water through a cord was replaced by Peleg's system of 1% agar agar. The mites were exterminated. Fine-coil humidifiers and heaters were installed, which made it possible to prolong the adult life span to 45 days, with 24 hours artificial light, resulting in an "economic" life span of 30 days.

2.1.1. Eggs

The eggs continued to be recovered from the waxed cloth domes. The dacron-cotton fabric was tried again, but with erratic results.

2.1.2. Larvae

Numerous problems arose here, mainly through decomposition of the nutrient medium infection by fungus (notably *Fusiarum*) and bacteria. The diets in Table I were tried out. The larvae, however, did not develop satisfactorily while the trays remained uncovered. Therefore the next step was to cover them with polyethylene or cloth for 1, 3, 4, 5 and 6 days. Development of the larvae was ensured as long as the trays remained covered. When left open for 1, 3 and 4 days larvae died because of decomposition of the medium in the trays. Since on the fifth and sixth days in the covered trays larvae left the medium in search of oxygen, it was decided that this was the right length of time to keep them covered, since two days later they were due to pupate.

2.1.3. Pupae

On the seventh day the nutrient medium was transferred to sieves. After being washed out, the larvae were placed in trays with sawdust,

where they pupated and remained 12 days in a room kept at 27°C and 75% r. h. ; at the end of this period they were transferred to smaller trays without sawdust, which were then moved to the cages for adults.

Thus, for the La Molina nutrient medium covering the trays for six days, the cycle was as follows at the end of 1967 [6]:

	No. of days
Eggs	3
Larvae	7
Pupae	12
Adult (pre-oviposition)	8
Adult (life-span)	45
Female (oviposition)	30

The nutrient medium continued to decompose, because of either the malfunctioning of the potentiometer or water distillation plant, or defects in the air-conditioning system. At present it is hoped to overcome these difficulties by installing automatically controlled air-conditioning equipment and an ozonizer. The results of the first week of tests up to 15 May 1968 were promising and it was observed that the medium had stopped decomposing and that oviposition seemed to be better in the ozonized room than in the non-ozonized one.

2.1.4. Field work

McPhail traps have been set up in the Ica Valley since 1965. In 1966 500 traps were placed and it was intended to service them on a weekly basis; this did not prove completely possible. Nevertheless, the incomplete data obtained from them suggest that there is a seasonal variation, which reaches a peak in July and August, decreases towards January, and rises again between April and August. The pattern was repeated in 1966 and 1967 [7].

2.1.5. Irradiation

Preliminary work involving six replications was started using 6000, 8000 and 10 000 rad; the lowest dose already caused sterilization.

3. THE MEDITERRANEAN FRUIT FLY, Ceratitis capitata Wied.

The first record of the Mediterranean fruit fly in Peru was in Huánuco in 1956. In the following six years the fly invaded the Departments of Piura, Lambayeque and Ancash, where it did not displace Anastrepha spp. and Lima, Ica, Moquegua, and Tacna, where it displaced Anastrepha, particularly in the last locality [8]. In the following years Ceratitis spread throughout the coastal and mountain regions attacking orange, grapefruit, mandarin, mango, peach, chirimoya, guava, apple, pear, coffee and medlar crops. The attractant ENT 21486 was used in McPhail traps to detect flies, and poisoned bait consisting of a 0.4% dipterex + 0.4% hydrolyzed protein mixture was used as control [9, 10]. Use was also made of

TABLE II. DIET FOR LARVAE OF Ceratitis capitata Wied.

	F	A	B	C	D	E
H ₂ O	200.00 ml	300.00 ml	377.92 ml	550.00 ml	289.00 ml	376.85 ml
Yeast	29.27 g	14.00 g	13.33 g	12.50 g	15.36 g	13.30 g
Sodium benzoate	0.41 g	0.60 g	0.42 g	1.50 g	0.28 g	0.41 g
Nipagin (methyl-p-hydroxybenzoate)	0.41 g				0.36 g	
HCl	2.04 ml	3.00 ml	1.75 ml	5.00 ml	2.14 ml	1.00 ml
Powdered carrot		50.00 g	50.00 g	50.00 g	50.00 g	50.00 g
Sugar	41.91 ml					
Bagasse	25.09 ml					

1% hydrolyzed protein + 2% borax to bait both the McPhail traps [3] and modified Steiner traps [11], and, finally, Trimedlure was introduced, along with Steiner traps, for the Tacna eradication campaign in December 1967.

3.1. Mass rearing of Ceratitis.

In 1965 attempts were made to breed the species Ceratitis capitata Wied. in the laboratory, but probably due to the small number of insects collected from naturally infested fruit it was not possible to maintain continuous cultures [11] until 1966. After a period of adaptation of specimens obtained from oranges from the Ica area in Peru several generations of the Mediterranean fruit fly [12] were reared. These deposited their eggs in the perforated polyethylene bottles, but not on dacron-cotton fabric woven in Peru. The larvae thrived on the Costa Rican diet consisting of bagasse and yeast, and completed their cycle in 29 days, the egg taking 2, the larva 7, the pupa 10 and the adult pre-oviposition period 8-10 days. Absence of an efficient air-conditioning system caused the insect cultures to die out after three generations.

During the summer of 1967, infection by fungus and bacteria developed in the larval nutrient media and the already small numbers of insects were reduced in May to 200-400 adults, but it was decided to carry out rearing tests with three replicates using the formulae in Table II.

The pH value was kept between 3.2 and 3.8 in all cases, but unfortunately a faulty power supply gave rise to wrong pH readings resulting in fungous infection of the nutrient. After this was corrected, more than 50% of pupae were obtained using formulae A and C. The latter was used with 10% less HCl during July and August; as a result 20 000 pupae a week were obtained although at a high price since a kilogram of carrot costs 70 Peruvian soles and of yeast 140 soles [13].

It was possible to replace the dry yeast by molasses made in Peru costing only 5.8 soles per kilogram, although we had to increase the amount of it in the diets by 10%, and eventually to introduce Formula F which, with slight modifications, is being used up to the present time (May 1968) at a cost of 4.21 soles per kilogram.

In each tray 4.5 kg of the diet and 1 ml of eggs are placed. The recovery factor from eggs is about 10% of the pupae with a cost of US \$225.59/million.

Between 1 March and 15 May the number of adult insects was raised from 180 000 in 6 cages to 1 000 000 in 50 cages at this cost, and a hatch of 54 000 eggs can be expected, which will result in 108 000 pupae daily, 60 000 of which will be used for reproductive purposes leaving 336 000 (48 000 × 7) each week for subsequent release.

With the introduction of ozonizers it is hoped to raise both the egg hatch as well as the recovery factor and to have at least 500 000 pupae available weekly for subsequent release.

3.2. Irradiation

Tests carried out on irradiation of six-day old pupae with 6000, 8000, and 10 000 rad confirm results obtained by other investigators regarding the sterilization dose, which is 10 000 rad.

3.3. Field work

In August 1966, some 500 McPhail traps, baited each week with 1% hydrolized protein + 2% borax, were placed in the Tacna and Moquegua valleys, but after May 1967 were not regularly serviced because of lack of personnel. Nevertheless, we were surprised to see that in Tacna 99.9% of the fruit flies belonged to the species Ceratitis capitata Wied., and less than 10 specimens of Anastrepha were captured.

In December 1967, new personnel were hired and the Steiner traps are now baited with Trimedlure fortnightly, the present number being more than 500 traps in each valley.

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ON THE POSSIBILITY OF A NEW METHOD FOR THE CONTROL OF INSECT PESTS *

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Abstract †

ON THE POSSIBILITY OF A NEW METHOD FOR THE CONTROL OF INSECT PESTS. The new principle of insect control consists in disturbing the propagation of the pest population by means of translocations. It is well known that individuals heterozygous for some translocations usually form a portion of aneuploid gametes and give a more or less inviable aneuploid progeny. On releasing, therefore, a sufficient number of individuals with a chromosome set altered by translocations into a wild population (with allogamous propagation), there will arise heterozygotes for translocations yielding a certain percentage of inviable offspring. Crosses inside this population will be similar to those between species with resulting sterility of hybrids. The theoretical analysis reveals that if a wild population is mixed in proportion 1:1 with some race containing only one translocation viable in homozygous condition and giving in heterozygotes 50% of aneuploid gametes, the reproduction of the population will be reduced by 43%. If several races with different allelic translocations are released the reduction of reproduction in the population can reach 75%, and if races with 4-5 independent translocations are used the reduction can attain 95%-99% and even more. A population consisting of races with different translocations cannot remain in balance. Those types of chromosomes which happened to be in minority are subjected to elimination. Yet this process of elimination will go on during many generations and thus the disturbance of reproduction will be protracted. By an additional releasing of eliminating race, this disturbance can be maintained permanently. Diverse variants of this method are possible, depending upon the biology and economic importance of injurious insects, the cost of breeding translocated races in laboratories, the difficulties of obtaining viable translocations, etc. It is possible, for instance, to release only males, a method in which there is evidently no danger at all. The present investigation is a purely theoretical one. For the purpose of verifying experimentally this idea work has been started with Musca domestica and Calandra granaria — two insects widely differing in their cytogenetics, ecology and the kind of damage caused.

1. In the last two years, while studying the question of the significance of translocations for natural selection and evolution, we arrived at a somewhat unexpected and very interesting conclusion about a completely new application of genetics — the control of insect pests. At the present time there has been quite a wide acceptance by geneticists of the "general theory", put forward by us in 1929, about the origin of various types of mutations, particularly chromosome translocations and inversions. From experiments on Drosophila it is known that because of the similarity, or even identity, of their mechanism of origin, translocations and inversions arise with comparable frequency, though translocations have in fact a better chance of being formed than inversions. It is already known with complete certainty from comparative genetics and population studies in Drosophila that, in the evolution of the karyotype, inversions are encountered incomparably more

* This paper, originally published in 1940 in Zoologicheskii Zhurnal 19 4, 618, is included in this report because of its historic significance; it contains much basic information on sterility and other genetic methods of insect control.

† Author's English summary.

frequently than are translocations. The causes of this are quite clear. While an inversion, provided that it is not accompanied by additional gene mutations or definite position effects, is a virtually insignificant change, leaving the viability and fertility of the organism unaffected, translocations in the overwhelming majority of cases, from the first generation onwards, begin to be eliminated by natural selection. This is because an organism which is heterozygous even in respect of a fully viable translocation begins to produce a greater or smaller percentage of unbalanced aneuploid gametes. The proportion of these varies but it may be as much as 50% even when there is only one translocation. Thus the reproduction of individuals

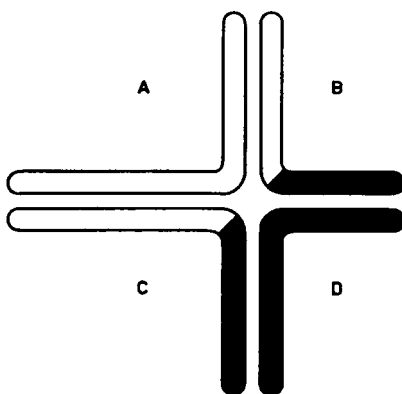


FIG.1. Diagram of the conjugation of four chromosomes in an individual heterozygous for one translocation.

inheriting a translocation is more or less markedly reduced, and the translocation is quite quickly eliminated by natural selection. An extremely fortunate, and almost incredible, coincidence is required for a translocation to be able to establish itself in a population with the status of a species characteristic.

While considering this question we came to the conclusion that since translocations are so deleterious to the reproduction of the organism, the possibility arises of the practical application of translocations to influence the reproduction of a harmful species. Our detailed examination of this question showed there are prospects here which are thoroughly practical and highly attractive.

2. The occurrence of various types of gamete in the presence of a heterozygous translocation is quite a complicated process, which has not yet been expressed in precise quantitative terms. As is well known, at conjugation two translocated and two normal chromosomes of a heterozygote usually form a ring or a cross (Fig.1), and the percentage of each type of gamete depends on how the chromosomes are distributed to each pole of this ring.

In a number of plants the chromosomes, as a rule, segregate regularly with A and D going to one pole and B and C to the other. In these cases there are obviously no aneuploid gametes formed. Gametogenesis of this kind was found in several cases in *Datura* (Blakeslee, 1927, 1929). In

Oenothera one ring gave not more than 6.4% aneuploids, but, on the other hand, in Tradescantia reflexia (Sax and Anderson, 1933) one four-chromosome ring gave 80.3% aneuploid gametes.

However, the more usual pattern of segregation of the chromosomes is that in which about 50% of aneuploids, or a little less, are produced (Drosophila, maize, Pisum, Tradescantia edwardsia, many cases in Datura, etc.). Aneuploids can be formed if the chromosomes segregate as follows:

A and B to one pole, C and D to the other, or A and C to one pole and B and D to the other. The final result is governed by the ratio between the

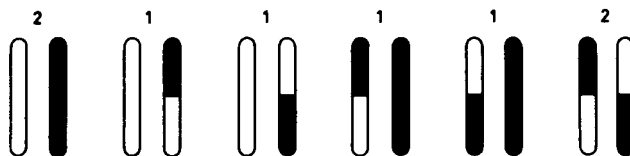


FIG. 2. Diagram of the six types of gamete from an individual heterozygous for one translocation. The types at each end are orthoploid and the four in the middle are aneuploid. At the top are shown the relative frequencies, which give a total of 50% of aneuploid gametes.

frequencies of these two aneuploid types and the orthoploid ($A, D \leftrightarrow B, C$). At the same time, however, there are often cases of non-segregation, in which three chromosomes go to one pole and one goes to the other, which further complicates exact calculations. The percentages of the various types of segregation apparently depend on the characteristics of the translocations, i.e. on the lengths of the sections of chromosome that have been exchanged.

For our purposes, however, it is important to consider that in many cases, especially in Drosophila (as a typical insect), the presence of a translocation gives 45-50% aneuploids, and this can easily be represented diagrammatically as shown in Fig. 2.

In the following account we shall proceed from the principle that, although in different examples of translocations the proportion of aneuploids is variable, nevertheless translocations do occur in which this is close to 50% and in these cases the formation of the various types of gamete can be basically represented by the simple scheme shown in Fig. 2.

3. The occurrence of the inversion and translocation types of chromosome aberration is accompanied, in most cases, not only by a change in the position and redistribution of the chromosomes, but also by a change in the genotype itself. The nature of these concomitant changes may vary. In some cases, at the sites of the chromosome breaks, destruction of small sections of chromosome occur and deletions result. In other cases, at the sites of breaks or adjacent to them, gene mutations occur. In the third type, which is difficult to distinguish from the second, the changes are regarded as position effects caused by the loss of contact between certain sections of chromosome and the establishment of contact between others.

As with all mutations, the majority of such genetic changes are lethal in the homozygous state, or at least reduce homozygote viability.

However, translocations were long ago obtained in which there was a redistribution of sections of chromosome not accompanied by any deleterious consequences for the organism, and the homozygotes were found to be viable. This category of viable translocations and inversions clearly includes all those which are preserved in the evolution of species. Recently four very interesting viable translocations were obtained in Crepis by Gerasimov (1939).

Since later on we shall be interested in translocations which are viable in the homozygous state, the above-quoted facts permit us to state a second guiding principle to the effect that, although in most cases, as with any mutations, translocations in the homozygous state are accompanied by lethal effects, nevertheless it is possible to obtain translocations whose homozygotes are fully viable, and these will be briefly referred to as "viable translocations".

4. The general idea of our proposed new method for controlling insect pests is as follows. If in a particular species of pest the chromosome apparatus can be modified by one or more translocations, and the translocated line bred and released among the wild population so that individuals of the translocated strain mate with normal ones, then heterozygous offspring will be produced which will show reduced reproduction. Thus the overall reproduction of the pest population will be reduced to a greater or lesser degree and this should have a positive economic effect. In order to estimate the magnitude of this effect it is necessary to investigate under what circumstances and to what extent the reproduction of the pest can be reduced.

5. We shall investigate the simplest case. Let us assume that we have bred a strain bearing one viable translocation among two non-homologous autosomes. By establishing a mixed population of normal wild individuals, A, and translocated individuals, T, we shall have four possible matings (fertilizations) by individuals of type A and type T, namely: $A\varphi \times A\sigma$, $A\varphi \times T\sigma$, $T\varphi \times A\sigma$ and $T\varphi \times T\sigma$. At relative frequencies (probabilities) of p for A and q for T, ($p + q = 1$), we obtain the following distribution of matings:

$$p^2 (A \times A) + 2 p q (A \times T) + q^2 (T \times T)$$

The $A\varphi \times A\sigma$ matings give entirely fertile progeny AA. The $T\varphi \times T\sigma$ matings give entirely fertile progeny TT. The $A\varphi \times T\sigma$ and $T\varphi \times A\sigma$ matings give heterozygous progeny AT with 50% of aneuploid gametes, i. e. their reproductive capacity is defective.

It is easy to see that the quantity $2 pq$ reaches a maximum when $p = q = \frac{1}{2}$. $2 pq$ then equals $\frac{1}{2}$ or 50%.

We thus obtain the optimum effect when we mix with the wild population an equal number of individuals of the T strain.

In the next generation we obtain the following distribution and frequencies for the matings of the various types of individual (substituting whole numbers

for the fractional coefficients):

$\sigma\sigma$ \ / \ ♀♀	AA	2AT	TT
AA	1	2	1
2AT	2	4	2
TT	1	2	1

The composition of the progeny from these matings are as follows (in order to obtain whole number coefficients we assume four offspring from each pair):

1	AA × AA	4AA			
1	TT × TT		4TT		
2	AA × TT			8AT	
4	AA × AT	4AA		4AT	8 die
4	TT × AT		4TT	4AT	8 die
4	AT × AT	1AA	1TT	3AT	11 die
		9AA	9TT	19AT	27 die
Total = 64					

In summary we obtain:

- (1) 27/64 (42.2%) embryos die;
- (2) The following generation has a composition of 9AA + 19AT + 9TT.

This composition (9:19:9) is obviously very close to that of the preceding generation (1:2:1); the difference lies in the direction favourable to us, thanks to the small excess of heterozygotes.

At the same time, the equality of numbers between AA and TT individuals was maintained, and in this respect the population was stable. In the next generation, the calculations for which we will not present here, the percentage of embryo mortality increases somewhat, and finally reaches a value of 43.

Thus we obtain an extremely encouraging result: by the release among the wild population of a single strain with a single translocation, in numbers equal to that of the wild population, we achieve a more or less stable mixed population, the reproduction of which has undergone an overall reduction of 43%.

6. If we rear a strain carrying two translocations among four pairs of chromosomes, then each translocation will exercise independent action as shown in the above scheme. Their overall effect can be expressed as follows:

Translocation I kills 42% of embryos, 58% survive.

Translocation II kills 42% of the 58%, i. e. 24.5%.

TABLE I. POSSIBILITY OF EMBRYONIC MORTALITY AS RELATED TO THE NUMBER OF CHROMOSOMES IN AN INSECT SPECIES WHEN APPLYING THE PRINCIPLE OF TRANSLOCATION AS A MEANS OF INSECT CONTROL

Group of insects	Number of pairs of autosomes	Number of possible independent translocations	Possible percentage of embryo mortality ^a
Mosquitoes	2 - 5	1 - 2	43 - 58
Flies	2 - 8	1 - 4	43 - 88
House fly	5	2	58
Locusts	6 - 11	3 - 5	67 - 93
Beetles	9 - 19	4 - 9	88 - 99
Bugs	6 - 19	3 - 9	67 - 99
Butterflies	12 - 30	6 - 15	99

^a Translator's footnote:

The figures given in this column by the author do not seem to be consistent with the figures given in the text for percentage lethality with different numbers of translocations. The column apparently should read:

42 - 67

42 - 88

67

80 - 93

88 - 99

80 - 99

99

The total mortality is then $24.5\% + 42\% = 66.5\%$. With three translocations among six pairs of autosomes, 80% of the embryos in the population are killed, with four translocations the mortality is about 88%, and with five translocations it is about 93%.

The possibility of obtaining a strain with many independent translocations, in which each pair of chromosomes is limited by only one translocation (I with II, III with IV, V with VI, etc.) depends on the number of chromosomes in the species of insect concerned. Table I illustrates the possibilities in this connection.

With regard to species with many chromosomes, however, it is possible that aneuploidy in respect of several sections of chromosome may not always

be lethal for the embryo. This question requires special experimental investigation.

7. In species with few chromosomes, as, for example, mosquitoes and most flies, where only one or two independent translocations can be obtained, there arises the question whether the method can be further developed. Analysis of this point has led us to the discovery of a further important principle. This is that the lethal effect could be considerably increased if we could produce and release not one, but two or more translocated strains.

Let us refer back to Section 5 above and see what will be the reproduction of a population consisting in equal parts of the normal type and two different translocated types T and U, where the translocated strains each have one translocation among the same chromosome pairs, and where the translocations are markedly different from each other.

The composition of the first generation will then be:

$$AA + TT + UU + 2AT + 2AU + 2TU$$

Whereas in the case of the population of A and T we had 50% heterozygotes in the first generation, here there are 67% heterozygotes.

In the next generation we shall have the following distribution of matings of the various types:

$\begin{array}{c} \sigma\sigma \\ \hline \varphi\varphi \end{array}$	AA	TT	UU	2AT	2AU	2TU
AA	1	1	1	2	2	2
TT	1	1	1	2	2	2
UU	1	1	1	2	2	2
2AT	2	2	2	4	4	4
2AU	2	2	2	4	4	4
2TU	2	2	2	4	4	4

In the boxes containing 1's there will be no embryo mortality and in those containing 2's there will be 50% embryo mortality. In the boxes containing 4's the proportion of lethals is either 11/16 (for the three boxes on the diagonal AT x AT, AU x AU and TU x TU) or 75% in the remaining six boxes.

In total:

0	lethals in	9 cases		0 x 9 =	0
50%	"	" 36	"	50 x 36 =	1800
68.7%	"	" 12	"	68.7 x 12 =	824
75%	"	" 24	"	75 x 24 =	1800
		<u>81</u>			<u>4424</u>

$$4424:81 = 54.6\%$$

Whereas by releasing a single translocated strain carrying one translocation we achieved in the second generation 42.2% embryo mortality in the population, by releasing two strains we achieve 54.6%. This difference is due to the fact that the frequency of those matings which give 100% viable embryos falls (9/81 against 4/16 or 11% against 25%), and correspondingly the frequency of matings giving a proportion of lethals increases and a new class of matings appears which gives 75% embryo mortality. This class of matings includes those of the AT x AU, AT x TU and AU x TU types, in which different types of translocation are involved.

It is easy to see that if the number of successfully selected strains is increased, the frequency of matings of the later type would increase, and it can therefore be concluded that the mortality of embryos after the release of many such strains will approach 75%. In the case of the release of many strains with two translocations each, the corresponding limit will be:

$$75\% + (75\% \times 25\%) = 93.75\%$$

For three translocations:

$$93.75\% + (6.25\% \times 75\%) = 98.4\%$$

and so on.

8. How can we evaluate the results given in the previous sections? The population dynamics of a species, particularly a pest, present a highly complicated phenomenon, depending on many factors — climate, food, the activities of parasites, predators, disease, etc. Reproduction¹ must also be included in this list of factors but, although important, it is only one factor among several others. The question may be asked what effect on the numbers of the species will be caused by, for example, a 40% lowering in reproduction, to take the minimum of the figures discussed above.

It is, of course, impossible to answer this question in its general form. For example, when the reproduction of a pest begins to be reduced by shortage of food, such a reduction may have no influence. Under other conditions, on the other hand, even a reduction by 40% could have a decisive influence. We can imagine, for example, a population which, after reaching a minimum, is beginning a new phase of increase, with conditions favourable for reproduction and parasites having almost disappeared. In these circumstances the rate of production of offspring is very important, since with a high reproductive rate the host can escape from the regulating influence of parasites by outstripping the parasite's own reproduction. A 40% reduction, in these circumstances, in the host's reproduction is equivalent to a 40% increase in the reproduction of the parasite, and would allow the parasites to begin to suppress the host's reproduction relatively early and hence prevent it from attaining the maximum that it could have reached with unrestricted reproduction. The more the host's reproduction is reduced, the greater will be the reduction in the population maximum, and the more pronounced will be the state of suppression in which it exists.

Naturally the extreme lowering of the reproduction rate referred to in the preceding sections would have even more influence. Let us assume that

¹ Author's footnote: We always use the word "reproduction" and not "fertility", because the special feature of translocation heterozygotes is not that their fertility is changed but that their embryos die at some stage of development.

we are dealing with a species in which one male and one female produce, on average, 100 eggs. A lowering in the reproductive rate by 98% would leave only two viable embryos per pair, i. e. only a replacement for the parents. In these conditions, even with 100% survival from the embryo to adult stages and to the time of egg-laying, the species will not increase in numbers. But because of well-known and inescapable factors, mortality of individuals in the larval, pupal and imaginal stages, and up to egg-laying is very significant and this mortality would lead to a decrease in numbers and eventual extinction. In other words, in order to deprive such a species of the ability to increase in numbers, it would be necessary to lower reproduction by translocations not to the extent of 98%, but to a much smaller extent—according to circumstances perhaps 70%, 60% or even only 40%—particularly in view of the fact that reproduction is reduced not for one generation but for a whole series of generations.

From these considerations we conclude that the utilization of translocation strains can produce veritably catastrophic results for the species subjected to the treatment.

9. We must now consider one weak aspect of the method. From population genetic theory and a number of actual observations it is known that in the case of a sufficiently large population with the structure

$$p^2 AA + 2pqAa + q^2 aa$$

where A and a are two alleles of any gene and are more or less equivalent in their significance for the viability and fertility in the organism, such a population may retain its structure (i. e. the quantities p and q) for a practically unlimited time for any values of p and q not too close to 1 or 0. In these circumstances the only factor which can change p and q will be stochastic processes (genetic drift) acting in large populations extremely slowly when there is complete panmixy and acting scarcely at all if the population is divided into more or less inbred groups.

Under other conditions a population may be found with structure $p^2 AA + 2pqAT + q^2 TT$ where A and T are two types of chromosome structure distinguished by the presence of one translocation. Such a population can be stable, preserving p and q from generation to generation, only on condition that $p = q$. The equilibrium is unstable and if it should happen that $p > q$ a process will begin of progressive increase in the inequality until $p = 1$ and $q = 0$. In other words, type T will be gradually eliminated. On the other hand if it should happen that $p < q$, a process of elimination of type A will begin.

This elimination occurs because, when the embryos are destroyed as a result of aneuploidy, equal numbers of chromosomes of type A and type T are also destroyed. If type A is commoner in the population than type T (i. e. $p > q$), these equal numbers of destroyed chromosomes will represent a greater percentage of the total number of T and a smaller percentage of that of A. Therefore in the following generation the inequality $p > q$ will increase still further and so on.

Figure 3 shows the approximate course, calculated by us, for the process of elimination for populations of A + T (top curve) and A + T + U (bottom curve). At first, near the equilibrium point, the process goes very slowly, then it accelerates sharply, reaching a value of 5-6% per generation, and then it decelerates again as it approaches the complete

displacement of one type. As shown in Fig. 3, in a population of A + T the change from 52.5% to 90% occupies roughly 12 generations and in a population of A + T + U one of the types displaces the others, in the range 36% - 90%, in approximately 15 generations.

Thus, if a panmictic population is constituted (i. e. a population in which mating between males and females of all types is absolutely random and depends only on the frequencies of the types), then over the course of a few generations one of the types practically displaces all the rest. The measure thus turns out to be a temporary one.

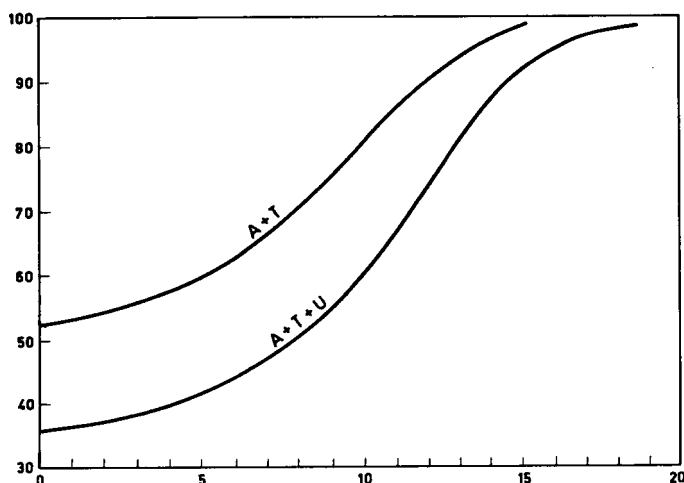


FIG. 3. Course of displacement by one type of the other types in populations of A + T and A + T + U; abscissa: generations; ordinate: frequency of eliminating type.

Before examining the possibility of preventing this "temporaryness", we shall consider what effect the temporary measure can have. For this purpose it is necessary to ascertain how the lethal effect of the translocations on the population varies with different ratios of types A and T. The curve corresponding to this relationship is given in Fig. 4.

As shown in the figure, the decrease in the percentage of embryo mortality proceeds much more slowly than the decrease in the percentage of T (or of A, if this is the type which is eliminated). With the ratio 1:1 the mortality is 42%, at 2:1 it is 37%, at 3:1 it is 32% and even at 9:1 it is still 17%. If there were two translocations in the strain which was released these figures would be even more striking; for the ratios in question they would be 64%, 60.3%, 53.8% and 31.1% respectively. In this situation, even if the release of translocation strains is a temporary measure and its effect continues for only 10-15 generations, nevertheless its effect will be very considerable and the numbers of the pest population will be dealt a severe blow.

Figure 4 shows us several other important possibilities as well. It can be seen that the release of translocated strains in the proportion 2A:1T and even 3A:1T has a very marked effect, particularly with two or three

translocations in the strain which is released. Therefore in a situation where it is difficult to make a release in the proportion 1A:1T it would be possible to release the translocated strain in an amount two or three times less and then, having thereby reduced the numbers of the pest, to effect a second release of strain T and thus raise the ratio to the most advantageous level (1A:1T); this is a considerably easier procedure. Using strains with two, three or four translocations it is possible to obtain a still greater reduction in the numbers to be released at this preliminary treatment of the population.

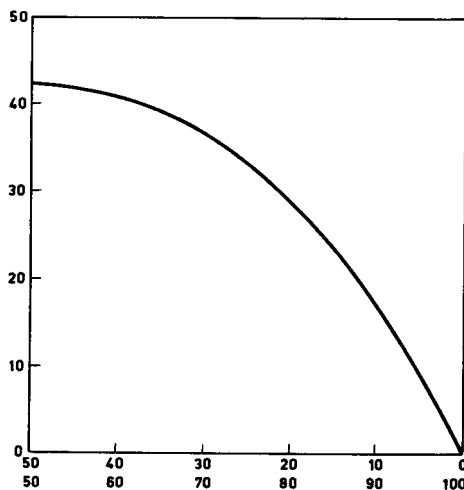


FIG. 4. Percentage mortality of embryos in a population of A + T with various ratios of A:T; the abscissa shows the percentage of A and T gametes in the population, the ordinate shows the percentage of embryo mortality.

10. Is there any method for controlling the process of elimination? Is it possible somehow to slow down the process or even to stop it when the population has been brought to equilibrium? Study of the process of elimination itself reveals that it could possibly be controlled and that the question can be answered affirmatively.

In general, the control of undesirable elimination should be based on the fact that the elimination process itself can proceed in either direction, i. e. either towards elimination of the translocated type or towards elimination of the normal type.

We can proceed, for example, as follows. We divide the territory which is to be treated into squares, like a chessboard, and in the white squares we release the translocated strain in excess (producing, for example, a population with 40A + 60T) and in the black squares we release them in a minority (producing, for example, a population with 60A + 40T).

There will then begin in the white squares the elimination of type A and in the black squares the elimination of type T. Thanks to the chessboard arrangement, each white square will be continually invaded by the opposite type from the neighbouring black squares and vice versa. This migration

will, in the first place, markedly slow down or even stop the actual elimination process. But even if elimination occurs in the centres of the squares, there will nevertheless result a chessboard network of mutually lethal forms, which will continuously invade one another and produce heterozygotes with consequent embryo mortality. Although in this situation the equilibrium will be of an unstable type, the process of removing one of the forms from the whole population will continue for a very long period and it requires comparatively slight periodic attention to the "chessboard" population in order to maintain it in the most advantageous state.

It is, of course, not our intention here to enter into a discussion of technical details. Our intention is only to show that the process of elimination, with which the method here proposed conflicts from the very outset, is not fatal to the method as a whole. Analysis shows, on the contrary, that this process has properties which can be exploited in the further development of the method, in respect both of different variants of the latter and of the peculiarities of different species of insect. In addition we should like to indicate the interesting problems which arise in connection with the further theoretical development of the proposed method.

11. However, what in the first place are the practical possibilities of the method? Here three main questions arise: (1) the feasibility of rearing and releasing sufficient numbers of individuals of the translocated strains; (2) the advisability of releasing these additional numbers of the pest; and (3) the possibility of obtaining the translocated strains themselves.

The problem of releasing sufficiently large numbers of individuals, for example in the ratio 1:1 to the wild population, may at first sight appear absolutely insoluble. This is only true if one has in mind, say, massed numbers of sugar-beet pests or swarms of beet webworm. But, as is well known, the beet webworm, like various other pest species, produces massive outbreaks only periodically, and in the intervals the species may decline to a minimum with far smaller numbers. There are also distinct oscillations as regards location, and in certain regions the pest may disappear almost completely in some years.

The disappearance is temporary and a new wave of activity with an increase in numbers then begins again. The opportune moment for release of translocated strains is precisely when the population is at its minimum. The release of sufficient numbers may then be much easier and, in addition, would protect the region concerned from the ensuing outbreak on its usual scale.

In other cases, use could be made of the seasonal minimum. In July and August millions of flies emerge in many areas and invade living quarters in vast clouds. In spring, however, in April and May, such clouds do not occur and, on the contrary, the number of flies after the winter is often insignificant. Clearly in autumn the release of a number of flies equal to the natural population would hardly be possible, but in spring this task would be thousands of times simpler.

Depending on the characteristics of the insect concerned, the application of the proposed method may vary considerably and to enter into details here would be premature. It may just be mentioned that the release need not be made in one operation but can be effected in several separate operations, and here there is scope for the theoretical investigations to

discover the most economic procedures for application of the method, to which we referred in Section 9.

If, for example, five translocated strains are obtained and it is desired to produce a population in the ratio 1:1:1:1:1, it would be necessary to release a number exceeding that of the natural population, by a factor of five. However, the operation can be performed quite differently. One can first release one strain in the ratio 1:1 with the wild population, and then pause until this release has had some effect. Then a third type is released in the ratio 1:2, i.e. the number released is half that of the diminished mixed population, and there is then another pause for a further reduction to occur. Then the fourth strain is released in the ratio 1:3, i.e. a number equal to one third of the new mixed population, and so on. The result is that the total of insects released is not in the ratio 5:1, but considerably less. In the end, however, the practicability of such an arrangement will be determined by economic considerations, taking into account the harm done by the pest and the cost of rearing the translocated strains, which vary greatly from species to species.

12. As regards the advisability or even safety of releasing additional numbers of pests (even though these are of the translocated strains), this question must be answered specifically for each species. In a number of cases these releases could be made without any misgivings. For example, in spring the small numbers of house flies can safely be increased by as many again or even by two or three times as many in the certainty that after 1-1½ months there will be a marked decrease in fertility and that in July and August there will be a big drop in the mass reproduction of flies in the field. In other cases, however, it may be necessary to be more cautious. In these cases there is at our disposal, however, a method of effecting the introduction of translocations into the population without any risk, even temporary, of increasing the reproduction of the pest. This can be done by releasing only males of the translocated stocks and retaining the females. The released males begin to compete with the wild males for the females, but since the eggs will only be laid by wild females, the number of their progeny resulting from the release of the translocated males will not rise at all. It is only necessary to prolong releases for several generations, although this will render the operation somewhat more expensive.

13. The greatest difficulty in the use of this proposed method will be the production of the translocated strains. The stages in this process will be approximately as follows: (1) the mastering of a technique for laboratory rearing the insects continuously over a number of generations; (2) the production of a small number of suitable mutations to serve as "markers", which are needed for the continued securing of translocations and the combinations of these marker mutations at least in pairs; (3) the production of the translocation; (4) the conversion of translocations into the homozygote state and the selection of viable translocations; (5) the combination of translocations two, three or more together in individual strains, if this is considered necessary; and (6) the mass rearing of the selected strains. All these stages will occupy a fair number of generations.

The rearing of some insects, for example, cereal-feeding ones such as the grain weevil, is very simple, but the rearing of others, such as

moths which feed on green plants, is much more difficult, while the breeding of yet others, such as mosquitoes or horseflies, is extremely difficult, and even for the time being impracticable. Another point is that the raising of ten generations of the horsefly or grain weevil can be completed in the course of one or two years; in insects producing one generation per year it would take ten years, while such species as cockchafers and wireworms, with two- or three-year life cycles, are hardly worth considering, unless a better method of working with them can be found.

However, there are enough species of insect pests with a short life cycle and which are more or less suitable for laboratory rearing, and so there is a wide field of work available without us having to consider the cockchafer or wireworm. As it proceeds this work will undoubtedly lead to the discovery of methods for shortening several stages of the process; thus, for example, marker mutations may be found in natural populations and translocations might be sought without markers by cytological methods or by observing embryo mortality in eggs, and so on.

14. Up to the present time the only practical applications of genetics have been the selection of domestic or semi-domestic animals and cultivated plants. Altogether, particularly in animal genetics, the number of suitable and practically significant subjects for treatment has been extremely limited.

It is, therefore, with a great sense of satisfaction that we note the emerging prospects for the practical application of genetics to a new, extraordinarily wide, and economically important field, the subjects of activity in which are numbered literally in hundreds.

Nature is certainly more complex than our theoretical models, and the new method proposed by us here for the control of pests (in addition to, and in no way in conflict with other methods—agronomic, chemical, mechanical and biological) requires practical verification before one can say that the method is fully worked out. It is possible that in some cases unexpected difficulties will arise in the production of translocations, in the maintenance of the viability of the translocated strains, in the lethal effects of aneuploidy on the embryo, and so on. However, genetic calculations are always found to be so accurate that there are no particular grounds for fearing that, in this case, they will not turn out to be correct, especially as the phenomena on which the present method is based occur in Drosophila, i. e. a species which is quite closely related to many insect pests.

On the other hand studies on translocations and the methods of obtaining them are a comparatively young branch of our science, being mainly confined to the last decade. There is therefore no doubt that as soon as the work we have in mind is under way, involving the pursuit of a variety of new objectives, many new advances in the study of translocations will be made and even more effective opportunities for their practical application will certainly be found. We are confident that in its efforts to serve practical purposes Soviet genetics will produce new theoretical achievements to the benefit and honour of our great socialist homeland.

CONCLUSIONS

1. The fact that individuals which are heterozygous for translocations form aneuploid gametes and produce aneuploid, inviable progeny opens up

the possibility of developing a new method for the control of (allogamous) insect pests.

2. Theoretical calculations show that the release into an insect pest population of strains of the same species possessing a chromosome apparatus modified by the presence of translocations should cause considerable damage to the reproduction of the pest.
3. The more translocations there are in each strain released, the larger the number of different strains released, and the nearer the approach to equality between the numbers of the pest and the numbers of each strain released, then the greater will be this damage to reproduction.
4. The utilization of translocations viable in the homozygous state has important advantages.
5. The mixed population thus produced cannot come to a stable equilibrium and will tend towards uniformity of type by elimination of all the chromosome types except one. However, this process should last many generations, and for this reason the disruption of the reproductive process of the pest population should last a long time.
6. Periodic supplementary releases of the chromosome type which is being eliminated should maintain the disruption of the reproductive process continuously at a high level.
7. It is possible to devise variants of the method in accordance with the biology of the pest, the cost of rearing it in the laboratory, the difficulty of producing translocated strains, the harmfulness of the pest, etc. One of these variants, which may hold out the best prospects thanks to its inherent safety, involves the release of males only.
8. The proposed method can be applied in combination with any other current method and without interfering with or suffering from it.
9. The present paper presents a purely theoretical investigation of the subject. Experimental development work on it has been started using the housefly Musca domestica and the grain weevil Calandra granaria, two insect which differ widely in their biology and the damage which they cause.

