EFFECTS OF SOME INTER- AND INTRA-SPECIFIC SIGNALS (KAIROMONES AND PHEROMONES) ON THE MATURATION OF THE DESERT LOCUST *Schistocerca gregaria* (Forskål) (ORTHOPTERA: ACRIDIDAE)

BY

Yousif Osman Hussein Assad

B.Sc. (Pesticides) University of Alexandria, *Egypt*

(1979)

M.Sc. (Pesticides) University of Gezira, *Sudan*

(1991)

Thesis

Submitted in partial fulfillment of the requirements for the degree of Ph. D.

In

Applied Entomology (Chemical Ecology)

In the

Faculty of Agricultural Sciences

University of Gezira, 1995

APPROVED BY:

EXTERNAL EXAMINER:

Prof. Siddig Ahmed Siddig..........

22.10.1995

SUPERVISORS:

Prof. Nabil H. H. Bashir.......... 22-10-95

Prof. Ahmed Hassanali..........

Dr. Baldwyn Torto..........

Dr. Hassane Mahamat..........

Prof. Syaid El Bashir..........

DECLARATION

I certify that the contents of my thesis are the product of my original work and none of the material has previously been submitted by me for a degree in any university.

signed. ________________________

Yousif O. H. Assad
Candidate

ACKNOWLEDGEMENT

I am grateful to my ICIPE supervisors Prof. A. Hassanali, Dr. B. Torto, Dr. H. Mahamat and Prof. S. Bashir and University supervisor Prof. Nabil H. H. Bashir, for their continued interest, personal guidance, constructive comments and critical supervision through this study.

My sincere thanks and gratitude also go to my ICIPE supervisor Dr. B. Torto, for the valuable discussion, suggestion, supervisions and help. I am grateful to Dr. P. Njagi for his valuable comments and help for GC-EAD analysis.

Thanks are extended to the staff of the Chemical Ecology department (ICIPE) for their great help and their technical assistance with special thanks to Mr. Amiani, Mr. Wanyama and Mr. Odongo.

I would like to express my sincere gratitude to the staff of the ICIPE sub-station Red Sea Coast, Sudan for their great help in the collection of plant materials and to those of the insectary (ICIPE-LOCUST DIVISION) for the supply of locusts for the study.

Thanks are also due to my colleagues in the Ph. D. programme, especially to those in the chemical ecology unit, for their assistance and encouragement.

Special thank are due to the ICIPE-ARPPIS programme for a scholarship and locust research project (semiochemical) for sponsoring part of the study and to my registering university (University of Gezira) for nomination. Special thanks are also extended to the government of Sudan for granting me a study leave. Sincere appreciation goes to biostatistics unit (ICIPE) for assistance in the statistical analysis and in preparing the manuscript.

Finally, I wish to express my deep gratitude to all ICIPE staff, my colleague Hassan Mahamat Abakar, my family and uncle Ibrahim Adam El Dein and his family for their support and encouragement.

DEDICATION

This thesis is dedicated to the souls of my dear parents in Heaven, God bless them.

To my dear wife, Samia for the sacrifices she made and the constant prayers she offered throughout my study period.

To my childern, Fahad and Osman for the many hours they had to spend without their daddy around which never understood but bore it so courageously.

LIST OF CONTENTS

LIST OF CONTENTS (CONTD.)

LIST OF CONTENTS (CONTD.)

PAGE

LIST OF CONTENTS (CONTD.)

LIST OF CONTENTS (CONTD.)

LIST OF TABLES

TABLE PAGE

LIST OF TABLES (CONTD.)

LIST OF FIGURES

LIST OF FIGURES (CONTD.)

LIST OF FIGURES (CONTD.)

FIGURE PAGE

LIST OF APPENDICES

APPENDIX PAGE

LIST OF APPENDICES (CONTD.)

ABBREVIATIONS APPEARED IN THE TEXT

AAMP	adult aggregation maturation pheromone
ANOVA	analysis of variance
Appen.	Appendix
BCN	benzylcyanide (phenylacetonitrile)
° C	degree(s) celsius (centigrade)
c.a.	corpora allata
CNS	Central Nervous System
cm	centimeter
cv%	coefficient of variation
D	dark
DCM	dichloromethane
DLCO-EA	Desert Locust Control Organization for East Africa
EI	Electron current
EPA	Environmental Protection Agency
eV	Electron volts
F	Female
FAO	Food and Agricultural Organization
FID	Flame Ionization Detector
Fig.	Figure (s)
g	gram(s)
GC	gas chromatograph
GC-MS	gas chromatograph-mass spectrometry
HP	Hewlett-Packard
HPLC	High performance liquid chromatograph

ABBREVIATIONS (CONTD.)

hrs	hour(s)
IABU	Insect and Animal Breeding Unit
ICIPE	International Center of Insect Physiology and Ecology
ID	Internal diameter
IPM	Integrated Pest Management
Imm.	Immature
JH	Juvenile hormone
Km	Kilometer
L	light
LSD	least significant difference
Ltd.	Limited
M	Male
m	meter
MAP	Maturation Aggregation Pheromone
Mat.	Mature
min	minute
M/Z	mass/proton weight
μl	microliter
ml	millitre
μm	micrometer
mm	milimetre
NAAP	Nymphal Anti-maturation Aggregation Pheromone
p.o.p	pre-oviposition period

ABBREVIATIONS (CONTD.)

rel-	Relative
R.H.	relative humidity
SAS	Statistical analysis system
SE	standard error
TPRs	Temperature and Photoperiod Regimens
UK	United Kingdom
VG	Vacuum Generals

ABSTRACT

The effect of the gregarious fifth instar nymphs on the maturation of newly moulted gregarious immature males and females of the desert locust *S. gregaria* was investigated by monitoring colour changes (yellowing of body), sexual activity, aggregation-maturation pheromone titres (as measured by phenylacetonitrile levels in males), ovulation (as determined by the length of oocyte in females), oviposition time, and the number of eggs/pod oviposited by females.

Maturation was significantly delayed in adults that had been reared together with nymphs (visual, tactile and chemical signals present) with respect to all the parameters monitored, thus confirming previous reports. Both male and female nymphs were equally effective in inducing this delay. However, the number of egg/pod oviposited by females was not affected.

Nymphs kept in an upper compartment of two-chambered cages (no visual or tactile contact possible) were similarly effective, but their faeces were ineffective suggesting the mediation of a volatile signal from the nymphs themselves.

This was confirmed by examining the effect of volatiles trapped from nymphs on the maturation of adults. These studies suggest a role for the volatiles as an adult maturation retardant, parallel to the adult volatiles which

have been shown to be an adult maturation accelerant. Our results are discussed in terms of the role of the two pheromone systems in synchornising maturation of the gregarious adults.

The effects of crude extract of a desert shrub, *Commiphora quadricincta* (Schweinf) before and after winter rains, on the maturation of immature males and females, was also investigated. Maturation was significantly accelerated in immature adults exposed to the extract before winter rains with respect to all the parameters, while those exposed to the extract after rains were significantly different from those exposed to mature males. The results confirm a previous finding that the essential oil of *Commiphora* shrubs accelerated the maturation of adults and also confirm that there is difference in the composition of the shrubs during two seasons.

The identification of volatiles of fifth instar hoppers and crude extract of *Commiphora* was carried out by GC-MS. About 23 compounds were identified in the fifth instar trapped volatiles; most of them were straight-chain alkanes, alkanoic acids, alkenals, alkanones and other compounds; and 55 compounds were identified in *Commiphora* crude extract most of which were terpenoids (monoterpenes) and other compounds.

INTRODUCTION

The desert locust *Schistocerca gregaria* (Forskal) (Orthoptera: Acrididae) is an important agricultural pest due to its polyphagous feeding behaviour. It has a vast invasion area covering about 29 million km^2 affecting 57 countries in Africa and Asia. This area represents more than 20% of the total land surface of the world. Due to its mobility and ability to fly long distances, the desert locust has become a principal concern to national, regional and international organizations, especially where locust outbreaks usually occur. The current locust control strategy is heavily dependent on the use of insecticides which have a broad spectrum of activity and affect a wide range of non-target species including other insects, birds, mammals and to some extent, human. So far no environmentally acceptable substitutes have been found.

Since the publication of Rachel Carson's Silent spring 25 years ago, the worried public has become more concerned about the underlying dangers of the use of insecticides on the environment, and in particular on wildlife.

Measures have been taken by the Environmental Protection Agency (EPA) of USA and other similar organizations in the past 15 years to prohibit or restrict the use of some pesticides on the environment. Recently, there has been widespread concern on the continued use of these insecticides in ecosystems of ecologically fragile areas such as those of the desert locust recession and breeding habitats. Nevertheless, the amount applied is still considerable and can not be tolerated.

Therefore, after 1985- 1988 plague, the ICIPE and other institutions stressed the need for establishing a sound scientific knowledge-base through a multidisciplinary approach, to develop long-term locust management strategies. Hence, research to devise alternative, environmentally friendly, biorational strategies for sustainable management of locust have been initiated. Alternative methods which are based on adequate understanding of the physiology, behaviour and chemical ecology of the desert locust are needed. In this connection, behaviour-modifying chemicals, i.e. semiochemicals, are being considered for developing an alternative, environmentally sound strategies for locust management and control.

Many processes vital to swarming behaviour and plague development, are believed to be mediated by certain pheromones. It is now largely accepted that understanding key factors which mediate the processes controlling locust phase transformation can provide new clues for practical control of these insects. Of these processes, synchronized accelerated maturation has an important role in sustaining the gregarization behaviour of the desert locust.

A number of inter- and intra-specific signals (kairomones and pheromones) have been implicated in the synchronous maturation of the desert locust during the gregarization process. Several aspects of earlier work were not undertaken in sufficient detail and needed further investigation. Therefore, the present work was undertaken with the objective of throwing further light on the factors responsible for inducing the process of accelerated/delayed maturation of gregarious desert locusts. The specific objectives of the study were as follows:

(1) To compare the effect of fifth instar nymphs (males and females) and their faeces on the maturation of immature male and female adults.
(2) To study the effect of trapped volatiles emitted by the 5th instar nymphs (crude extract) on the maturation of immature adult males and females, and to identify the compounds involved.
(3) To investigate a possible role of the desert plants *Commiphora quadricincta* (Schweinf) on the maturation of the gregarious desert locust.
(4) To identify the plant kairomones which are likely to be responsible for the maturation of the desert locust.

REVIEW OF LITERATURE

1. Locust

Locusts are a special group of grasshoppers which belong to the order Orthoptera and family Acrididae. Locusts differ from grasshoppers due to their ability to aggregate and to migrate for long distances. There are four major species of migratory locusts that are of economic importance in Africa, namely:.

- The Desert Locust, *Schistocerca gregaria* (Forskal);
- The African Migratory Locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire);
- The Red Locust, *Nomadacaris septemfasciata* (Serville).
- The Brown Locust, *Locustana pardalina* (Walker).

Of these four species, the desert locust is regarded as the single most serious threat to agriculture, due to its polyphagous feeding behaviour and migratory aptitude (Uvarov, 1977 and Steedman, 1988).

During recession periods, the desert locust is restricted to the arid and semi-arid part of a broad belt covering some 16 million km^2, extending from the Atlantic Ocean to north-west India (Fig. 1) (Steedman, 1988, and FAO, 1993). However, during plagues, the gregarious swarms may reach a much wider area and covering some 29 million km^2, or

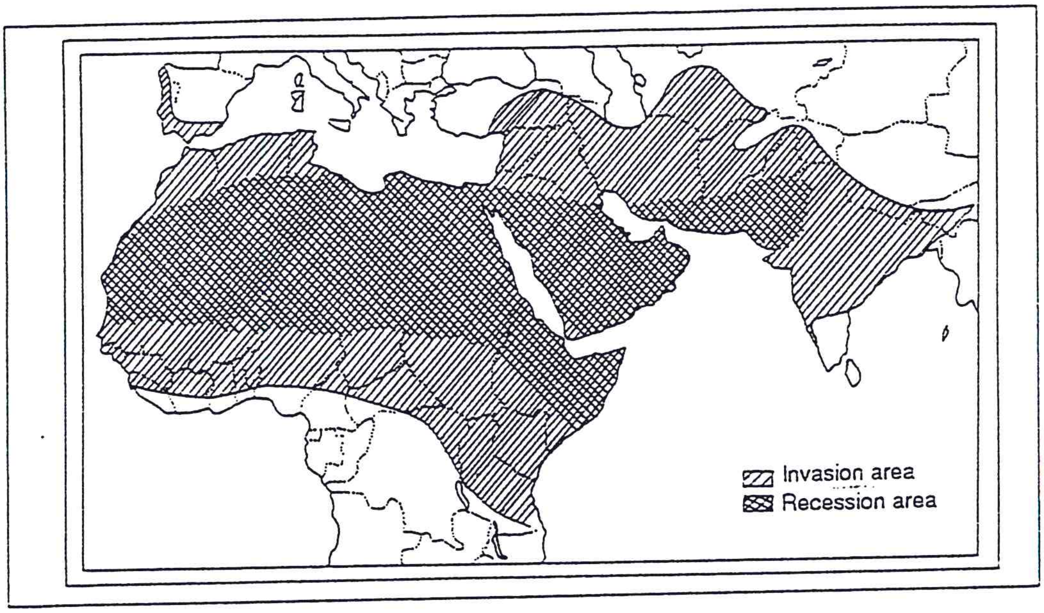


Fig. 1. Desert locust (*S. gregaria*) recession and invasion areas (from Steedman, 1988).

about 20% of the world's land surface (Fig. 1). *S. gregaria* is very sensitive to changes in population density. Phase transformation from the solitarious phase towards the gregarious phase and vice versa are believed occur too rapidly and frequently. As a result, during recessions it is believed that many populations may be in the transient phase rather than the solitarious phase, whereas during plagues most populations may be in the gregarious phase (FAO, 1993).

2. Biology of The Desert Locust

The life cycle of the desert locust comprises three stages: i.e. eggs, hopper and adult (Fig. 2). The time spent in each stage varies considerably depending on the weather conditions (Steedman, 1988).

Immature adults of the gregarious desert locust are usually pinkish in colour during the first 6-7 days after emergence. In both sexes the pink colour disappears, and a beige or brownish colour becomes apparent about 9 to 10 days after emergence. After 1 to 3 days, some yellow flush appears on the abdomen and/or on the base of the wings of males as well as on the base of the wings of females, (Pener, 1967). On the other hand, the immature adults of the solitarious desert locust are usually pale grayish brown in both sexes; males change to pale yellow on sexual

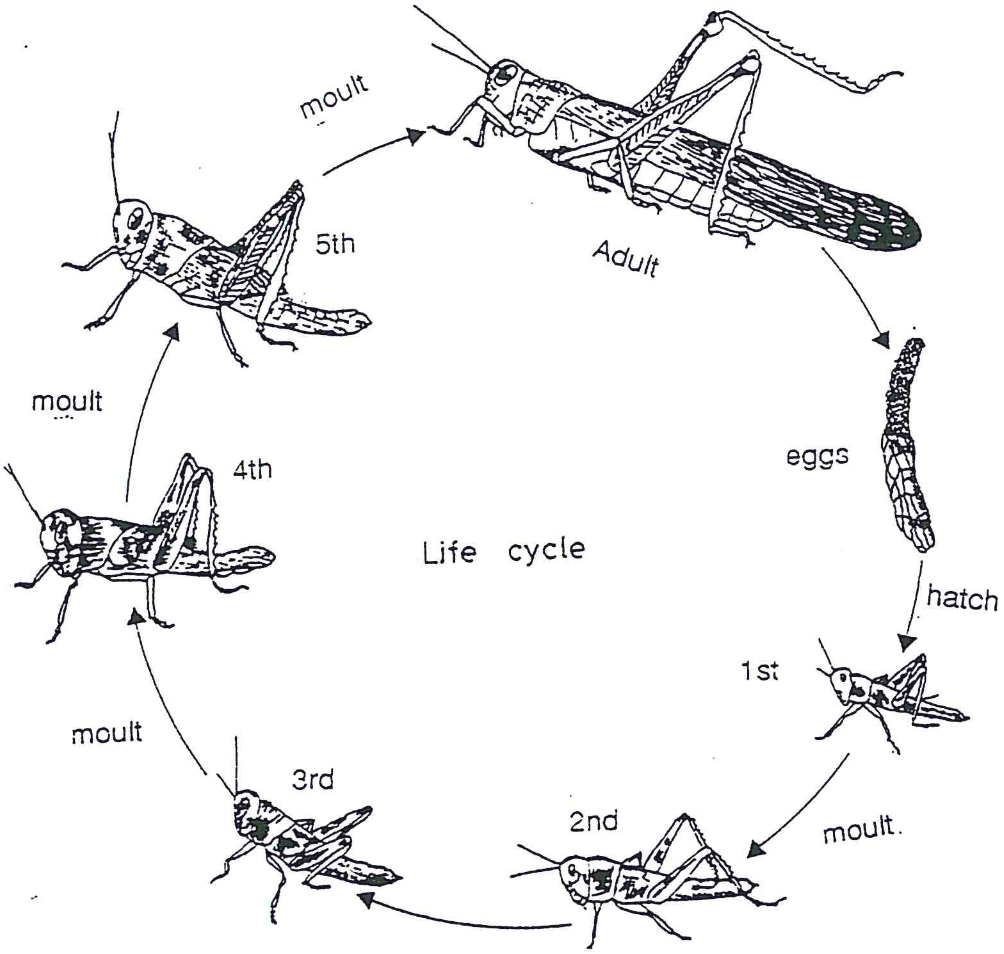


Fig. 2. Life cycle of the gregarious desert locust *S. gregaria*.

maturation, and females may show no colour change on maturation when at very low densities (FAO, 1993). Adults may become sexually mature in few weeks or few months, according to the environmental conditions. At low temperatures and under drought conditions, maturation may take as long as six months, whereas under optimal food and weather condition, maturation occurs within 3-4 weeks (Pener, 1967, and Steedman, 1988). Together with the appearance of the yellow colour, males start to show sexual behaviour, and the female's ovaries can easily be seen when the abdomen is pulled away from the thorax. At this time, copulation takes place; spermatozoa are passed into the females' genital organs and the eggs are fertilized. The time spent in copulation varies from 3-14 hrs. Several females can be fertilized by one male and the spermatozoa can be stored inside the female's body (spermatheca) and used to fertilize more than one set of eggs (Pener, 1967, Uvarov, 1977, Steedman, 1988).

Once eggs are fully developed inside the female, the latter can only keep them for about 3 days; then the eggs must be laid whether a suitable soil is available or not (Uvarov, 1977). Oviposition starts when females become beige or yellow in colour, especially at the base of the hind wings; and most females lay their first egg pod during the third week (14-21 days) after fledging (Pener, 1967). Males mature before females, but oviposition usually commences within about 2 days of copulation; a gregarious female usually lays 2-3 egg pods each with about 60-80 eggs; a solitarious female mostly lays 3-4 pods, each pod containing 100-160 eggs, with egg pods laid at an interval of 7-10 days (COPR, 1982).

The period of egg development (the incubation period) varies according to the soil temperature, e.g. in the summer breeding areas, the incubation period takes 10-14 days, but this is extended to 25-30 days in the cooler spring and winter breeding sites. When the eggs are fully developed, the young hoppers burst their way out of the egg shells, crawl up the froth tube to the surface; all the hoppers from one egg pod normally hatch on the same day. It usually takes three days for the complete hatching of a whole egg field, but longer periods have been recorded (Uvarov, 1977, and COPR, 1982). When hatching is complete and hoppers are a day old, they start to feed. The gregarious and solitarious hopper stage undergoes 4 and 5 moults, respectively. The life cycle of the gregarious hoppers is thus divided into five instars. The colour is heavy black pattern on yellow or orange background. The solitarious phase has six instars with a uniform green colour in early instars, which may become brown in the last two instars. The final moult from the last instar hopper results in the fledgling adult which does not grow in size, but gradually increases in weight (COPR, 1982, and Steedman, 1988).

3. Environmental Factors Affecting Maturation in Insects

Reproduction is regulated by both biotic and abiotic conditions and, in temperate areas, it is seasonally restricted. In order to synchronize reproductive activity with favourable seasons, many insects adjust their development according to environmental cues such as temperature, day length, moisture (R.H.), and food quality (Tauber, Tauber and Masaki, 1986; Danks, 1987, and De Wilde, 1962). Food quality and quantity are also known to affect the rate of insect development and the rate at which insects attain maturity (Woodward, 1952; De Wilde, Bongers and Schooneveld, 1969; Uvarov, 1977). Blood-sucking insects, for instance, require blood meal for the development of their eggs (Norris, 1964a). Some form of response to the day length, temperature or food, are extremely common among majorities of arthropods possessing a facultative diapause (Woodward, 1952; De Wilde, Dulntfer, and Mook, 1959).

Generally, the earlier developmental stages of insects require abundant food supply and favourable climatic conditions. Adults normally emerge when the environmental conditions are favourable, but when these conditions are unfavourable, development is retarded or arrested (Norris, 1964a).

Adult diapause is usually associated with an all- or - none reproductive delay response, either diapause and no reproduction or maximum reproduction and no diapause, although the duration of the reproductive delay may vary between individuals. If diapause occurs in the adult stage, it is directly antagonistic to reproduction (Dingle, 1978).

The environmental factors which influence maturation in different insects vary. In some cases one factor may be dominant, whereas in others a combination of factors may operate. In some insects, such as the Lymantriid and Bombyiid, moths emerge as mature adults with all their eggs ready to be laid, whereas most insects require some time for their development and maturation before eggs are laid. In the following overview the effect of different factors are summerised.

3. 1.Temperature

The most widely studied factor affecting maturation in insects is temperature. Andrewartha (1952) showed that diapause in the last larval instar of *Spalanngia drosophilae*, was largely determined by the age of the mother and the temperature at which it was reared. Similarly, the rate of maturation in the Colorado beetle, *Leplinotasa decimlineata* (Say), and *Notosira erratica* L. is affected by temperature. In these insects the females hibernate with undeveloped ovaries at temperatures as low as - 4 °C. Ovarial development is reversed or stimulated by high temperature before hibernation (Woodward, 1952, and De Wilde *et al.*, 1959).

Tracy and Nechols (1988) studied the biology of *Ooencyrtus anasae* and *Ooencyrtus sp.*, two parasitoids of the coreid *Anasa tristis*, in the laboratory at 20.8, 23.0 and 26.6 °C. They found that females of both species emerged with undeveloped ovaries at these temperatures. However, the oocytes developed during the preoviposition period (P.O.P) when females were exposed to 26.6 °C for about 35 hrs.

In other insects, the onset of diapause is sustained irrespective of changes in temperature. The chrysomelid beetle *Phytodecta olivaceae* (Forster) emerges from the soil after hibernation and oviposit from April to June when temperature rises, then burrows again and remains in diapause until the following year. The offspring, which emerges from July till September, also burrows and hibernates after a short feeding period. This means that these beetles enter an extended period of diapause from about June to October. Diapause will not be prevented at a temperature of 25 °C in this beetle (Waloff and Richards, 1958).

In temperate countries, blood sucking insects such as adult mosquitoes hibernate during the winter and take blood meals in the autumn which lead to the development of fat bodies instead of ovaries. In some species this hibernation can be prevented by high temperatures (Vinogradova, 1969).

3. 2. Day Length

In some insects, the initiation of diapause may be associated with the exposure of the early developmental stages to changes in day length. Small changes in day length herald the seasonal changes, which either encourage or discourage breeding. Short photoperiods tend to induce delayed ovarian development and promote diapause, whilst high temperatures generally tend to counteract that effect (Norris, 1964b). In blood sucking insects, such as some species of *Anopheles*, autumnal day-length is mainly responsible for the initiation of a reproductive diapause. Strains from southern latitudes have shorter critical photoperiods than those from northern latitudes. However, in *Culex pipiens molestus* L., diapause occurs independently of the photoperiod (Vinogradova, 1969).

An interesting example of an insect that emerges from the soil under conditions of short photoperiod, but soon burrows back into the soil entering a reproductive diapause, is found in the Colorado potato beetle, L. decimlineata.

This beetle shows no muscle development and oogenesis does not progress with undeveloped ovaries (De Wilde, 1954; De Wilde *et al.*, 1959).

Adults of the Collembola *Orchesella cincta* and *Tomocerus minor* (Lubbock) also show reproductive diapause. In early autumn, diapause is induced by a short photoperiod. The sexual maturation of juveniles of both species is retarded by a short photoperiod during which these insects hibernate (Woude and Verhoef, 1988).

In *Orius insidiosus* (Say), nearly 100% of the adult females entered reproductive diapause when reared under short day photoperiod (i.e. 10:14 LD), whereas at long day photoperiods (i.e. 12:12, 13:11, 14:10, 15:9 LD), insects initiated diapause (56.8, 29.7, 5.3, 15.9 %, respectively). The critical photoperiod fell between 12:12 LD and 13:11 LD. The duration of the P.O.P. was found to be inversely related to the photoperiod (Ruberson, Bush, and Kring, 1991).

3. 3. Quality and Quantity of Food

In addition to temperature and photoperiod, it has been found that differences in quality as well as quantity of food consumed by the insect may influence fecundity. The female of the moth *Ephestia kuhniella* (Zell) needs between 0.125g and 0.15g of whole meal flour in its larval stages.

If the amount of food per larva is reduced to about half (0.075 g), fecundity is reduced by 44% (Norris, 1934).

The effect of food plant age and nutrient content on the growth of larvae of *Papilio polyxenes asterius* (Fabricius) was studied by Finke and Scriber (1988); they found that larvae feeding on plants which had leaf-water contents of less than 75%, were unable to increase their nitrogen utilization for optimal growth rate.

Other studies showed that the effect of the food quality of various plant tissues, such as fresh silks, tassels or young ear tips of maize, sunflower head and male blossom of squash, affected the average lifespan which varied from 29 to 46 days on these foods and egg production varied from 16 to 128 eggs/female of the adult of the corn rootworm *Diabrotica barberi* (Smith and Lawrence). The chrysomelids lived for only 9-17 days with less than 4 eggs/female when they were given maize leaves or a mixture of 3 weed species common in South Dakota maize field (Lance and Fisher, 1987). Adult beetles of *D. barberi* failed to mature and survived poorly when provided only with food sources from immature maize plants. Also reduction in the quality of food associated with maize plant maturity significantly reduced oviposition period, fecundity and lifespan (Naranjo and Sawyer, 1987).

3. 4. Combination of Factors

In some cases, a combination of factors such as day length and temperature may operate dependently. For instance, in the homopteran *Stenocranus minutus* Fabr, Muller (1957) showed that hibernation occurs in the adult stage. The young adults do not emerge until August and reproduction is arrested as a result of long days during larval life. Also, Norris (1964a) showed that diapause can be prevented by high temperature and short days during the first month of adulthood.

Reproductive diapause in females of the carrot weevil, *Listrontus oregonensis* (Le Conte), is controlled by an interaction between temperature and photoperiod. Immature adults (not sexually mature) when placed at test regimens did not oviposit at certain temperature and photoperiod regimens (TPRs), whereas reproductive diapause was induced in sexually mature females after periods of exposure to similar TPRs. The photoperiod which induced diapause decreased with increasing temperature. At 16 °C no oviposition occurred at day length less than 18 hrs, whereas at 28 °C there was oviposition at all day lengths (Stevenson and Boivin, 1990). Two strains of *Drosophila funebris* from Japan showed a clear-cut reproductive diapause in response to the photoperiod and the temperature, but these strains differed from each other in the intensity of diapause (Watabe, 1988). In *Drosophila melanogaster* (Meig) ovarian diapause is regulated by the photoperiod and the temperature. Newly emerged females exposed to short days (less than 14 hrs of light per day) at 12 °C or 10 °C entered reproductive diapause. On the other hand, females exposed to long days (16 hrs of light per day) at the same low temperature underwent ovarian maturation (Saunders, Henrich, and Gilber, 1989).

In the chrysomelid *Diabrotica undecimpunctata howardi* (Barber), rearing of the insect at various combinations of temperatures (20 and 25 °C) and photoperiods (12 and 13 hrs), inhibited the ovarian development, causing the insect to enter into a reproductive diapause. Photophases of 12 and 13 hrs at 30 °C and 14 hrs at 20, 25 and 30 °C favoured normal ovarian development, while short photophase at 20 °C inhibited ovarian development for 30 to 60 days (Elsey, 1988).

Javahery (1990) demonstrated that the pentatomid *Acrosternum hilare* (Say) occurs in several plant species, and found that the temperature and the humidity directly influenced the incubation period and nymphal development. The bugs aestivated in late September and October on either side of the leaves of the deciduous trees and migrated to the overwintered under leaf litter, where they remained from

November until April. It was noted that reproductive development and fecundity are influenced by the photoperiod.

Investigations of the effects of constant and variable temperatures on the development of larvae of the *Podisus maculiventris* (Say) have shown that under conditions of diurnal thermorhythms with different amplitudes, the duration of the larval development was similar to that at the corresponding constant temperatures. The maturation period of the females was, however, reduced by an average of 4 days; temperatures of 25-28 °C lessened the short day effect (Goryshin, Volkovich, Saulich, Vagner, and Borisenko, 1988).

3. 5. Reversibility and Irreversibility of Environmental Effects

The effects of environmental factors on insect maturation and development may be either reversible or irreversible. For instance, under the conditions of cool temperatures, short photoperiods and poor food supply (quantity), the Colorado potato beetle, *L. decemlineata*, emerges from the soil, but soon burrows back entering a reproductive diapause. Exposure of the insect to a warm temperature, long photoperiod and adequate food supply, favours female emergence, production of vitellogenin, onset of oogenesis and development of ovaries. During hot summer, the adults oviposit, but hibernate later in response to short day length. The oocytes are resorbed and the hibernating females can be found with the eggs in all stages of degeneration. Therefore, maturation is retarded and at marginal photoperiods is influenced by temperature, e.g. at 25 °C oviposition will stop and within 3-5 weeks insects enter into diapause (De Wilde *et al.*, 1959).

Laboratory experiments carried out by Gara and Wood (1989) to determine the role of the cold temperature and host material in reversing the reproductive diapause, have shown that diapause was not broken in females of Sitka spruce weevil, *Pissodes strobi* (Peck), exposed to temperatures of 4.4, 10, 15.5 and 21.1°C for periods of 20, 40 and 60 days. However, females fed on lateral branches of *P. sitchensis* continued to have undeveloped ovaries, while females fed on terminal shoots under long-day conditions (16:8 LD) developed ovaries. At a low temperature (i.e. -4 °C), maturation is inhibited. Woodward (1952) showed that in the Mirid *Notosira erratica* L. the females hibernate with undeveloped ovaries, but development can be reversed or stimulated at a temperature of 25°C before hibernation.

In many insect species of the temperate zone, the induction of diapause (a dormant overwintering state) or its prevention can be controlled in the laboratory by manipulation of the photoperiod. Exposure of most species for 1 to 3 weeks to short days with 13 or less hours of light induces diapause, whereas exposure to long days prevents it. Diapause can also be prevented by interruption of the scotophases (dark period) of otherwise inductive (short day) photoperiod (De Wilde, 1962, and Danilevskii, 1965).

Some insects, such as the adults of the face flies, enter a facultative diapause in which mating and ovarian maturation do not take place, and their fat bodies become hypertrophied. Laboratory studies by Evans and Krafsur (1990) emphasized the short photoperiods as the primary inducers of diapause. However, the response is temperature-dependent, e.g. at 16°C most face flies enter diapause regardless of photoperiod (even in the 18:6 LD).

A few populations of univoltine species enter into obligatory diapause in each generation irreversibly, regardless of the environmental conditions, e.g. gypsy moth, *Lymantria dispar* (Linnaeus) (Masaki, 1956), and the bagworm, *Thyridopteryx ephemeracformis* (Haworth) (Morden and Waldbauer, 1980).

4. Maturation Control in Migratory Insects

Insects inhabiting variable environments often face living conditions which are unfavourable for development and reproduction. Such adversities can be overcome either by delaying development and reproduction to some future time (i.e. by entering diapause), or by combination of diapause and migration. The power of movement in insects is often an important element in their life histories. Insects migrate to habitats most suitable for the growth and the development of their offspring, and many species also migrate to escape unfavourable breeding conditions (Dingle, 1978, and Solbreck, 1979).

The options are largely dependent upon the degree of synchrony of the environmental changes in the different habitual patches (Solberck, 1978). Migration and diapause are adaptations for insects exploiting temporary habitats; temporariness being a function of both space and time. Accordingly, migration can be regarded as escape in space and diapause as escape in time (Solberck, 1978). However, insect migratory flights are of different kinds, migration by young adults is soon followed by breeding. Those undertaken to and from diapause sites are intimately linked to the general diapause development. The pre- and postdiapause migrations can be regarded as marking the beginning and the end of the diapause period (Dingle, 1978, and Solberck, 1978).

In patchy habitats, where the availability of suitable conditions for breeding are less predictable and can be synchronized, migration is bound to have a higher reproductive value. Populations may spend the unfavourable season as reproductively quiescent adults rather than as immobile immature stages, because the former can search out for suitable habitat patches for reproduction as soon as they become available (Farrow, 1990).

One of the main characteristics of insect migration is the so-called "oogenesis-flight syndrome" described by Johnson (1969). It is a situation in which young pre-reproductive females become migrants. This delays reproduction until they arrive and settle at a new site. The additive effect of diapause to that of migration and reproduction can have an important role to play in the life histories of insects. The seasonal patterns of movement, as reported by Dingle (1985), may be over shorter or longer distances, depending on the species and circumstances. Migration often begins when the ovaries are immature and when the activity of the corpus allatum is diminished. Prolonged migration often ceases when the ovaries become mature (Johnson, 1969). A good example of relatively short-distance movement is that of the lygaeid bug *Lygaeus equestris* (L.) on the island of Gotland. In the winter, diapausing individuals cluster in sheltered rock outcrops or around stone buildings, using energy stored in the fat bodies. As the winter progresses, the fat bodies shrink as the energy is utilized, and the ovaries, which are undeveloped in the autumn, become more sensitive to stimulation by warm temperatures. However, in May, warm weather stimulates the reproductive system and flight, and the insects migrate to the host plants growing in the surrounding terrain. Here, feeding produces a rapid development of eggs and reproduction begins. The new generation matures through the remainder of the summer and migrates to the overwintering sites in autumn (Solbreck, 1971, 1972 and 1976).

Induction of diapause in the migratory seed bug, *Neacoryphus bicrucis* (Say), was studied by Solbreck (1979) who demonstrated that the insects were found to hibernate in the adult stage and exhibit a facultative reproductive diapause. Constant photoperiods of the durations encountered in the field did not evoke the diapause response, but shortening of the photoperiod did. It has been suggested that the response to decreased day length in *N. bicrucis* is an adaptation to ensure seasonal synchronization in a highly migratory species where successive generations may breed at different latitudes.

Environmental cues such as photoperiod, temperature, and food availability appear to influence the degree of migratory behaviour displayed by an *Oncopeltus* population. When reared in a short photoperiod (12:12 LD, at 23 °C), *Oncopeltus* entered an adult reproductive diapause (Dingle, 1974). The resulting delay in reproduction results in a longer period of time prior to egg maturation during which females may be stimulated to make long flights (Caldwell, 1974, and Rankin, and Riddiford, 1977).

Moreover, it was reported that in many predaceous coccinellid beetles, viz. *Coccinella septempunctata* (L.), long-distance migrations are associated with the reproductive diapause requirements for hibernation in hilly areas. The females fly to low land areas, where the food (aphid prey) necessary for their ovarial development is available. The males mature without delay and copulate before and during hibernation as well as afterwards. Although females are fertilized before leaving the hibernation areas, and do not mature until they arrive at feeding grounds, the photoperiod, temperature and food are all involved in the induction of the diapause, which can be reversed by keeping cultures at fairly high temperatures, fluctuating between 22-28 °C at a 16 to 18 hours photoperiod and with sufficient food (Hagen, 1962).

In some insect species, both sexes are immature when they migrate to hibernation or aestivation sites. The males mature during hibernation and mate before the immature females migrate to the oviposition sites. For example, both sexes of *Eurygaster integriceps* (Put.) migrate to the aestivation sites and later they hibernate with the gonads still immature. The testes begin to develop, slowly at first, and then in February more rapidly, and are ripe in March or April when the ovaries in most of the females are still immature. Mating occurs at the end of the hibernation period when temperature rises (Brown, 1965).

In addition to migration to and from the aestivation or the hibernation sites, diapause can be involved with migration more directly, as in the case of *Oncopeltus fasciatus* (Dallas) (Dingle, 1978). In this North American lygaeid bug, short-day diapause increases the duration of the migratory period in the adult and, hence the time available to escape the oncoming winter. Since migration and diapause occur simultaneously in *O. fasciatus* and permit a considerable long-distance movement, the response to the short days may be a key adaptation in allowing this species to invade the north temperate zone during the summer months (Dingle and Baldwin, 1983). The delay in reproduction under short days allows a sufficient time for the escape from the unfavourable conditions in the autumn (Dingle *et al*., 1980).

Migration in insects is not just an alternative to diapause, but often it is a feature of pre-diapause behaviour. Flights to and from mountain diapause areas are not confined to coccinellids. Several species of Hemiptera also show similar seasonal patterns. The pentatomid *E. integriceps* is the best known of these. Studies on *E. integriceps* suggest that at least this species makes use of the wind in its spring return flights. Once the insects have risen clear off the ground, they turn and fly down-wind. They are thus dependent on wind patterns to find the suitable breeding sites (Dingle, 1985).

5. Factors Affecting Sexual Maturation of Acridids

Many tropical insects migrate between seasonally available habitats, and locusts are probably the best known of these (Uvarov, 1977). When locusts are in the gregarious phase, they form swarms that are able to migrate over long distances, mainly during day time (Uvarov, 1977). A tendency for mass migration is also found in some species of grasshoppers, e.g. the Senegalese grasshopper, *Oedaleus senegalensis* (Krauss), which migrates in large aggregations, mainly at night.

Locusts and grasshoppers lay their eggs in moist light soils and may have more than one generation during a single rainy season. Many species undergo reproductive diapause in order to cope with unfavourable conditions, such as decreasing day length as in the case of the Senegalese grasshopper (Stein, Bie, Herstad, Olafsson, and Somme, 1989). Moreover, in the red locust, *N. septemfasciata*

(Serville), maturation begins after a time, apparently without any stimulus from a changed environment, and is gradual. Ovarial development and weight increase begin many weeks before copulation and oviposition, provided that the photoperiod remains short. The length of the diapause interval is approximately constant, irrespective of the time of the year, since it is internally controlled (Norris, 1962). It occurs simultaneously over a large area, seemingly triggered by the general change in the conditions rather than by the actual contact with the rain or by the improved vegetation (Norris, 1962). Nymphs develop during the autumn and spend about eight months (including the hot summer, dry winter and spring periods) in an adult diapause. As in all acridids, there is a period of intensive feeding for a few weeks after the adult emergence. In the diapaused females, this does not happen as feeding declines to a low level, weight no longer increases and the ovaries remain threadlike. The males also feed less and maintain a constant weight (Norris, 1962).

Reproductive diapause of the red locust is terminated at the beginning of the rainy season. This is followed by intensive feeding of the immature adults on the new vegetation and a subsequent synchronized maturation. Maturation may, however, be arrested as females resorb the contents of their developing gonads due to unfavourable conditions. The development of the gonads, or at least of

the ovar
environm
A s
conducte
developm
season.
insect
14 hrs.
develope
without
is incre
natural
1962, 19
Alt
the temp
species
hoppers.
Anacridi
the autu
the next
but reta
affectin
demonstr
emerged
the inse
counterp

had a very prolonged diapause even at a favourable temperature. The results of submitting females to a range of photoperiods led Norris to suggest that in the field, where hoppers and young adults develop during the summer, the onset of the female diapause is induced by a continuous long photoperiod. In the laboratory, diapausing females could be induced to mature in the winter by increasing the temperature. Norris suggested that diapause is terminated by that time, but maturation in the field would be prevented by low temperature.

Study carried out by Tanaka, Hakomori, and Hasegawa (1993) on migratory locusts showed that photoperiod, temperature and rearing density affect the rate of the sexual maturation. They found that the time required for 50% of the females to start oviposition was longer when they were crowded as hoppers and isolated as pairs of adults at a longer photoperiod. A similar photoperiodic response was reported for some Japanese strains of *L. migratoria* (Hakomori and Tanaka, 1992). Long days not only delay the time of the first reproduction by locusts, but also reduce the frequency of oviposition as compared with locusts reared at short-days (Tanaka, 1982). A study carried out by Wardhaugh (1986) on the Australian plague locust *Chortoicetes terminifera* (Walker) showed that photoperiod and the temperature during the nymphal and early adult stages, play an important role in regulating the induction of diapause.

6. Influence of Host Plants on Acridids

Host plants may contribute much to locust and grasshopper dynamics through their influence on key population parameters. Variation in host plant quality and quantity alter a variety of key life-history traits in grasshoppers including survivorship, developmental rate, rate of egg production, total fecundity, and oviposition rates. Although the key studies that directly link large-scale population processes to changes in host plant quality have yet to be preformed, a variety of carefully crafted experiments indicated the likelihood of their importance. There is a direct relationship between the species of host plant and grasshopper survival, growth, and reproductive output (Mulkern, 1967).

Generally, the quality and quantity of specific food plants have marked influences as well. Numerous accounts suggest that poor-quality food plants associated with extreme drought results in a poor reproductive performance (Chapman, Page, and Cook, 1979).

The physiological responses such as oocyte production in response to the quality and the quantity of protein in the food plants and the hormonal processes mediating the responses suggest a close tie. Protein composition of ingested food affects the synthesis of proteins (qualitatively and quantitatively) in the fat body of *S. gregaria* (HILL, 1965).

Reproductive cycles in grasshoppers may be modified by changes in food plant quality mediated by plant growth hormones. For example, adults of *S. gregaria* do not mature sexually during the long, dry periods when they feed on senescent vegetation. But when new green foliage is available after rains, the locusts mature very quickly. This response has been attributed to high concentrations of the plant growth hormone gibberellin found in the leaves of the new growth, but only in small amounts in the senescent foliage (Ellis, Carlisle, and Osborne, 1965).

Detailed studies have demonstrated the importance of particular chemical constituents in the host plants to grasshopper survival, including both defensive secondary chemicals (Mulkern and Toczek, 1972; Bernays, Horsey, and Leather, 1974, and Bernays, Chaberlain, and Mc Carthy 1980) and nutrients (McGinnis and Kasting, 1966). For example, nitrogen content is very important to nymphal growth of *Melanoplus bivittatus* (Say.) (McGinnis and Kasting, 1966). *Melanoplus sanguinipes* (Fabricius) fed on wheat with low phosphorus content developed faster, with increased survival and fecundity, compared with individuals fed on plants with higher phosphorus content (Mulkern, and Toczek, 1972).

7. Factors Affecting Sexual Maturation of The Desert Locust

True locusts differ from grasshoppers in their ability to alter their behaviour, physiology, colour and shape in response to variations in population density caused by changes in the environment. The desert locusts in a solitary phase usually live in very low densities well separated apart. As in the gregarious phase, sexual maturity in the solitary locust is associated with the onset of the rainy season, and oviposition occurs at sites where soil moisture is adequate and vegetation is sufficient to support the development of their progeny (i.e. the hoppers). If these conditions are maintained throughout a few generations, the process of gregarization begins which leads to the formation of swarms (Uvarov, 1977).

7. 1. Environmental Factors and The Maturation of The Solitarious Desert Locust

Environmental cues and some biotic factors have been shown to influence the rate of development and maturation of solitarious desert locust (Norris, 1964b). Under favourable conditions, young adults become sexually mature within three weeks, but maturation may be delayed for several months when unfavourable conditions prevail (Norris, 1957; Stein *et al.*, 1989).

The exact conditions that cause maturation of locusts are not known, but rainfall appears to play an important role (Norris, 1964b). Prolonged delays in maturation often occur which are believed to be due to the effects of cold weather and drought (Norris, 1957).

It was found that when solitarious desert locusts are reared in the laboratory, rapid maturation can occur at quite low humidities and a minimum of fresh food (Norris, 1957). But under field conditions, maturation tends to be delayed during the summer months without any change in humidity. These delays, which are of very variable incidence and duration, are now known to be induced mainly by the action of long days (Norris, 1957).

Another factor shown to influence reproduction of the insect is temperature. Cantacuzene, Lauverjat and Papillon (1972) have shown that *Schistocerca* laid sterile eggs when kept at air temperature of 20°C by night and 28°C by day. They also observed that the ovaries developed normally, but the spermatheca which appeared normal, did not contain spermatozoa.

Maturation in the desert locust can be recognized by changes in colour. The immature adult male of the solitary phase is likely to be pale grey or beige, while the mature is pale yellow. In contrast, an adult from a swarm will be pink when immature and bright yellow when mature (Steedman, 1988).

7. 2. Environmental Factors and The Maturation of The Gregarious Desert Locust

Environmental cues have different effects on the development and maturation of the gregarious desert locusts. For instance, day light regime affects the rate of ovarial maturation of locusts in laboratory reared crowded colonies of *Schistocerca*. Norris (1957 and 1964b) showed that ovarial maturation was inhibited by the long day-length, particularly at hopper stage. Hoppers reared in 12 hours light regime produced adults which mature more rapidly than those reared in 13 hours light regime. Norris (1954) also demonstrated that in 13 hours light regime in crowded desert locust, ovarial development of the females was arrested and the accessory sexual glands of the male remained empty although spermatogenesis proceeded. Other changes which are associated with diapause, including formation of a large fat-body, reduced feeding and lowered tissue water-content were observed.

Dudley (1961, cf. Uvarov, 1966) found that crowded *Schistocerca* kept at a rigidly controlled constant temperature of 35 °C, with all the other conditions kept constant, failed to mature for as long as seven to eight months and then died.08

The occurrence of a large number of locust hoppers of a similar age in the field can only be the result of the simultaneous hatching of a large number of eggs which were laid in close proximity to one another. This in turn ensured the simultaneous sexual maturation (Carlisle and Ellis, 1967). Norris (1954) suggested that one factor which synchronizes sexual maturation within a swarm is the maturation pheromone, produced by a mature male desert locust, which stimulates the maturation of the other individuals of both sexes. Carlisle and Ellis (1967) indicated that mature females of the desert locusts produce the substance in a lesser amount, and that males which have begun to mature induce maturation in others.

The beginning of the maturation process can be recognized by the disappearance of the pink colour from the hind tibiae, coupled with the deposition of yolk in the eggs (Steedman, 1988). Change in colour (yellowing) in accordance with stage III classification developed by (Norris, 1954) in gregarious desert locust well marked yellow flush on the hind wings and often on the elytra as well; noticeable fad of the brown colour at the tip of the abdomen and along the lateral margins of the abdominal tergites, then yellow colour extending to the pronotum, sides of the thorax and the head was used. The colour change in the gregarious adult *Schistocerca* was used by Pener (1967) to distinguish between the sexually immature (pink) and mature (yellow) stages. Crowded fledglings of *S. gregaria* are pink, but after a few days the colour turns to pinkish-beige, then to beige or brown; eventually females become yellowish and males bright yellow after the onset of full sexual maturation. Although adult coloration is known to vary in relation to sex, phase status and environmental conditions, it is, however, risky to depend on the colour changes alone to determine exactly the developmental and maturation state of an individual locust (Amerasinghe, 1977 cf. Amerasinghe, 1978a). According to Amerasinghe (1978b) bioassay based on the ability of the pheromone to induce yellow coloration, is not always a reliable guide to sexual maturity. In attempt to find biochemical markers Mahamat *et al.* (1991) reported that the haemolymph proteins of locust showed distinguishable differences between immature and mature gregarious individuals.

Richard and Mangoury (1968) showed that the ovarial development in virgin females was accelerated by the presence of mature males, but was unaffected by the presence of immature adults or hoppers. Ovarial development in females is normally accelerated and oocytes mature as a result of copulation.

Recent experiments by Mahamat, Hassanali, Odongo, Torto, and Bashir (1993) confirmed previous findings that exposing immature males to mature males, or their abdominal extracts, for a period of 8 days accelerates the yellowing process in the gregarious immature adults of the desert locust.

7. 3. Semiochemicals Mediating Maturation in The Desert Locust

a. Pheromones

Pheromones are important chemical substances which mediate various behavioural and biological processes in insects, including locusts. The mediators of phase transformation are pheromones of which three types have been implicated, viz. gregarization, sex maturation and oviposition pheromones. Each of these pheromones induces gregarization differently at different stages of the locust development (Loher, 1990, and Byers, 1991). It was suspected that mature males of *S. gregaria* produce pheromones which accelerate the maturation of the immature individuals of both sexes. These pheromones were considered to be secreted by the epidermal cells of the mature male (Norris, 1954 and 1964a, and Loher, 1960).

The experimental work of Norris (1962 and 1964a) on the sexual maturation in *S. gregaria* led to the consideration that pheromones play an important part in attaining the sexual maturity, as expressed in the onset of the sexual behaviour, a change in body coloration, ripening of the gonads resulting in earlier copulation, egg production and oviposition.

In addition to the stimulatory effect of the mature male on the immature adults, there appears to be an inhibitory effect originating from the nymphs or the immature adults, which was hypothesized to be pheromonally based (Norris, 1962 and 1964a). Obeng-Ofori, Torto, and Hassanali (1993) showed that in gregarious *S. gregaria* aggregation is mediated by two sets of pheromone systems: a juvenile aggregation pheromone produced by the nymphal stages to which nymphs respond and, an adult aggregation pheromone produced by the older adults and specific to adults. Gas chromatographic examination of the locust volatiles has confirmed significant qualitative and quantitative differences in the composition of nymphal, male and female adult emissions (Torto, Obeng-Ofori, Njagi, Hassanali and Amiani, 1994). Norris and Pener (1965) and Richard and El Mangoury (1968) proposed that in both the desert locust and the migratory locust, a substance inhibiting the production of the male maturation pheromone is released by the immature adults, which ensures that maturation of the group is synchronized.

Norris (1954) and Amerasinghe (1978b) demonstrated that both crowded and isolated mature males of *S. gregaria* are equally capable of accelerating the sexual maturation in the immature adults of both sexes and, the effect was attributed to a contact-transmitted maturation pheromone. Loher (1960) demonstrated that this was an oil-soluble substance probably produced in the vacuolated epidermis of the different parts of the body, especially on the abdominal tergites.

Mahamat *et al.* (1993) confirmed the mediation of maturation- accelerating pheromone and demonstrated conclusively that it is associated with volatile emissions of older male. They also demonstrated that the degree of acceleration attained with the mature males volatiles alone (in the absence of visual and tactile cues) is comparable with that obtained when immature insects were kept in direct contact with mature males. The results showed that the pheromonal effect is the dominant factor in accelerated maturation due to phenylacetonitrile, benzylaldehyde, vertarole, anisole and vinylveratrole. Ferenz, Luber and Wieting (1994) confirmed that only yellow, mature males produced phenylacetonitrile (benzylcyanide) (BCN). The role of this compound, however, was not investigated.

Maturation itself is controlled by the corpora allata (c.a.) and the cerebral neurosecretory system. So the maturation pheromone in some way may be stimulating the activity of the neuroendocrine system. The central nervous system (CNS) may certainly be involved in at least part of the effect of the pheromone (Loher, 1960).

It was reported that the maturation pheromone of *S. gergaria* is under the influence of the JH. it has been speculated that the epidermis of one individual produces a pheromone which stimulates the endocrine system of the other individuals, probably by way of chemoreceptor and the nervous system; the consequent production of JH in the recipient individuals stimulates the production of more pheromone (Loher 1960).

b. Allelochemicals(Kairomones)

Interaction among locusts within and between trophic levels may have important implications on the locust population and their life histories. Carlisle, Ellis, and Betts (1965) reported that maturation of the adult desert locust coincides with the bud burst of certain desert shrubs at the beginning of the rainy season and a few weeks before the appearance of the annual vegetation. These shrubs include many species of *Boswellia neglecta* S. Moore and *Commiphora myrrha* (Nees) Engler (Gaffal) which have resinous buds that are the source of the biblical frankincense and myrrh.

It appears that the desert locusts respond to the scent of the shrubs that first break bud (Marshall and Disney, 1957). Carlisle *et al.* (1965) demonstrated, on the basis of the field observations and the laboratory experiments, that contact with terpenoids of the aromatic shrubs present in the highest concentration just at bud-burst, trigger the maturation process in the desert locust. Therefore, it was postulated that essential oils produced by many desert shrubs initiate maturation of the locusts in many desert areas (Carlisle and Ellis, 1967).

Certain seasonal changes such as the onset of the drought or infrequent rain are considered to delay maturation in the desert locust (Ellis, Carlisle, and Osborne, 1965). This may be because hoppers feeding on lush green vegetation will have to feed on senescent plants by the time they fledge. Under these conditions, young adults will not become mature. A diet of senescent *Brassica sp* delayed sexual maturation of the desert locust, an effect ascribed to a deficiency of gibberellic acid, the addition of which restored the normal maturation process (Ellis *et al.*, 1965).

Furthermore, food plants have been shown to have markedly different effects on the growth and development of crowded locusts. Jackson, Popov, Ibrahim, Alghamedi, and Khan (1978) demonstrated that *Pennisetum, Dipterygium, Tribulus* and *Chrozophora* supported rapid growth and development, and closely synchronized moulting. Of these four plants, *Dipterygium* was found to be outstanding. It was further shown by the same authors that a pure diet of sorghum allowed some hoppers to reach the adult stage in a normal period, but many were found to be retarded, resulting in poor synchronization of moulting, low body weight and delayed sexual maturation. However, crowded desert locusts which were fed on pure diets of *Tribulus* and sorghum failed to mature. The introduction of the leafing twigs of *Commiphora opababamum* (L.) Engl. into the diet had no effect at all in inducing maturation, despite the consumption of the leaves by the locusts.

Similarly, if locusts were fed long after fledging on senescent vegetation without any dietary supplement of gibberellic acid, no maturation is observed within a short time. Ellis *et al.* (1965) showed that when gregarious desert locusts were fed on senescent vegetation, which was supplemented with gibberellin from the day of fledgling, the locust matured as quickly as if they were feeding on green leaves. It was found that there was a relationship between insect colour and the freshness of grass on which they were fed on. Okay (1953) observed that the colour change from brown or yellow to green is entirely based on the formation or disappearance of the blue pigment, and this blue pigment depends mostly on the freshness of the grass on which the insects are fed.

It was demonstrated that there is a close relationship between adult development, feeding activity, and the attainment of sexual maturation. Norris (1961) demonstrated that an early period of intense food consumption and a concomitant rapid body growth, followed by a levelling off of both feeding and growth, is associated with sexual maturity.

7. 4. Host and Non-host Plants of The Desert Locust

Vegetation in the recession and breeding zones of the desert locust generally consists of short perennial bushes and herbs less than a metre high and annuals which come up after the rain (Steedman, 1988).

Desert plants such as *Dipterygium glaucum* Oecn., *Schouwia purpurea*, and *Heliotropium spp.*, are found on the moist silty and clay soils which are often covered by sand. Field observations showed that *Schouwia* may stay green for 3-4 months after a heavy rainy season (Uvarov, 1977, and Steedman, 1988).

Steedman (1988) further reported that plants with which solitarious desert locusts are often associated include: *Heliotropium spp.*, *D. glaucum*, *Tribulus terrestris* L., *Schouwia purpurea*, *S. thebaica*, *Aerva persica*, and *Hyoscyamus muticus*. Uvarov (1977) reported that in the semi-desert sahelo-saharan zone, with 50-200 mm rain, sand plains bear a diffuse vegetation of short perennial tussock grasses (*Panicum turgidum* Forsk., *Lasiurus hirsutus*, *Aristida pallida*) and shrublets (*Aerva javanica*, and *Lepladenica spp.*). In silty-clayey depressions, lush communities of annual herbs, particularly *S. thebaica, T. ochroleucus* and *H. muticus* as well as annual grasses (*Cenchrus biflorus,* and *Schoenfeldia gracilis*) are found and these ephemeral grasses provide the main food for hoppers.

Keay (1959) reported that the term savanna has always been used for a type of subtropical country with wide expanses of predominantly short grass and scattered trees of moderate height, mostly acacias, but also *Adansonia, Comretum, Commiphora* and others localized thickets of shrubs, often thorny, and herbs.

Gillett (1991) further reported that the desert shrubs *Boswellia* and *Commiphora (Burseraceae)* are distributed in West, Central, North-East and Southern Africa, where the annual rainfall ranges between 200mm to 1400mm and altitude range between 5m to 1650m.

MATERIALS AND METHODS

1. Insects

The desert locust *S. gregaria*, was reared in a crowded colony at the Insect and Animal Breeding Unit (IABU) of ICIPE. The colony originated from a stock kept by The Desert Locust Control Organization for Eastern Africa (DLCO-EA) in Addis Ababa, Ethiopia. Insects (300-400) of both sexes were reared under crowded conditions in aluminum cages (50x50x50 cm). Rearing took place in a special, well aerated room (4.5x4.5 m) with a ducting system that maintained a negative pressure, with a temperature of 33±1 °C, R.H. 60%, and a light cycle of 12:12 hrs light-dark. The insects used for the experiments were fledgling males and females from the same batch (1-2 day-old) to eliminate possible variability in their physiological status (Fig. 3A) and mature males (Fig. 3B). Fifth instar nymphs which have been implicated in the delay of maturation of immature adults were used to confirm previous work. The fifth instar nymphs (2-3 day-old); (Figs. 4a and 4b) were changed every three days to avoid any introduction of adult volatiles at moult.

For bioassays, standard aluminum cages (20x20x20 cm) with glass front and wire gauze on the four sides, one top, one bottom and two at the sides (Fig. 5) were used when

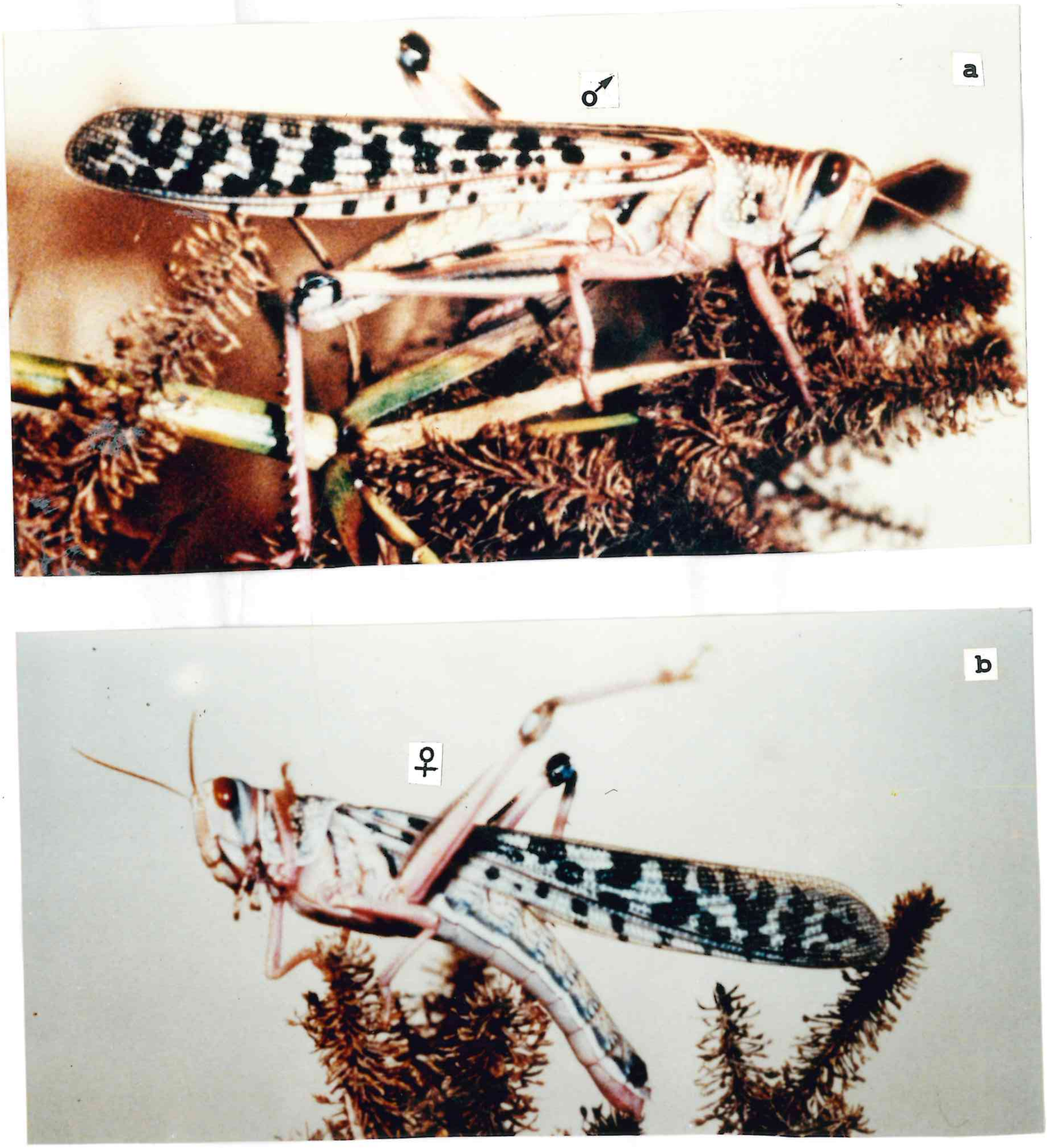


Fig. 3A. Fledgling (immature) adult (a) male and (b) female.

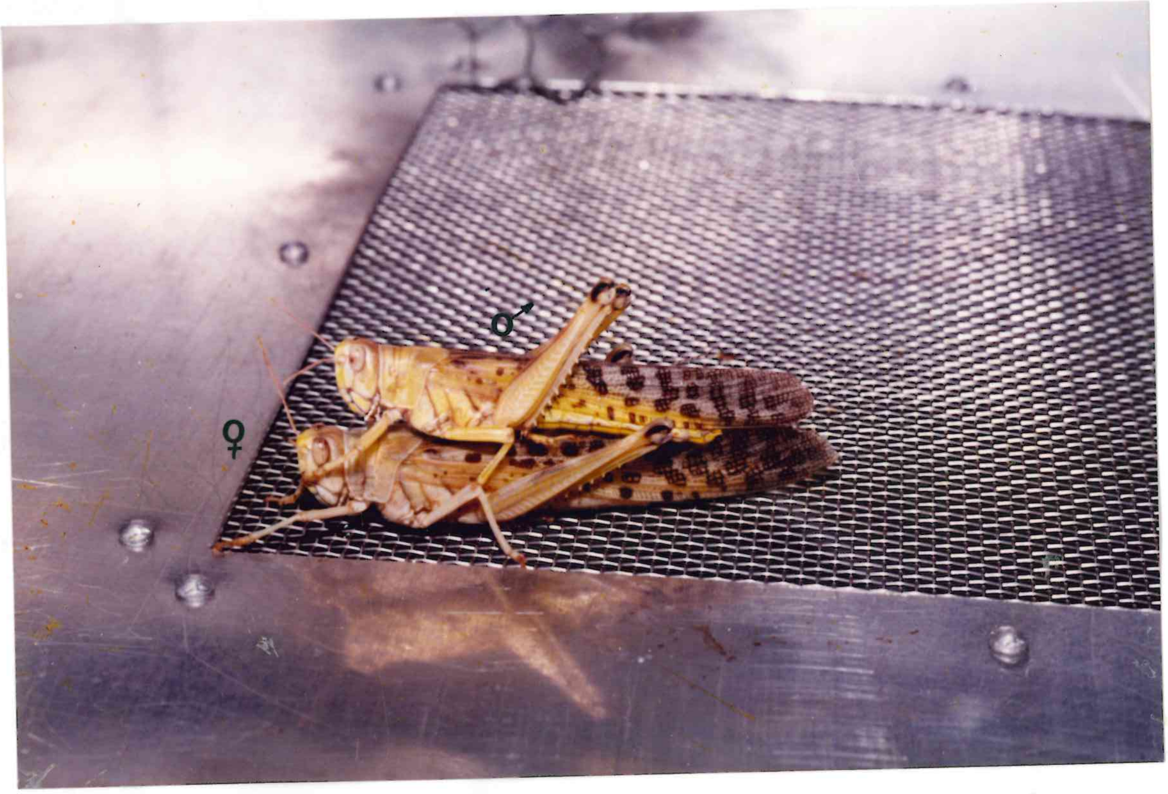


Fig. 3B. Mature male and female.

Fig. 4a. Fifth instar nymph of the crowded desert locust *S. gregaria*.

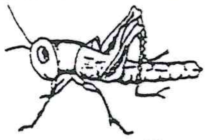
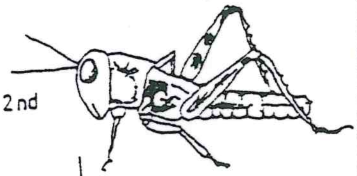
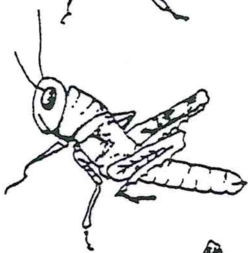
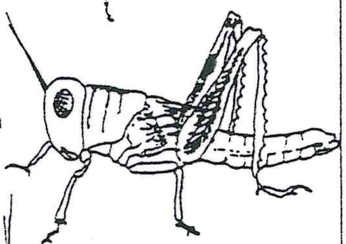
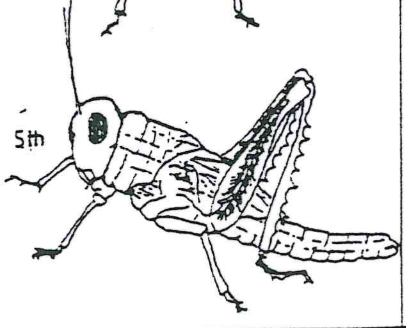
Nymphal instar		Length (mm)	Weight (mg)	Description
1st		7	30–40	Black turning to pale when moulting
2nd		15	50–80	Pale colour becomes more obvious. Head larger. No sign of wing growth
3rd		20	120–200	Black and yellow. Wing buds largers and more obvious, but shorter than length of the pronotum.
4th		33	500–700	Black and yellow. Wing buds largers and more obvious, but shorter than length of the pronotum.
5th		50	1000–1200	Brighter yellow with a black pattern. wing buds longer than the pronotum.

Fig. 4b. Distinctions between the different hopper instars of the desert locust.

Fig. 5. Aluminum cage used in experiments.

olfactory, visual and tactile cues are tested in combination. Aluminum bichamber bioassay cages (15x15x15 cm) with the upper portion similar to the lower portion (Fig. 6) were also employed when only volatiles were being tested. Cages were kept under the same conditions as above throughout the experimental period.

2. Trapping of Volatiles from Adults and Fifth Instar Nymphs

This was performed as described by Torto *et al.* (1994). Before use, the charcoal was cleaned by Soxhlet extraction with dichloromethane (Merck) for 72 hrs followed by activation under nitrogen (20 ml/min) at 250 °C for 30 min (Fig. 7).

2. 1. Monitoring adult emission

Volatiles were collected on charcoal traps by aeration. Briefly, air from a compressed air cylinder was passed through a charcoal filter, over locust contained in a trapping chamber (10 cm long x 3.5 cm-ID glass chamber) and through the charcoal trap (2.5g) packed between two glass wool plugs in 6 cm long x 8 mm - ID glass tubes at 106 ml / min for 16-24 hr at 30±1 °C. Collections were done from sets of nine adult males in groups of three (aged 12-16, 16-

Fig. 6. Aluminum bichamber bioassay cage.

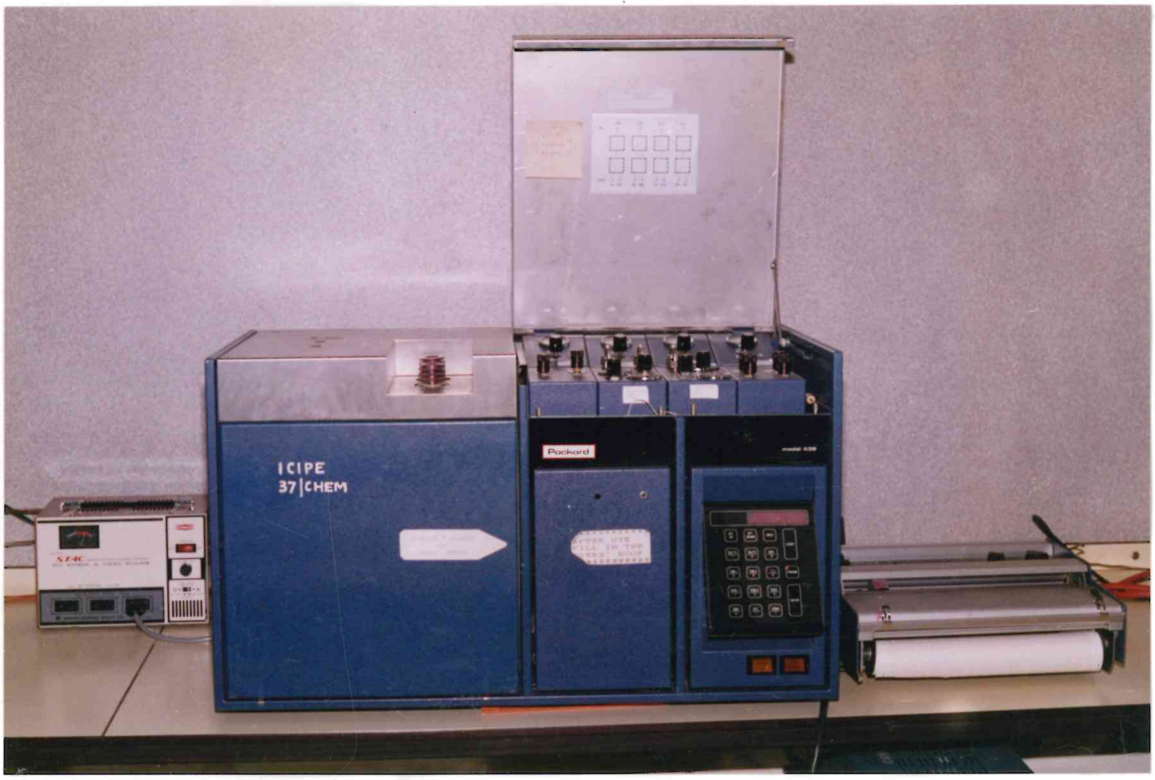


Fig. 7. Packard Becker GC chromatograph used for activation the traps.

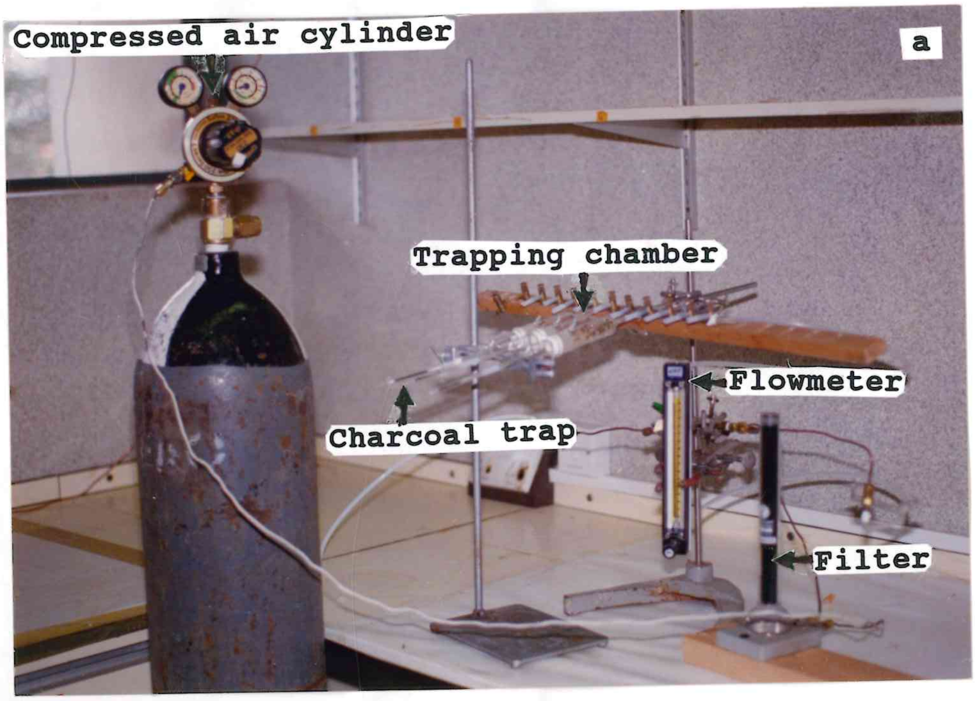
20, 20-24, 24-28, 28-32, 32-36 and 36-40 days) exposed to (a) fifth instar nymphs (Experiment I); (b) fifth instar nymphs faecal volatiles (Experiment II); and (c) volatiles trapped from fifth instar nymphs (Experiment III); (d) those which were left unexposed (control) (Fig. 8). Trapped volatiles were eluted with 5 ml HPLC grade dichloromethane (Aldrich Ltd., UK) and stored at -15 °C in a freezer before analyses.

2. 2. Collection of nymphal volatiles

Volatiles emitted by fifth instar nymphs (50 insects, aged 3-5 days old, mixed sex) were collected similarly for 24 hrs but with charcoal traps held in an ice-bath and the insects contained in a 1-litre-three-necked flask (Fig. 9). Trapped volatiles were eluted with 5 ml HPLC grade dichloromethane (DCM) (Aldrich Ltd., UK) and concentrated under a gentle stream of nitrogen at 0 °C to 1000 μl (Fig. 10) and stored at -15 °C in a freezer before use.

3. Analysis of Volatiles

The procedure described by Torto *et al.* (1994) was used. Volatile extracts were concentrated to 100 μl and then 250 ng of *o*-methylacetophenone (internal standard) were



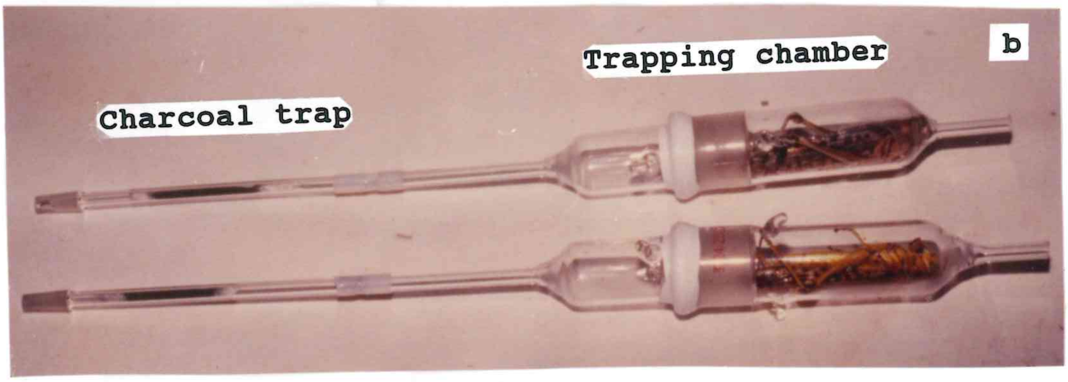


Fig. 8. (a). Volatiles collection assembly for adult *S. gregaria* and (b) Quickfit trapping chambers connected to charcoal traps.

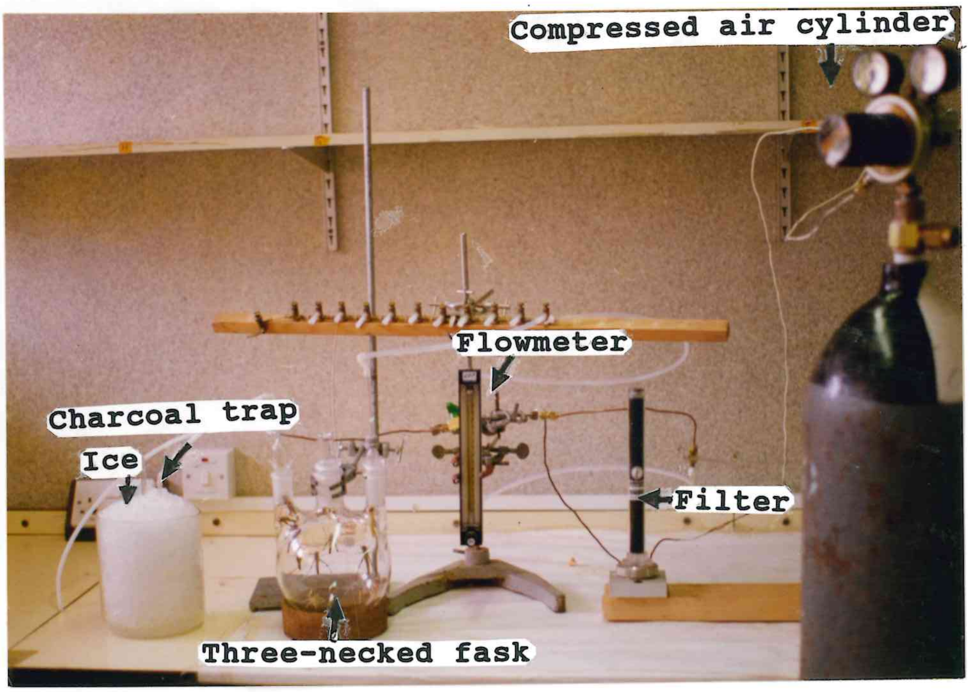


Fig. 9. A cold trap assembly for collecting 5th instar nymphal volatiles.

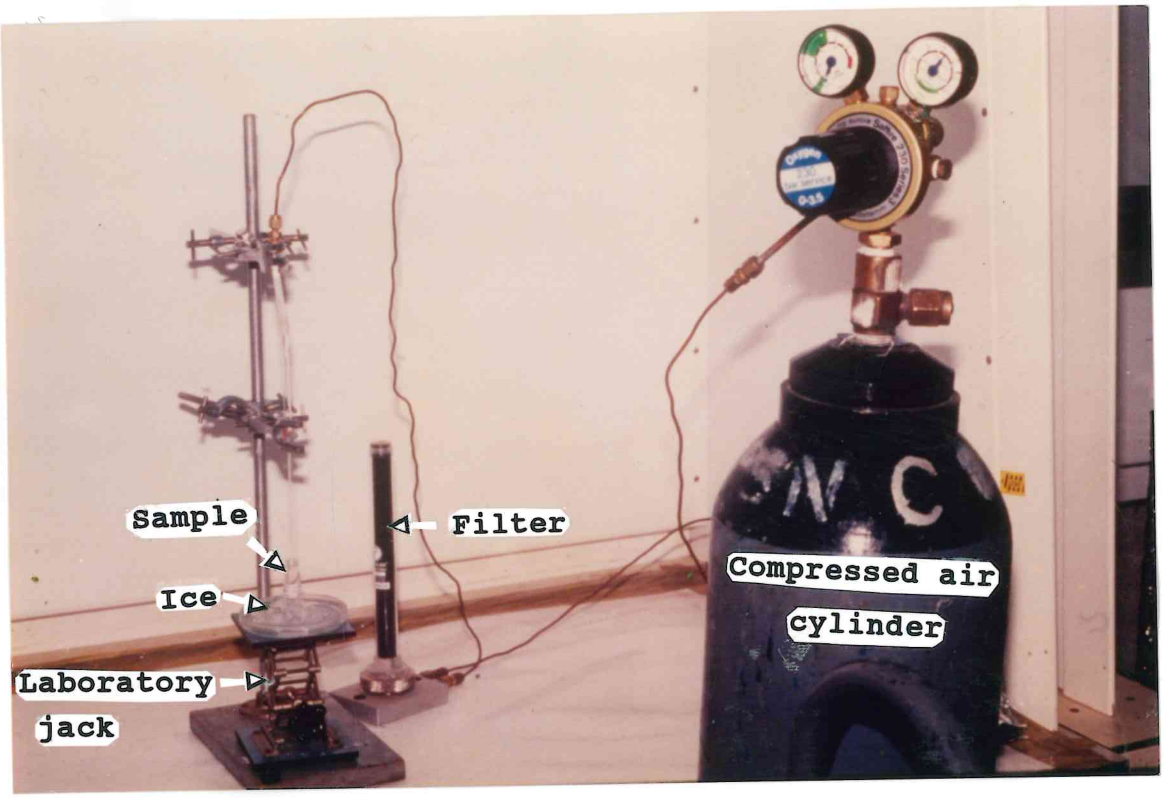


Fig. 10. Concentration of trapped volatiles from insects under a stream of nitrogen.

added. 2.5 μl aliquot of the extract, were analyzed by capillary gas chromatography (GC) (Fig. 11). Analyses were performed on a Hewlett-Packard (HP) 5890 series II gas chromatograph equipped with a flame ionization detector (FID) and a HP capillary column (carbowax, 50 m X 0.2 mm ID X 0.2 μm film thickness) using nitrogen as the carrier gas at a flow rate of 0.35 ml/ min. The oven temperature was initially isothermal at 60 °C for 10 min, then programmed at 5 °C/ min to 180 °C for 5 min and to a rate of 10 °C/ min to 220 °C for 15 minutes. Chromatographic peaks including that of phenylacetonitrile, were integrated using a SP 4400 chromjet or a HP 3393 integrator.

4. Experiment I: Effect of The Fifth Instar Nymphs on The Maturation of Immature Adults Males and Females of Gregarious Desert Locust

Newly moulted immature adult (1-2 day old) males and females (referred to as recipients) from the gregarious colony were exposed to fifth instar nymphs (mixed sex), mature males, immature males or immature females (referred to as signal sources) in standard aluminum cages (20x20x20 cm) with a sliding glass front and wire gauze on the four sides, one top, one bottom and two at the sides. Thus, the recipient insects had visual, tactile and olfactory contact

Fig. 11. Hewlett-Packard "GC" system.

with the signal source. Treatments involved the following:

Recipients	Signal source	Number of insects recipient:signal source
(a) imm. ♂	5th instar ♀	4:4
(b) imm. ♂	5th instar ♂	4:4
(c) imm. ♂	5th instar ♀ or ♂	4:1
(d) imm. ♂	5th instar ♂ or ♀	4:2
(e) imm. ♂	mature ♂	4:4
(f) imm. ♂	immature ♂ (control)	4:4
(g) imm. ♂	immature ♀ (control)	4:4
(h) imm. ♀	5th instar ♂	4:4
(i) imm. ♀	5th instar ♀	4:4
(j) imm. ♀	mature ♂	4:4
(k) imm. ♀	immature ♀ (control)	4:4
(l) imm. ♀	immature ♂ (control)	4:4

Each treatment was replicated 5 times. For (h) to (l) treatments, additional 5 replicates were set up to allow measurements of length of oocytes to be made. The insects were supplied with fresh wheat seedlings and wheat bran daily.

The recipient insects were checked daily for signs of maturation as assessed by:

(1) Change in colour (yellowing) in accordance with stage III classification developed by (Norris,

1954) and recently applied by Mahamat *et al*. (1993).

Stage 1: Pink or fading of the brown colour, at least on the hind tibia. No yellow colour at all; pale yellow colour at the base of the hind wings sometimes present (Immature).

Stage 2: Well marked yellow flush on the hind wings and often on the elytra as well; noticeable fad of the brown colour at the tip of the abdomen and along the lateral margins of the abdominal tergites; or bright yellow flush on the wings and elytra; most of the abdominal tergites are partially or fully yellow (Maturing).

Stage 3: Yellow colour extending to the pronotum, sides of the thorax and the head (Mature).

Observations were taken daily and the external colour change of each individual insect group was recorded.

(2) Copulation time. Young males which had begun to develop the yellow colouration on the abdomen were paired with fully mature females for about 6 hrs daily. Their ages at first successful copulation were noted; likewise, the test females were each paired with mature males and evidence of copulation

was similarly noted.

(3) Time to oviposit. The ages for the test females to oviposit first egg pods were recorded.

(4) Ovulation was monitored by the length of oocytes in females from day 12 to day 40 every 2 days. The abdomens of the adult females were cut open longitudinally and the ovaries were examined under a binocular microscope; the length of six developing terminal oocytes was measured in each individual using a micrometer.

(5) Number of eggs/pod. Number of eggs/pod oviposited for each treatment was recorded.

(6) Phenylacetonitrile titres. The presence of phenylacetonitrile and its amount was monitored in the volatiles of exposed and unexposed adult males at different ages (12-16, 16-20, 20-24, 24-28, 28-32, 32-36 and 36-40 days). The released amounts of phenylacetonitrile were quantified by GC (see trapping and analysis of volatiles).

5. Experiment II: Comparison of The Effect of Volatiles of Fifth Instar Nymphs and Their Faeces on The Maturation of Adult Males and Females of Gregarious Desert Locust

Three groups of immature adults were exposed to faeces (6 or 9g) of fifth instar nymphs (four nymphs were estimated to produce about 3g of faeces every day in the colony at ICIPE; the experimental faecal doses, therefore, represent, respectively double and triple the average droppings of fifth instar nymphs). The test insects (newly moulted fledgling adult males and females) were placed in the lower compartment of the bichamber cage (as described above) and the faeces, which was replaced with fresh material daily, in the upper compartment. In the controls, the recipient immature adults were placed in the lower compartment of the cage and the signal sources (immature males or females) placed in the upper chamber of the cage. The following combinations were compared:

	Recipients	Signal sources
(a)	imm. ♂ (4)	5th instar faeces (1g)
(b)	imm. ♂ (4)	5th instar faeces (3g)
(c)	imm. ♂ (4)	5th instar faeces (6g)
(d)	imm. ♂ (4)	5th instar faeces (9g)
(e)	imm. ♂ (4)	5th instar nymphs (mixed sexes)
(f)	imm. ♂ (4)	imm. ♂ (control) (4)
(g)	imm. ♀ (4)	5th instar faeces (1g)
(h)	imm. ♀ (4)	5th instar faeces (3g)
(i)	imm. ♀ (4)	5th instar faeces (6g)
(j)	imm. ♀ (4)	5th instar nymphs (mixed sexes)
(k)	imm. ♀ (4)	imm. ♀ (control) (4)

Each treatment was replicated 5 times. For (g), (h), (i), (j), and (k) treatments, additional 5 replicates were set up to allow measurement of ~~the~~ lengths ~~of~~ oocytes to be made. Maturation was monitored as described in Experiment I.

6. Experiment III: Effect of Fifth Instar Nymphal Volatile Extracts on The Maturation of Immature Adult Males and Females of Gregarious Desert Locust

Volatiles collected from 50 fifth instar nymphs were concentrated to 1 ml before use (20 μl of this represents an equivalent of 24 hrs emission from 1 nymph). Five immature males or females were placed in the lower compartment of the bichamber cage (each chamber 15x15x15 cm, the upper portion similar to the lower portion) and exposed to (a) nymphal volatile extract (100 μl; equivalent to 24 hrs emission of 5 nymphs) in light paraffin oil (1000 μl) to moderate the release of the volatiles, (b) fifth instar nymphs of mixed sexes (2+2), (c) immature adult, and (d) dichloromethane (100 μl) in light paraffin oil (1000 μl) as control. The test and control signal sources were placed in the upper compartments of the bichambers. Each set was replicated 5 times. For treatments involving females, additional 5 replicates were set up to allow measurement of lengths of oocytes to be made. Maturation was monitored as in Experiment I.

7. Identification of Fifth Instar Nymphal Volatiles

The trapped volatiles from 5th instar were analyzed by gas chromatography (GC) and gas chromatography-mass spectrometry (GC-MS). The extracts (3 μl) were injected into a Hewlett Packard gas chromatograph 5890 A fitted with a 50 m carbowax column 20 M (0.2 mm ID and 0.2 μm film thickness) and equipped with a FID. Nitrogen was used as the carrier gas at a flow rate of 0.35 ml/ min and the GC conditions were as follows: the oven temperature was initially at 60 °C for 10 minutes, then programmed at 5 °C/ min to 180 °C for 5 minutes and at a rate of 10 °C/ min to 220 °C for 15 minutes. Chromatographic peaks were integrated using a SP 4400 chromjet integrator. For the identification of the component peaks, GC-MS analyses were carried out using a VG Masslab 12-250 mass spectrometer (El, 70 eV) coupled to a Hewlett Packard 5790 gas chromatograph programmed under the same condition as above.

8. Effect of The Desert Shrub *Commiphora quadricincta* Schweinf on The Maturation of Immature Adult Males and Females of Gregarious Desert Locust

8.1. Collection of The Desert Shrub *C. quadricincta*

Twigs and leaves of the shrub *C. quadricincta* (Fig.

12), were collected from Klanieb South West Port-sudan, Red Sea Coastal areas in the Sudan in October 1994 before winter rains and in March 1995 after winter rains. The shrubs were interspersed among the other acacia trees and other plant species.

8. 2. Collection of Volatiles from The Desert Shrubs

Volatiles from the plants were collected by steam distillation on the clavenger apparatus (Fig. 13). The plant material was boiled in water and the generated blend of steam and plant volatiles cooled by the condenser and condensed into the clavenger which contained hexane (Fig. 13). The hexane extract was concentrated by Kontes short steam distillation apparatus (Fig. 14) and the crude extract stored at -15 °C until use.

8. 3. Experiment IV: Effect of Crude Steam Distillate Extract of The Desert Shrub *C. quadricincta* on The Maturation of Immature Adult Males and Females of Gregarious Desert Locust

The fledglings were placed in the lower compartment of the bichamber cages as described above and supplied with the food plant, The experimental groups were subjected to the

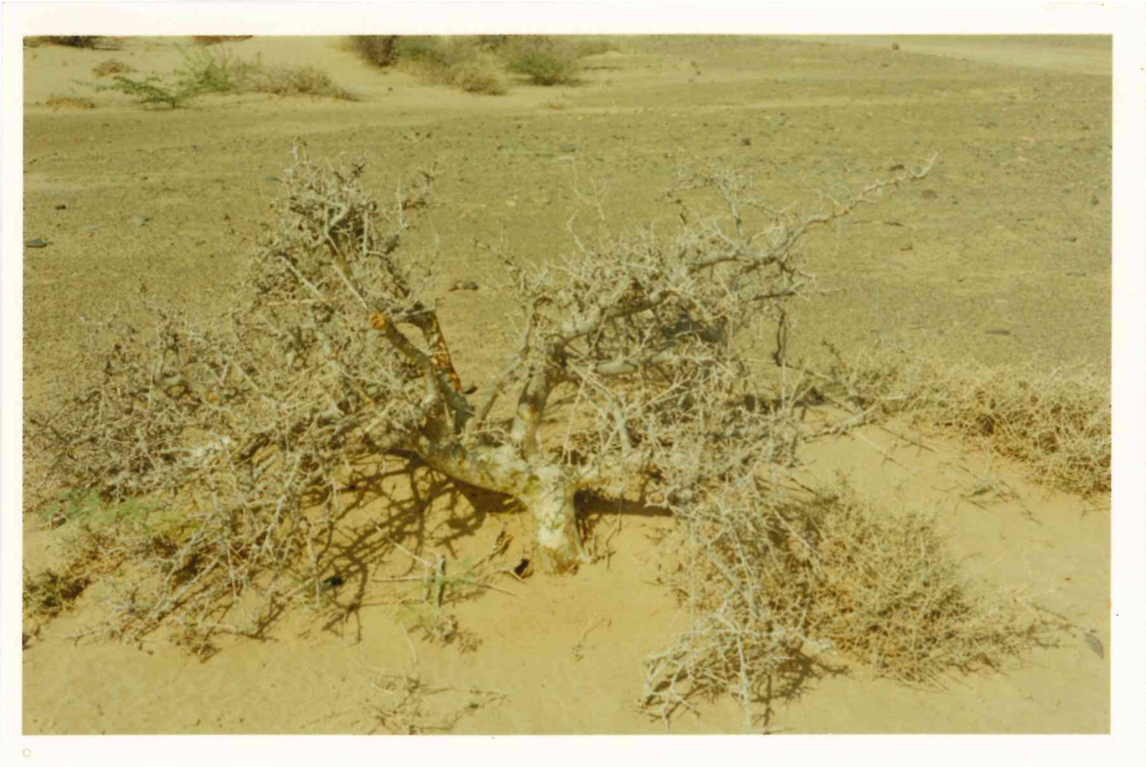


Fig. 12. Desert shrub *Commiphora quadricincta* from the Red Sea Coast, Sudan.

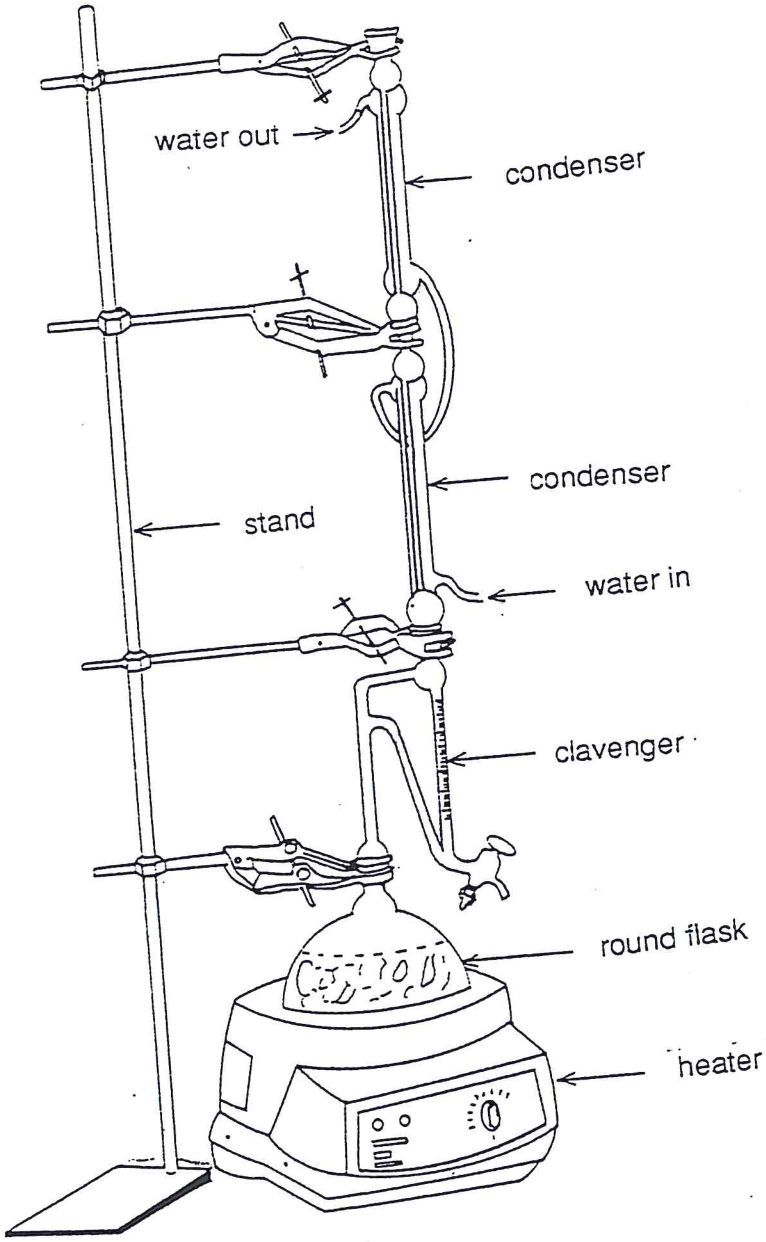


Fig. 13. Apparatus for collecting steam distillate from *C. quadricincta*.

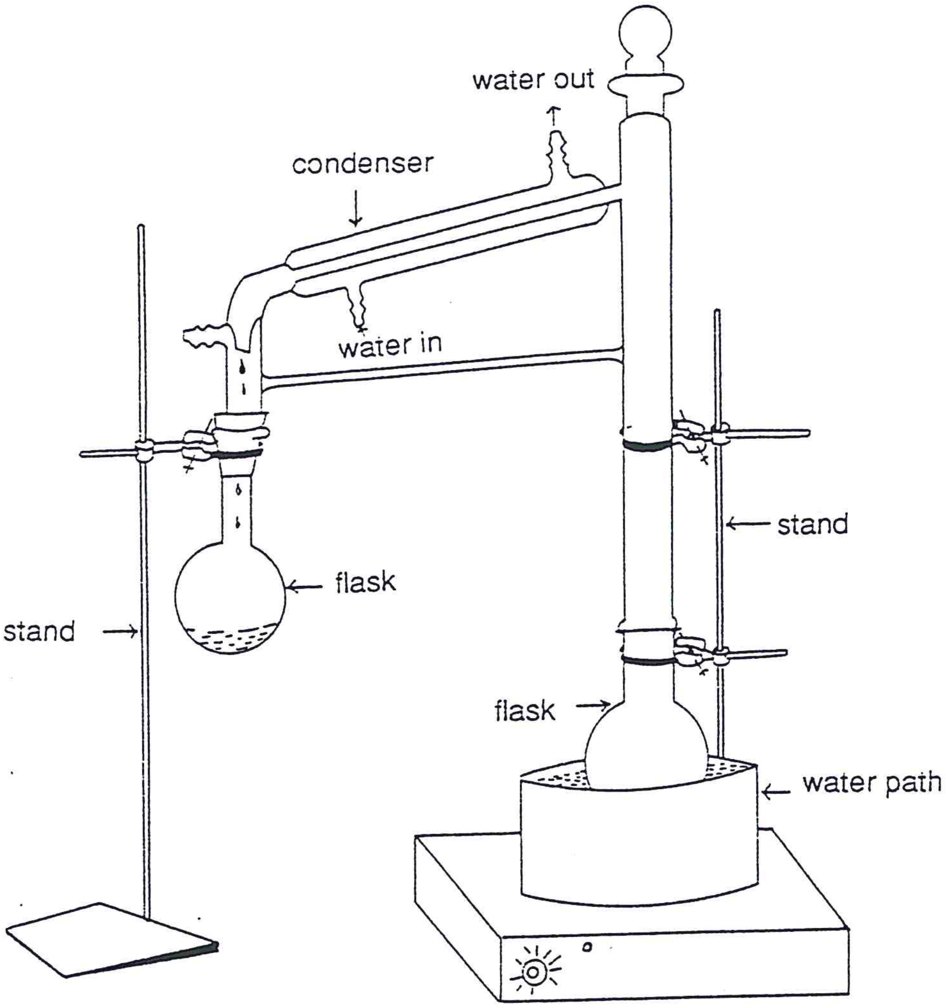


Fig. 14. Kontes short path distillation apparatus for solvent removal from Commiphora spp extract.

same laboratory conditions and precautions were taken to avoid contamination between the groups.

The crude volatile extract before winter rains (see 8.2) was tested for its maturation effects on fledglings (by placing it in the upper compartment of the bichamber referred to as signal source) at the following concentrations: (a) 100 μl (b) 10 μl (c) 0.1 μl (d) 0.001 μl, each in 1000 μl light paraffin oil to moderate the release of the volatiles . In the control bichambers (e) only light paraffin oil (1000 μl) with hexane (100 μl) was used. For comparison purposes mature males were placed in the upper compartment of another set of control bichambers (f). Also, immature adults were used as control. The signal sources and control were placed in the upper compartment, the lower compartment contained immature adults (2-3 days old; i.e. newly moulted). Each set was replicated 4-times and paraffin oil + the signal sources was changed every 3 days. For treatments involving females, additional 5 replicates were set up to allow measurement of lengths of oocytes to be made. The effect of the desert shrub volatiles were assessed by studying the sexual maturation as in Experiment I.

For the extract after winter rains the following concentrations (a) 10 μl and (b) 0.1 μl, were tested.

8. 4. Identification of The Volatiles Extracted from *C. quadricincta*

The crude steam distillate of the plant volatiles were analyzed by gas chromatography (GC) and GC-MS. The extracts (2 µl) were injected into a Hewlett Packard gas chromatograph 5890 A fitted with a 50 m Carbowax 20M column (0.2 mm ID and 0.2 µm film thickness or methyl silicone column (0.2 mm ID and 0.11 µm film thickness) and equipped with a FID. Nitrogen was used as the carrier gas at a flow rate of 0.35 ml/ min and the (GC) conditions were as follows: the oven temperature was initially at 60 °C for 10 minutes, then programmed at 5 °C/ min to 180 °C for 5 minutes and to a rate of 10 °C/ min to 220 °C for 15 minutes or (the oven temperature initially at 60 °C for 5 minutes, then programmed at 3 °C/ min to 200 °C for 15 minutes where a methyl silicone column was used). The peaks were integrated on a SP 4400 chromjet integrator. For the identification of the component peaks, GC-MS analyses were carried out using a VG Masslab 12-250 mass spectrometer (El, 70 eV) coupled to a Hewlett Packard (HP) 5790 gas chromatograph.

Electrophysiologically-active components were isolated by coupled gas chromatography-electroantennography (GC-EAD), performed on both the Carbowax and Methyl silicone columns and employed the same GC conditions as for analyses of the crude extract. The column effluent was split 1:1 into two 50-cm-long deactivated fused silica column connected to the FID and the antenna, respectively. A makeup gas (40 ml/min) was added just before the split point to accelerate the effluent through a deactivated columns. The effluents were driven from the chromatograph through the a transfer line maintained at 150 °C by a THC-3 temperature control unit (Syntech) and into a moistened airstream (4.0 ml/sec, 90% relative humidity, 25 °C) focused onto the antennal preparation via a stainless steel tube (5 mm ID). The return time constant (RC) was set at 2 sec. FID and EAD signals were monitored synchronously using a program on a GC/EAD interface card (Syntech) installed in a PC (Harvard Professional Computer, American Megatrends Inc.).

9. Statistical Analysis

All data collected was subjected to statistical analysis of variance (ANOVA) using SAS (SAS Institute Inc., cary. Nc 27512-8000 USA, 1987). The means were compared by the Least Significant Difference (LSD) test.

RESULTS AND DISCUSSION

1. IMMATURE ADULT MATURATION

A. Maturation Time as Assessed by Colour, Copulation and Oviposition

A. 1. Effect of live fifth instar nymphs

The effect of the fifth instar nymphs (in the presence of visual, tactile and olfactory cues) on the maturation time of the immature males (Experiment I) as monitored by yellowing and copulation, are summarized in tables 1 and 2, and Appens. A and B. The results show that significant delay in the maturation time ($P<0.05$) of the immature males was obtained in all cases independent on the number of fifth instar nymphs used as the signal source. Insects in the controls matured in about 18-20 days whereas those exposed to nymphs took over 30 days to show signs of maturation. On the other hand, in the presence of mature males, the immature males matured in 13.2 days, which represents a significant acceleration relative to the control insects. The times taken by the adult males to develop stage III colour characteristic (as described by Norris, 1954) are well correlated with copulation time; there were no

Table (1). Mean maturation time of immature males in the presence of fifth instar nymphs, mature males, immature females (control) and immature males (control)

Treatment (test insects/signal source)	Maturation Time in Days (X±S.E)		N	*t* Test
	By colour	By copulation		
Imm. ♂ / 5th instar ♂	33.67±0.66 a	34.67±0.67 a	18	NS
Imm. ♂ / 5th instar ♀	30.79±0.74 a	32.32±0.98 a	19	NS
Imm. ♂ / Imm. ♀	19.56±0.39 b	20.22±0.35 b	18	NS
Imm. ♂ / Imm. ♂	18.79±0.28 b	20.05±0.29 b	19	NS
Imm. ♂ / Mat. ♂	13.15±0.24 c	14.55±0.41 c	20	NS

Means with the same letter in column are not significantly different at P=0.05 according to LSD.
NS = Not significantly different between the pair in the row
N = No. of surviving insects at the end of the experiment

Table (2). Mean maturation time of immature males in the presence of fifth instar nymphs (four, two and one), and immature males (control).

Treatment (test insect/signal source)	Maturation Time in Days ($X \pm S.E$)		N	t Test
	By colour	By copulation		
Imm. ♂ / four 5th instar	33.67±0.66 a	34.67±0.67 a	15	NS
Imm. ♂ / two 5th instar	31.47±0.75 a	33.00±1.14 a	15	NS
Imm. ♂ / one 5th instar	33.00±1.14 a	33.27±1.04 a	15	NS
Imm. ♂ / Imm. ♂	20.60±0.47 b	21.27±0.50 b	15	NS

Means with the same letter in column are not significantly different at P=0.05 according to LSD.
NS = Not significantly different between the pair in the row
N = No. of surviving insects at the end of the experiment

significant differences between the two ($p \leq 0.05$); (Table 1). Moreover, there is no significant difference ($p \leq 0.05$) between the retardation effect of fifth instar males and females on the maturation of the immature adult males (Table 1). Interestingly, maturing males in the presence of fifth instar nymphs failed to become bright yellow in colour when compared to the control even after maturation and copulation.

With regard to the immature females reared in the presence and absence of fifth instar, the results of the maturation time as assessed by colour, copulation and oviposition are shown in Table 3 and Appen. C. The results showed that the development of yellow colour of the immature females in the presence of fifth instar (males or females), was delayed significantly ($\approx$22 days) compared to the control (18-19 days). Copulation activity was delayed even longer ($\gtrsim$27 days) which shows that colour change does not, in this case coincide with copulation activity. On the other hand, in the presence of mature males, there was significant accelerated maturation, the recipient insects maturing in about 14 days. Delayed maturation in test insects exposed to immature males and females is also reflected in delayed oviposition (Tables 3).

Table (3). Mean maturation time of immature females in the presence of 5th instar nymphs, mature males, immature females (control) and immature males (control).

Treatment (test insects/signal source)	Maturation Time in Days (X±SE)			N
	By colour*	By copulation*	By oviposition	
Imm. ♀ / 5th instar ♂	22.00±0.23 a	27.25±0.39 a	33.30±0.72 a	20
Imm. ♀ / 5th instar ♀	22.11±0.37 a	27.47±0.58 a	31.00±0.38 b	19
Imm. ♀ / Imm. ♀	18.75±0.18 b	20.00±0.37 b	23.75±0.23 c	20
Imm. ♀ / Imm. ♂	19.16±0.21 b	20.88±0.33 b	23.56±0.49 c	18
Imm. ♀ / Mat. ♂	14.37±0.16 c	11.34±0.21 c	18.37±0.40 d	20

Means with the same letter in a column are not significantly different at P=0.05 according to LSD.
* = Significant difference between times of colour change and copulation for female insects exposed to 5th instar nymphs ($p>0.05$, *t* test).
N = No. of surviving insects at the end of the experiment.

A. 2. Effect of fifth instar faecal volatiles

This set of experiments was aimed at obtaining information on the effect of fifth instar faecal volatiles (pheromonal cues only) on the maturation of immature adult males and females. The mean maturation times of immature males exposed to 1, 3, 6 and 9g of fifth instar faeces as assessed by colour and copulation are summarised in table 4 and Appens. D. The results showed that immature males when exposed to fifth instar faeces, the latter caused colour change to yellow which was observed on the 17^{th}, 17^{th}, 20^{th} and 19^{th} days after fledging, respectively, compared to the control on about 19^{th} days after fledging. There is no significant difference ($p > 0.05$) between experimental insects and the control groups. The same results were obtained when the maturation time was assessed by copulation. Copulation in the immature males exposed to fifth instar faeces was observed on days 18.60, 18.40, 20.20 and 19.30 after fledging, respectively. The control groups copulated on days 19.58 after fledging. On the other hand, immature males exposed to fifth instar nymphs as signal source (pheromonal cues only) showed significant delay in the maturation time ($p \leq 0.05$). Insects in the controls matured in about 20 days whereas those exposed to nymphal volatiles took 33 days to show signs of maturation (Table

Table (4). Mean maturation time of immature males and females exposed to 5th instar nymphs, (1, 3, 6 and 9g) of 5th instar nymphal faeces and immature males.

Treatment (test insects/signal source)	Maturation Time * in Days (X±S.E) By colour	Maturation Time * in Days (X±S.E) By copulation	N	*t* Test
Imm. ♂ /5th instar nymphs	33.40±0.30a	33.65±0.32 a	20	NS
Imm. ♂ /5th instar faeces(1g)	17.63±0.55c	18.05±0.55 c	19	NS
Imm. ♂ /5th instar faeces(3g)	17.84±0.32c	18.37±0.38 bc	19	NS
Imm. ♂ /5th instar faeces(6g)	20.00±0.85b	20.15±0.81 b	20	NS
Imm. ♂ /5th instar faeces(9g)	19.16±0.28bc	19.26±0.27 bc	20	NS
Imm. ♂ / Imm. ♂	19.53±0.46bc	19.58±0.44 bc	40	NS

Means with the same letter in a column are not significantly different at P=0.05 according to LSD.
* = No significant difference between maturation times by colour and copulation ($p>0.05$, *t* test).
N = No. of surviving insects at the end of the experiment.

4). Similarly, no significant difference ($p > 0.05$) was detected. The results showed that immature females when exposed to fifth instar faeces (1, 3 and 6g), the latter caused colour changes which was observed on the 19th, 20th and 21th days after fledging, respectively, compared to the control on about 20th days after fledging. There is no significant difference ($p > 0.05$) between experimental insects and the control groups with regard to the maturation time of females exposed to faeces (3g and 6g) as assessed by colour changes. Copulation in immature females exposed to fifth instar faeces was observed on days 20.60, 20.60 and 21.40 after fledging, respectively. The control groups copulated on days 21.30 after fledging. The same results were obtained when the maturation time was assessed by oviposition (Table 5 and Appens. E).

A. 3. Effect of fifth instar nymphal volatiles extracts

The effects of fifth instar nymphs trapped volatiles extract (pheromonal cues only) on the maturation of the immature adult males and females are summarised in table 6 and Appen. F. These results show that the mean maturation time of the immature males, as assessed by their colour and copulation, are about 34 and 35 days after fledging, respectively, compared to significantly earlier maturation

Table (5). Mean maturation time of immature females exposed to 5th instar nymphs, (1, 3 and 6g) of 5th instar nymphal faeces and immature males.

Treatment (test insects/signal source)	Maturation Time * in Days (X±S.E)			N
	By colour	By copulation	By oviposition	
Imm. ♀ /5th instar nymphs	33.40±0.30a	35.35±0.24 a	37.45±0.54 a	20
Imm. ♀ /5th instar faeces(1g)	19.57±0.27d	20.61±0.22 c	23.04±0.17 c	23
Imm. ♀ /5th instar faeces(3g)	20.17±0.22c	20.57±0.25 c	23.17±0.17 bc	23
Imm. ♀ /5th instar faeces(6g)	21.03±0.14b	21.37±0.14 b	23.82±0.13 b	29
Imm. ♀ / Imm. ♀	20.73±0.14bc	21.33±0.14 b	23.80±0.15 b	30

Means with the same letter in a column are not significantly different at P=0.05 according to LSD.
* = No significant difference between maturation times by colour and copulation ($p>0.05$, *t* test).
N = No. of surviving insects at the end of the experiment

in the control treatments (22 and 23 days, respectively); (p= 0.0001).

Table 6 (Appen. G. summarises results obtained when immature females were exposed to the fifth instar trapped volatiles extract. Again, mean maturation times of the immature females which were exposed to the trapped volatiles extract were 34.20 days by colour (control 17.7 days) and 36.40 days by copulation (control 19.5 days). Delayed maturation is also reflected in oviposition time which took 38.70 days (control 22.8).

The present study confirms the maturation-retarding effect of nymphs previously observed by Norris (1962, 1964; see also Richards and Mangoury, 1968), and demonstrates conclusively that it is associated with the volatiles emitted by fifth instar nymphs (Tables 1 and 3). In view of previous observations on the similarity in the volatiles of 2nd to 5th instar nymphs, a similar effect may be expected from the other instars (Obeng-Ofori, *et al.*, 1993). The signal involved appears to be quite potent and no significant reduction in its effect occurred even when the proportion of nymphs to young adults was reduced from 1:1 to 1:4 in bioassays (Table 2). It has been suggested that in nature the retarding influence of hoppers tends to delay the maturation of the early fledgers until the majority of the nymphs have completed development and moulted into adults

Table (6). Mean maturation times of immature males and females exposed to trapped volatiles of nymphs (5th instar) and 5th instar nymphs.

Treatment (test insects/signal source)	Maturation Time * in Days (X±S.E)			N
	By colour	By copulation	By oviposition	
Imm. ♂ /volatiles in CH2Cl2/paraffin	34.89±1.17a	35.00±1.15 a		18
Imm. ♂ /5th instar nymphs(mixed sexes)	33.40±0.30a	33.65±0.32 a		20
Imm. ♂ /control (CH2Cl2/paraffin)	22.32±0.51b	22.63±0.43 b		19
Imm. ♂ / Imm. ♂	20.80±0.69b	21.15±0.65 b		20
Imm. ♀ /volatiles in CH2Cl2/paraffin	34.17±1.10a	36.39±0.84 a	38.70±0.77 a	23
Imm. ♀ /5th instar nymphs(mixed sexes	33.40±0.30a	35.35±0.24 a	37.45±0.54 a	20
Imm. ♀ / Imm. ♀	18.70±0.29b	19.49±0.31 b	22.83±0.20 b	24
Imm. ♀ /control (CH2Cl2/paraffin)	17.70±0.29b	19.49±0.31 b	22.83±0.20 b	23

Means with the same letter are not significantly different at P=0.05 according to LSD.

* = No significant difference between maturation times by colour and copulation ($p>0.05$, *t* test).

N = No. of surviving insects at the end of the experiment

(Norris, 1962, 1964; and Richards and Mangoury, 1968). In time, an increasing number of male adults would start to produce the adult pheromone, which would accelerate the maturation of other adults, resulting in maturation synchrony of the entire population (Norris, 1962; Norris and Pener, 1965; and Mahamat, *et al.*, 1993). This would result in simultaneous mating and facilitate communal oviposition critical for spatial and temporal cohesiveness of the progeny (Popov, 1958; Norris, 1963; and Mahamat, *et al.*, 1993).

The results of this study also parallel those reported earlier which demonstrated a parsimonious role for the adult pheromone: as an adult aggregant (a releaser effect) and as a maturation accelerant (a primer effect) for young males and females (Mahamat, *et al.*, 1993; and Torto, *et al.*, 1994). In the present case, the results suggest that the same volatile emission shown earlier to act as a nymphal aggregant (Obeng-Ofori, *et al.*, 1993) is a maturation retardant for the young adults. Whether common constituents are involved in the releaser and primer activities remain to be established. Both nymphal sexes are equally effective in inducing retardation of maturation (Tables 1 and 3) consistent with the previous finding that there is no sex differentiation in the production of the nymphal pheromone (Obeng-Ofori, *et al.*, 1994b). This is unlike in the adults where only the males produced the pheromone (Mahamat, *et* *al.*, 1993; Torto, *et al.*, 1994; and Obeng-Ofori, *et al.*, 1994b).

Since adults of whatever development stage are behaviourally indifferent to the nymphal pheromone (Obeng-Ofori, *et al.*, 1993) the manner by which the latter exerts its influence on the young adults merits a special comment. It has been shown that although young adults do not emit significant aggregation signals of their own, they nevertheless aggregate strongly in response to volatiles of nymphal faeces and those of their own (Obeng-Ofori, *et al.*, 1994a). In field observations, we have found invariably large amounts of faecal droppings on areas where nymphs and fledglings co-occur. Volatiles derived from these two sources, unlike those from older and mature adults, are compositionally identical and consist of guaiacol and phenol (confirmed also by the present study, Appen. H) which account largely for the activity of the faeces (Obeng-Ofori, *et al.*, 1994a). This explains the close association of nymphs and young adults in the field when the former are fledging (Uvarov, 1977). In the present study, the results show that nymphal faecal volatiles have no measurable influence on the maturation of young adults (Table 4). Thus, the maturation retarding influence would end once most nymphs have moulted into fledglings when these are exposed only to faecal volatiles.

B. Effect on Pheromone (phenylacetonitrile) Production in Males

B. 1. Effect of live fifth instar nymphs

Figure 15 shows that there is a significant difference between experimental groups and the control groups in terms of the phenylacetonitrile titres emitted by the recipient insects compared to that of the control. These results show that the emissions of this pheromone compound was delayed, and the amount produced was lower in the recipient insects than that of the control.

B. 2. Effect of fifth instar faecal volatiles

Figure 16 shows that the effect of 1, 3, 6 and 9g of fifth instar faecal volatiles on phenylacetonitrile titres. The results show that no significant difference between the treatments and the control, and there is no effect in the amount produced by the recipient insect and the control.

B. 3. Effect of fifth instar nymphal volatile extracts

Figure 17 shows that there is a significant difference between experimental groups and the control groups in terms of the phenylacetonitrile titres. The results show that

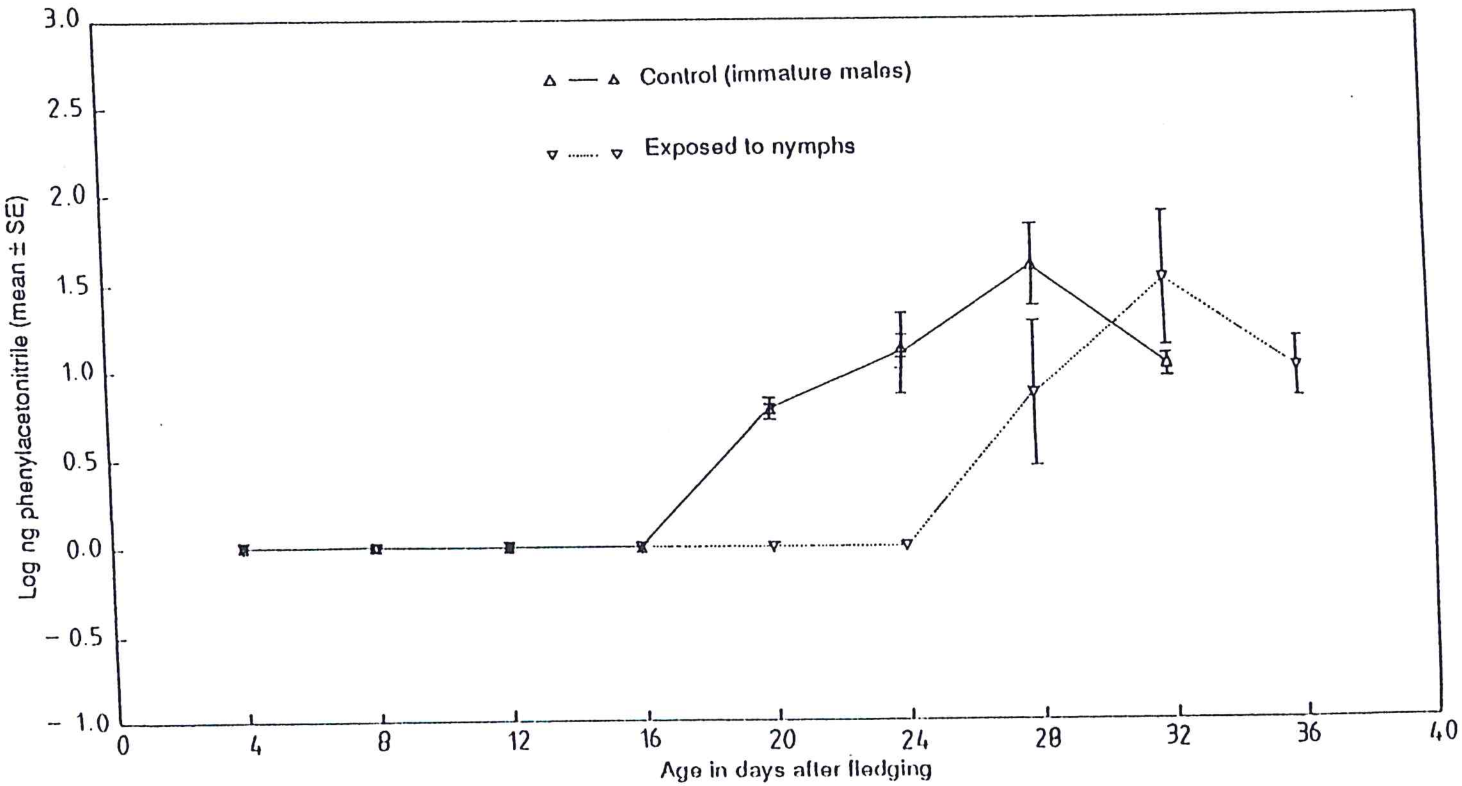


Fig. 15. Phenylacetonitrile produced by immature males in the presence of 5th instar nymphs and control (immature males).

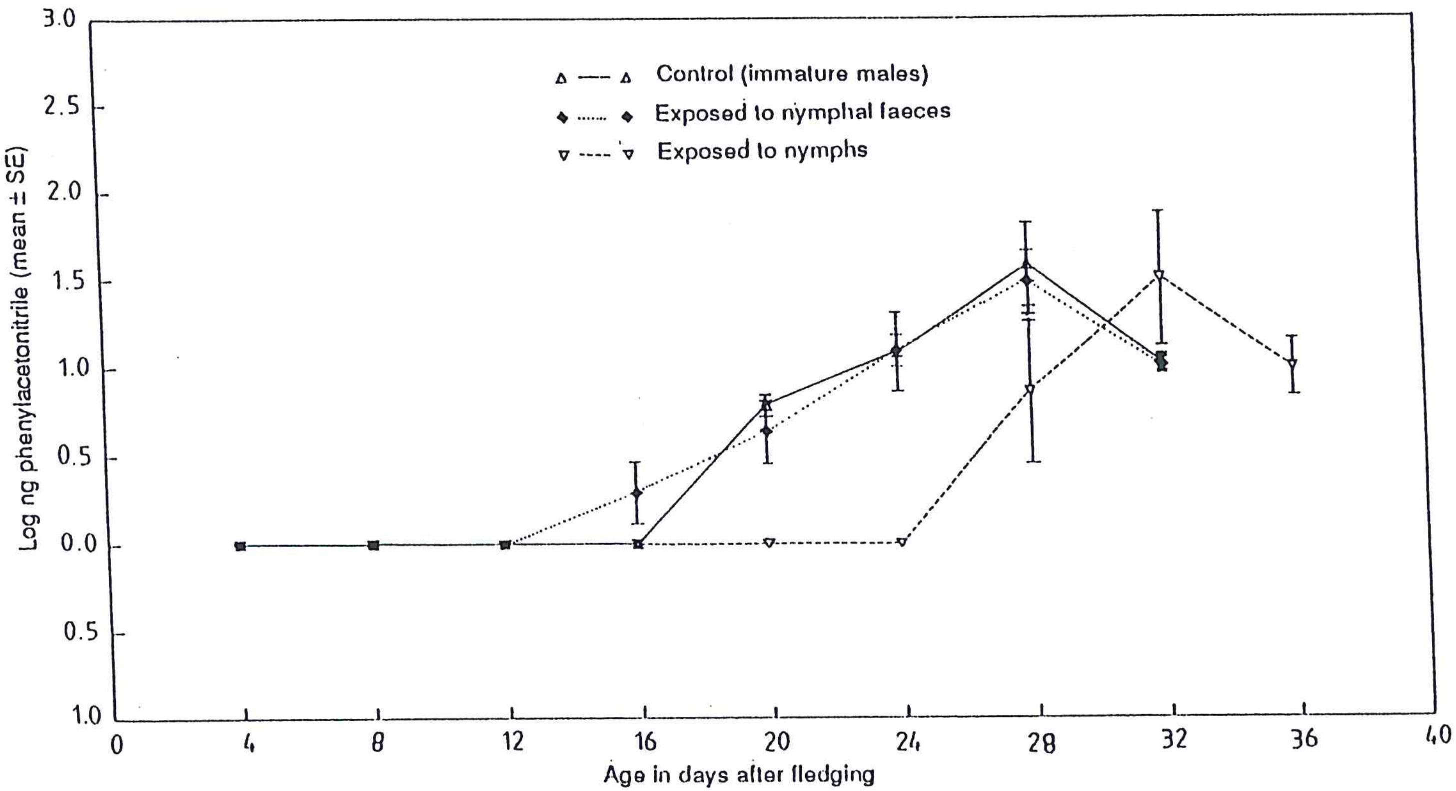


Fig. 16. Phenylacetonitrile produced by immature males exposed to 5th instar nymphs, 5th instar faeces and control (immature males).

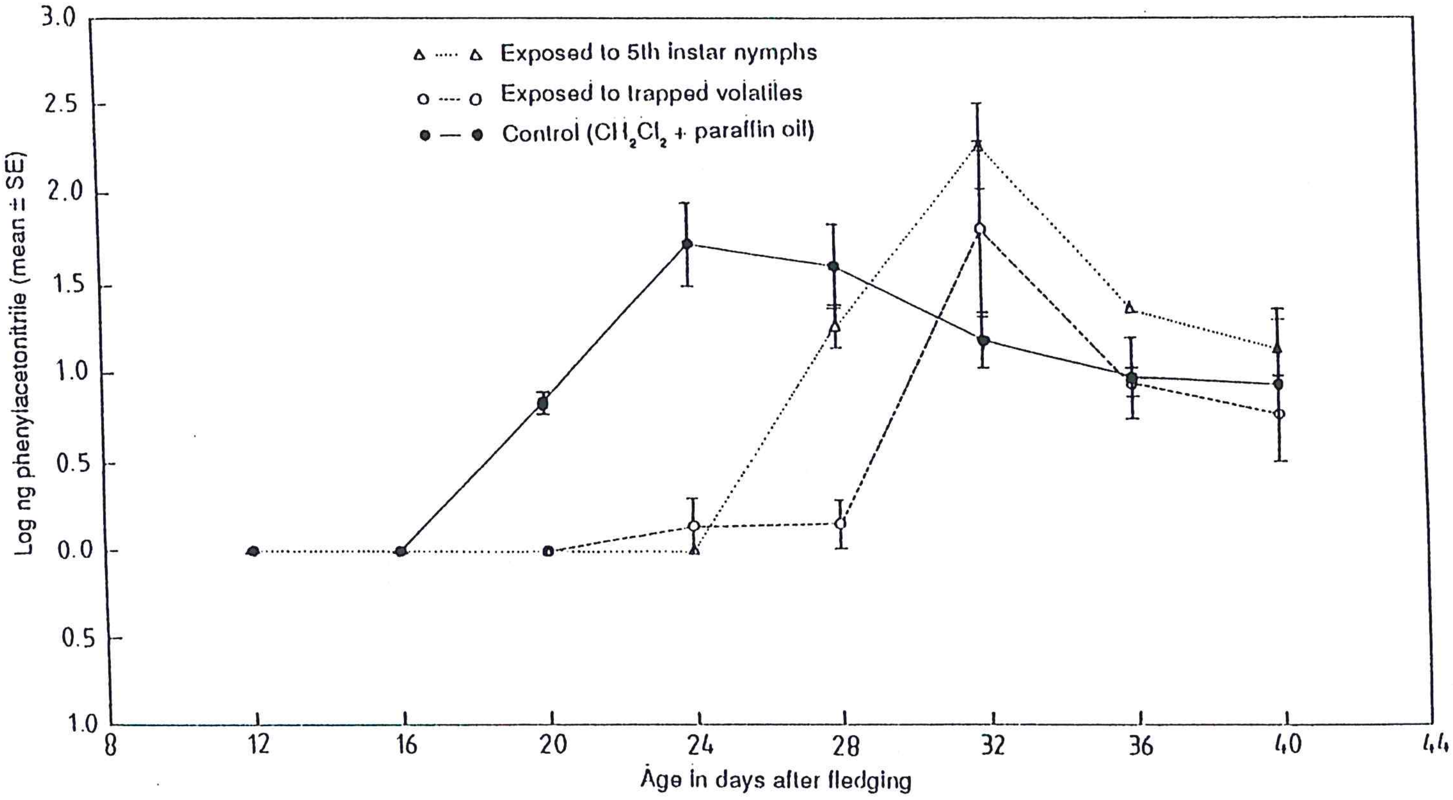


Fig. 17. Phenylacetonitrile produced by immature males exposed to 5th instar nymphs, 5th instar nymphs trapped volatiles and control (CH_2 Cl_2 + paraffin oil).

phenylacetonitrile emission was delayed and the amount produced is somewhat lower in the recipient insects than that in the control reaching the highest level 32 days after fledging.

These results provide further insight into the way maturation synchrony may be achieved in a gregarising population. They show that associated with the delay in maturation in young males continuously exposed to nymphal volatiles is a delay in the production of the adult pheromone as measured by phenylacetonitrile titres (Fig. 15). No such effect was noticed when the insects were exposed to the nymphal faecal volatiles (Fig. 16). Since the adult pheromone is both an aggregating signal in the adult and a maturation accelerant for young males and females (Mahamat, *et al.*, 1993; Torto, *et al.*, 1994), a delay in its production means a further delay in the maturation of early fledgers. In earlier stages of gregarization, when locust populations may not have attained a high degree of developmental synchrony, early fledgers may co-exist with not only the final nymphal stadium at different stages of development, but also with earlier stadia. Consequently, their maturation would be slowed down not only by their prolonged contact with hoppers, but also by the resulting delay in the production of the adult pheromone. However, as the population develops greater synchrony, contact with nymphs would become shorter and the adult pheromone would be produced earlier. The role of the two pheromone systems would be then increasingly reduced to fine-tuning the synchronization process.

C. Effect on Ovulation and Number of Eggs/pod in Females

C. 1. Effect of live fifth instar nymphs

In order to compare the reproductive development and potential of females reared in the presence and absence of fifth instar nymphs the following parameters were measured: (a) the length of the basal oocytes from day 12 up to the end of the first or second gonotrophic cycle (Fig. 18); and (b) the number of oviposited eggs per pod (Table 7). The results showed that the length of terminal oocytes of the immature females, reared in the presence of fifth instar nymphs, exhibited a longer gonotrophic period with the first mature oocytes being detected 38 days after fledging compared to 22 days in the control insects (Fig. 18). On the other hand, in the presence of the mature males the first gonotrophic cycle took significantly shorter time and lasted 16 days after fledging. In the case of the number of eggs per pod, the results showed that there is no significant difference ($p > 0.05$) between the treated and the control. Thus, despite delayed maturation, there is no effect on the reproductive capabilities of the immature females reared in

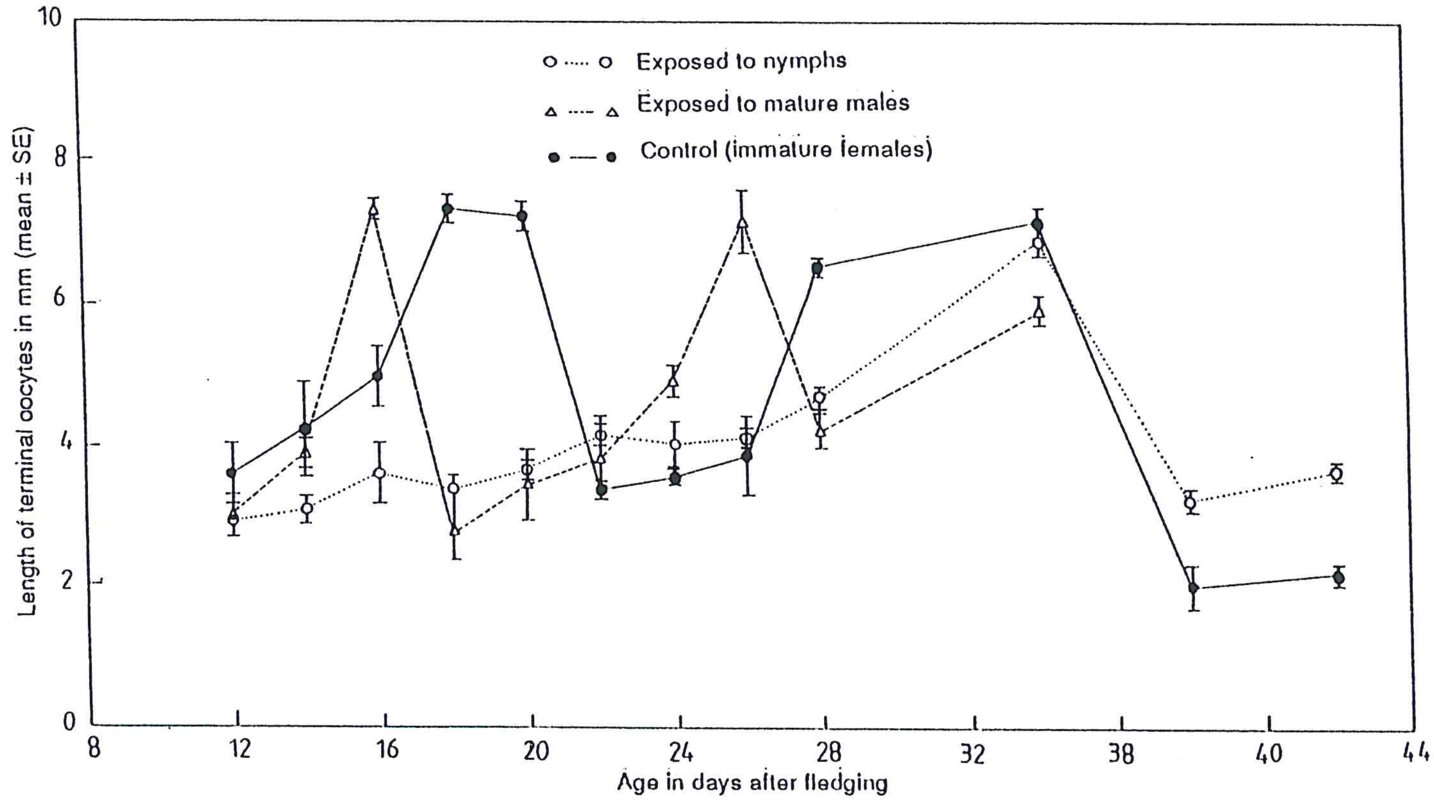


Fig. 18. Length of terminal oocytes of immature females in the presence of 5th instar nymphs, mature males and control (immature females).

Table (7). Mean number of eggs per pod of immature females in the presence of 5th instar nymphs, mature males, immature males and females (control).

Treatment (test insects/signal source)	Eggs/pod/female±S.E	N
Imm. ♀ / 5th instar nymphs	44.31±4.16 a	16
Imm. ♀ / imm. ♀ (control)	44.44±2.12 a	16
Imm. ♀ / imm. ♂ (control)	39.56±2.64 a	16
Imm. ♀ / mat. ♂	44.62±2.62 a	16

Means with the same letter in column are not significantly different at $P=0.05$ according to LSD.
N = No. of eggs pod counted for each treatment of the experiment

the presence of fifth instar nymphs. These results confirm the maturation-retarding effect of nymphs and maturation-accelerating effect of mature males on the maturation of the immature males and females; there being no significant difference of the effect of the presence of fifth instar nymphs on the maturation of immature adults of both sexes.

C. 2. Effect of fifth instar faecal volatiles

Figure 19 shows the effect of the fifth instar faecal volatile on the length of oocytes during development. The results indicate that faecal volatiles have no effect on oocytes growth when compared to the control. With regard to the number of eggs per pod the results showed that there is no significant difference ($p > 0.05$) between the treated and the control (Table 8).

C. 3. Effect of fifth instar nymphal volatile extracts

Figure 20 shows that the change in oocyte length and the ovarial development of the immature females which were exposed to the fifth instar nymphal volatiles extracts were delayed to a significant extent when compared to those of the control. In the case of the number of eggs per pod the results (Table 9) showed that there is no significant difference ($p > 0.05$) between the treated and the control.

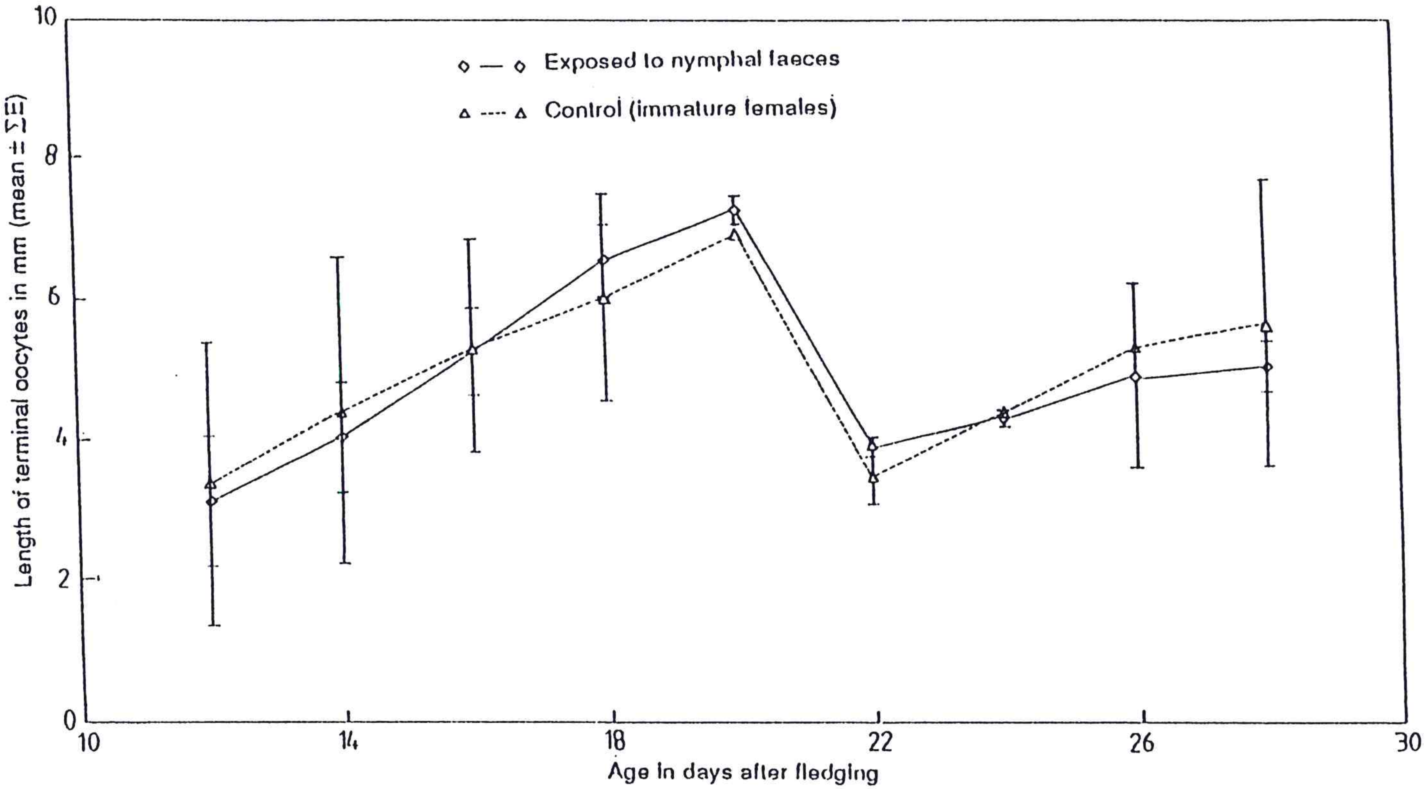


Fig. 19. Length of terminal oocytes of immature females exposed to 5th instar faeces and control (immature females).

Table (8). Mean number of eggs per pod of immature females exposed to 5th instar faeces and immature females (control).

Treatment (test insects/signal source)	Eggs/pod/female±S.E	N
Imm. ♀ / 5th instar faeces (1g)	56.25±1.58 a	16
Imm. ♀ / 5th instar faeces (3g)	55.75±4.07 a	16
Imm. ♀ / 5th instar faeces (6g)	49.00±3.57 a	16
Imm. ♀ / Imm. ♀	48.00±1.88 a	16

Means with the same letter in column are not significantly different at P=0.05 according to LSD.
N = No. of eggs pod counted for each treatment of the experiment

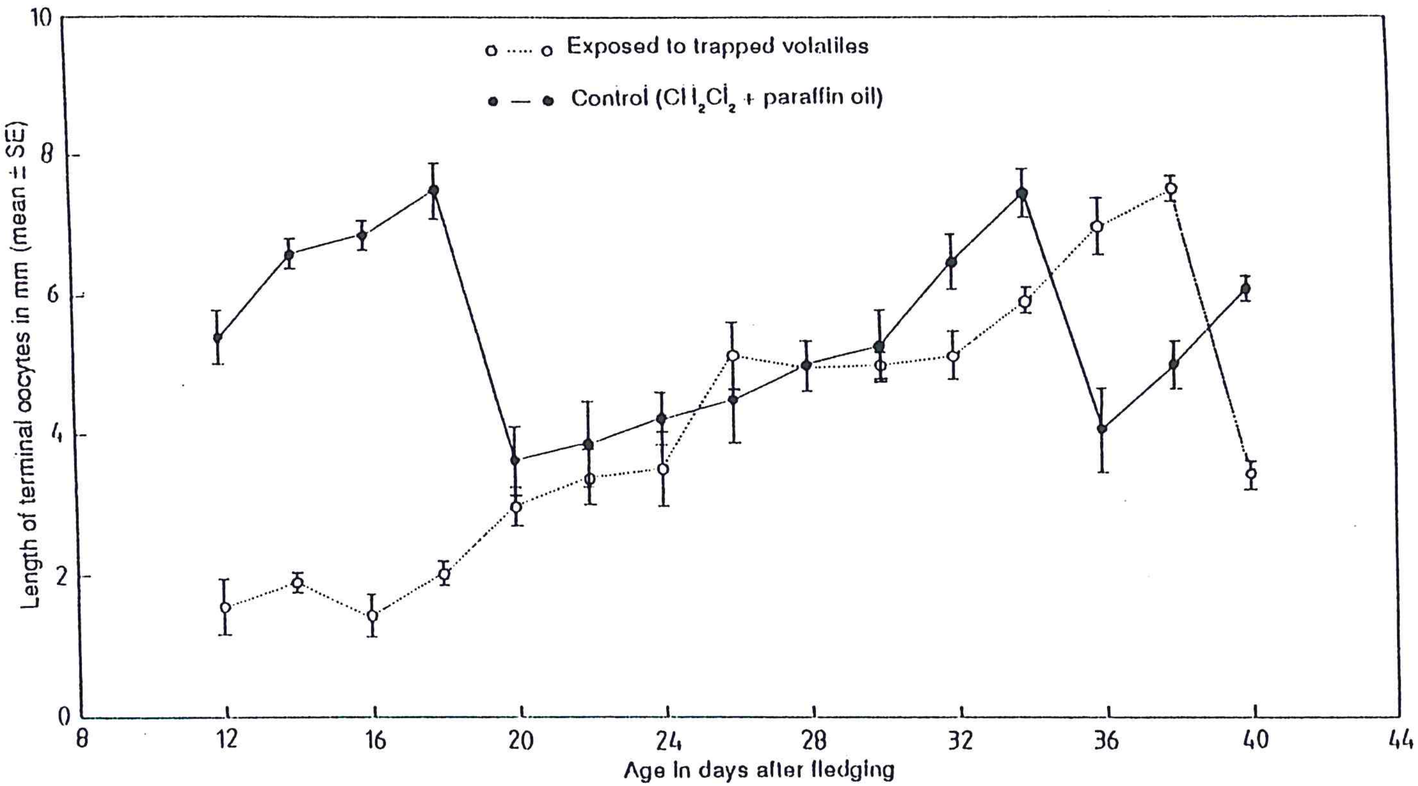


Fig. 20. Length of terminal oocytes of immature females exposed to 5th instar nymphs trapped volatiles and control (CH_2 Cl_2 + paraffin oil).

Table (9). Mean number of eggs per pod of immature females exposed to 5th instar trapped volatiles, paraffin oil + dichloromethane (control).

Treatment (test insects/signal source)	Eggs/pod/female±S.E	N
Imm. ♀ / 5th instar volatiles	53.56±4.92 a	9
Imm. ♀ / Control(CH_2Cl_2+paraffin oil)	60.56±2.21 a	9

Means with the same letter in column are not significantly different at P=0.05 according to LSD.
N = No. of eggs pod counted for each treatment of the experiment

The results showed that there is no effect on the reproductive capabilities of the immature females exposed to the fifth instar trapped volatile extract compared to the control. These results confirm the volatile nature of the pheromone and its effectiveness in the absence of visual and tactile cues.

Thus, delay in maturation in females in the presence of nymphal volatiles is reflected in colour changes, mating and oviposition time (Table 3 and 6), as well as in ovarial development (Figs. 18, and 20). Thus, the growth of oocytes of females reared in the presence of nymphs and their volatile extracts exhibited a relatively longer gonotrophic cycle with the first mature oocytes being found 38 days after fledging. That of control females lasted only 22 days and those exposed to mature males exhibited even a shorter cycle of 16 days reflecting, in this case, an accelerated development of oocytes. However, those exposed to fifth instar faecal volatiles were not affected (Fig. 19).

2. Identification of The Gregarious Fifth Instar Nymphal Volatiles

Fifth instar nymphs trapped volatiles were analyzed by GC as shown in (Fig. 21). The trapped volatiles were then submitted to a structural analysis by coupled gas chromatography-mass spectrometry (GC-MS). The results are

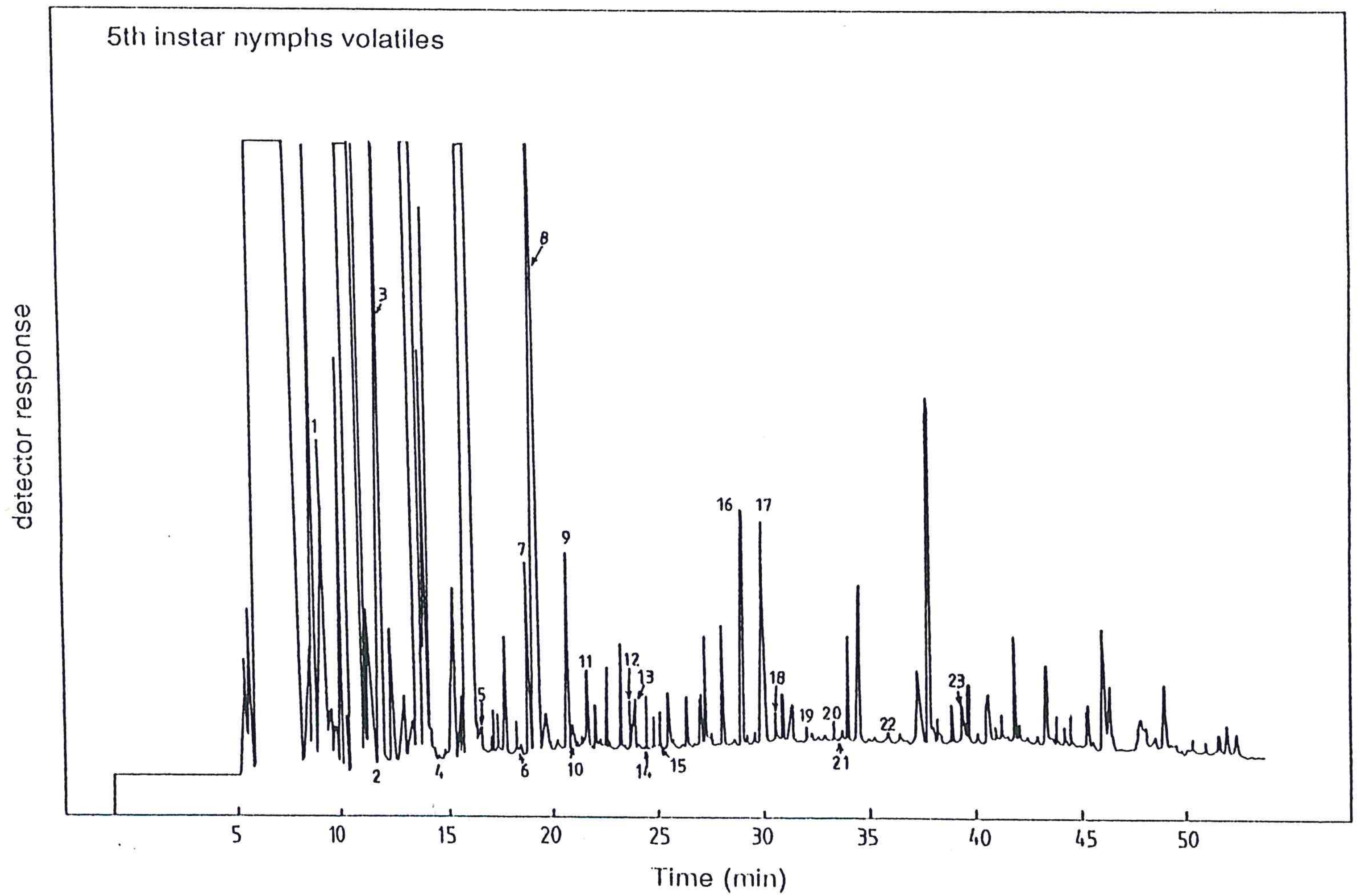


Fig. 21. Gas chromatogram of volatiles collected from gregarious fifth instar nymphs of *S. gregaria*. injected onto a 50-m Carbowax 20 M capillary column.

summarised in (Table 10). About 23 compounds were identified, six of the twenty three visible products on the GC chromatogram (Fig. 21) were linear carboxylic acids: isobutyric acid, hexanoic acid, heptanoic acid, octanoic acid, nonanoic acid and decanoic acid. The remaining peaks were the ketones of the above acids and other cyclic compounds (Table 10). The mass spectrum obtained for the peaks visible in GC (Fig. 21) gave mass spectra characteristic of the following: isobutyric acid, m/z (rel-intensity) at 102(100), 48, 50, 60, 63, 97 and 99(99), 96(45), 38 and 83(34), 85(24), 94(19), 66(15), 70(10), 72(6); *p*-xylene, m/z (rel-intensity) at 91(100), 106(53), 39 and 75(30), 77(23), 70 and 110(10), 51(8), 79 and 103(6); *m*-xylene, m/z (rel-intensity) at 91(100), 106(53), 39 and 77(13), 51(11), 63, 65, 79 and 103(8); styrene, m/z (rel-intensity) at 104(100), 78(42), 50(13), 43, 93 and 103(8); *n*-octanal, m/z (rel-intensity) at 43(100), 41(70), 57(53), 55(44), 84(32), 39(29), 69(23), 67 and 81(15), 100(10), 71 and 95(8); anisole, m/z (rel-intensity) at 108(100), 65(82), 78(76), 39(36), 51(17), 79(17), 93(15), 63(12), 50(11), 38(10); 3-hexen-1-ol,m/z (rel-intensity) at 41(100), 67(61), 55(43), 38(37), 100(25), 82(9), 85(6); nonanal, m/z (rel-intensity) at 57(100), 41(71), 70 and 98(23), 82(19), 95(15), 67(14), 54(11), 87(6); *n*-decanal, m/z (rel-intensity) at 41(100), 57(94), 70(43), 82(40), 67(29), 112(23), 95(22), 54(17), 128(6); benzaldehyde, m/z (rel-

Table (10). Compounds identified in 5th instar nymphal volatiles

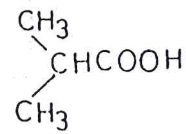
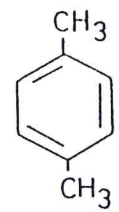
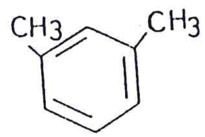
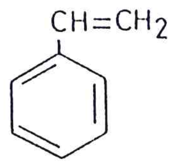
No.	name	Structure
1	Isobutyric acid	
2	*p*-Xylene	
3	*m*-Xylene	
4	Styrene	

Table (10). Contd.

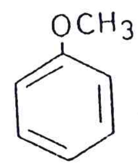
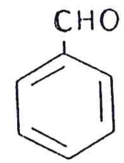
NO.	name	Structure
5	Octanal	$CH_3(CH_2)_6CHO$
6	Anisole	
7	3-Hexen-1-ol	$HOCH_2CH_2CH{=}CH\,CH_2CH_3$
8	Nonanal	$CH_3(CH_2)_7CHO$
9	Decanal	$CH_3(CH_2)_8CHO$
10	Benzaldehyde	

Table (10). Contd.

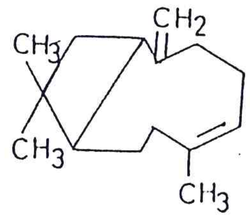
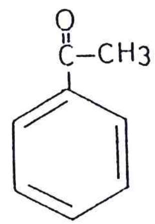
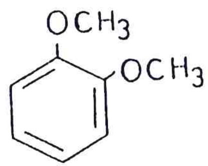
No.	name	Structure
11	2-Butyl-1-Octanol	$CH_3(CH_2)_3\overset{(CH_2)_5CH_3}{\overset{\vert}{C}H}CH_2OH$
12	Caryophyllene	
13	Undecanal	$CH_3(CH_2)_9CHO$
14	Acetophenone	
15	Veratrole	

Table (10). Contd.

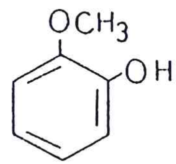
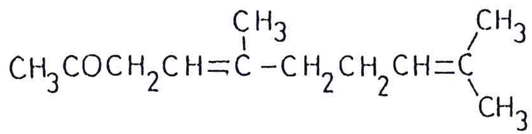
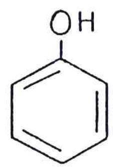
No.	name	Structure
16	Hexanoic acid	$CH_3(CH_2)_4\,COOH$
17	Guaiacol	
18	Geranylacetone	
19	Heptanoic acid	$CH_3(CH_2)_5\,COOH$
20	Phenol	

Table (10). Contd.

No.	name	Structure
21	Octanoic acid	$CH_3(CH_2)_6COOH$
22	Nonanoic acid	$CH_3(CH_2)_7COOH$
23	Decanoic acid	$CH_3(CH_2)_8COOH$

intensity) at 77(100), 106(88), 105(84), 51(48), 50(27), 78(17), 76(17), 52(11), 39(7); 2-butyl-1-octanal, m/z (rel-intensity) at 57(100), 43(76), 71(51), 85(37), 39 and 99(11), 67(8), 127(6); carophyllene, m/z (rel-intensity) at 41(100), 93(88), 69, 79 and 91(60), 81 and 133(56), 67(50), 105(48), 107(47), 39 and 55(40), 53 and 119(38), 161(37), 147(36), 65 and 189(20), 175(10), 51 and 204(8) ; undecanal, m/z (rel-intensity) at ; acetophenone, m/z (rel-intensity) at ; veratrole, m/z (rel-intensity) at 138(100), 95(64), 77(54), 123(42), 65(28), 52(28), 41(22); hexanoic acid, m/z (rel-intensity) at 60(100), 73(43), 41(38), 55(20), 87(13); guaiacol, m/z (rel-intensity) at 109(100), 81(68), 124(64), 53(12), 40(10), 34 and 51(8); geranylacetone, m/z (rel-intensity) at 43(100), 69(42), 107(13), 136 and 151(11), 39(10), 53, 83, 93 and 125(6); heptanoic acid, m/z (rel-intensity) at 60(100), 73(99), 41(72), 88(67), 55(50), 101(19), 116(11), 69 and 177(10), 83(8), 97(6); phenol, m/z (rel-intensity) at 94(100), 66(36), 34(29), 65(27), 40(18), 55 and 38(17); octanoic acid, m/z (rel-intensity) at 60(100), 73(59), 41(53), 55(38), 101(23), 85(20), 69(13), 115(10); nonanoic acid, m/z (rel-intensity) at 60(100), 73(70), 41(54), 55(48), 69 and 129(20), 115(16), 87 and 98(13), 83(8); decanoic acid, m/z (rel-intensity) at 60(100), 73(72), 41(62), 55(60), 129(36), 69(23), 87(21), 83(14), 97 and 115(10), 101(8), 135 and 156(7) (Appen. I).

Most of these identified compounds have been previously reported as components of emissions from a wide variety of plant residues (Bradow, 1991). Some are highly inhibitory to seed germination (Bradow, 1991). The C_7 and C_8 compounds were the most inhibitory, and of the different classes of chemicals the 2-alkenals were the most inhibitory, followed by the 2-alkenols, n-alkanals and 2-alkanones, which were equally effective as seed germination inhibitors; the straight-chain alkanes and alkanoic acids were relatively non-inhibitory. Bardow (1991) found that the aldehydes were most effective in preventing onion seed germination during the seven day incubation. After the seven day exposure, (E)-2-hexenal, 2-heptanol, and three C_7 aldehydes, 2-octanol, (*n*)-octanal, (E)-2-octenal, 2-octanone, 2-nonanone, and *n*-nonanal caused the most inhibition of carrot seed germination.

Most of these compounds which were identified in fifth nymphal volatiles were either totally absent in the chromatogram of trapped adult volatiles or present only in trace amounts. However, about five compounds identified in fifth nymphal volatiles were also identified in mature male volatiles (anisole, benzaldehyde, veratrole, guaiacol, and phenol), but no phenylacetonitrile which is present in about 80% in mature males volatiles (Mahamat *et al.*, 1993; Obeng-Ofori *et al.*, 1994a and Torto *et al.*, 1994). Obeng-Ofori *et* *al.* (1994a) demonstrated that two distinct releaser pheromone systems mediate the aggregation propensity of the insect: a juvenile pheromone produced by nymphs and specific to nymphs and an adult pheromone specific to adult. The present study implicates the same pheromone blend in a parsimonious role as nymphal aggregation pheromone signal and as an anti-maturation pheromone signal.

The compounds that are important in maturation retardation were not identified in this study in view of the large numbers of compounds involved and the possibility of a synergistic effect of different components. A substraction bioassay with blends of major components might lead to the identification of the important components.

3. Effect of *C. quadricincta* Crude Steam Distillate Extracts on The Maturation of Immature Adult Males and Females

3. 1. Maturation time as assessed by colour, copulation and oviposition

The effects of *C. quadricincta* crude steam distillate extracts obtained before and after winter rains on the maturation of immature males are summarised in Table 11. Significant, but different responses, were obtained at the doses ranging from 0.1 μl and 10 μl for the two extracts (Table 11 and Appen. J). Significant accelerated maturation

Table (11). Mean maturation time of the immature males exposed to the different doses of crude extract of *Commiphora quadricincta* before and after the winter rains, mature males and paraffin oil+n-hexane (control).

Treatment (test insect/signal source)	Maturation Time in Days (X±S.E)		N	*t* Test
	By colour	By copulation		
Imm. ♂ / Control (Hexane+paraffin oil)	22.67±0.71 a	23.07±0.83 a	15	NS
Imm. ♂ / 0.1μl crude extract (AWR)	18.85±0.49 b	19.50±0.55 b	20	NS
Imm. ♂ / 0.001μl crude extract (BWR)	15.55±0.84 c	16.55±0.84 c	20	NS
Imm. ♂ / 100μl crude extract (BWR)	15.25±0.10 c	16.05±0.15 c	20	NS
Imm. ♂ / 10μl crude extract (AWR)	14.50±0.11 cd	15.05±0.17 cd	20	NS
Imm. ♂ / 10μl crude extract (BWR)	14.50±0.80 cd	15.50±0.77 cde	20	NS
Imm. ♂ / 0.1μl crude extract (BWR)	13.50±0.38 cd	14.25±0.30 de	20	NS
Imm. ♂ / Mat. ♂	13.00±0.36 d	13.75±0.30 e	20	NS

Means with the same letter are not significantly different at $P=0.05$ according to LSD.
NS = Not significantly different between the pair in the row
N = No. of surviving insects at the end of the experiment
BWR= before winter rains, AWR= after winter rains.

was observed in immature adults exposed to the *C. quadricincta* extract before winter rains at 0.1 μl and 10 μl extract and at 10 μl of extract after winter rains, which were all comparable to those exposed to live mature males (Table. 11). The maturation time in immature adults exposed to 0.1 μl of extract after winter rains was significantly longer compared to the presence of mature males, but significantly different from control (hexane + paraffin oil).

Similar results were obtained when immature females were exposed to the different doses (10, 0.1, 0.001 μl) of the *Commiphora* crude extract before and after winter rains (Table 12 and Appen. K).

3. 2. Effect on Pheromone (phenylacetonitrile) Production in Males

Figure 22 shows the effect of the *C. guadricincta* crude extract on the phenylacetonitrile titres. The results show significant difference between the treatments and the control. On the other hand, immature males exposed to the mature males were not different from those exposed to the crude extract before the winter rains.

Table (12). Mean maturation time of the immature females exposed to the different doses of crude extract of *Commiphora quadricincta* before and after the winter rains, mature males and paraffin oil+n-hexane (control).

Treatment (test insect/signal source)	Maturation Time * in Days (X±S.E)			N
	By colour	By copulation	By oviposition	
Imm.♀ / Control(Hexane+paraffin oil)	22.31±0.81a	22.56±0.82a	24.94±0.70a	16
Imm.♀ / 0.1μl crude extract (AWR)	18.50±0.47b	18.81±0.44b	22.75±0.65b	16
Imm.♀ / 10μl crude extract (AWR)	16.76±0.36c	17.06±0.35c	19.18±0.37c	17
Imm.♀ / 0.001μl crude extract (BWR)	14.69±0.45d	15.25±0.49d	17.19±0.40d	16
Imm.♀ / 10μl crude extract (BWR)	14.59±0.23d	14.76±0.25d	17.35±0.31d	17
Imm.♀ / 0.1μl crude extract (BWR)	12.75±0.34e	13.38±0.26e	15.13±0.30e	16
Imm.♀ / Mat. ♂	12.00±0.00e	12.44±0.13e	14.94±0.14e	16

Means with the same letter are not significantly different at $P=0.05$ according to LSD.
* = significant difference between maturation times by colour and copulation ($p>0.05$, *t* test).
N = No. of surviving insects at the end of the experiment.
BWR= before winter rains, AWR= after winter rains.

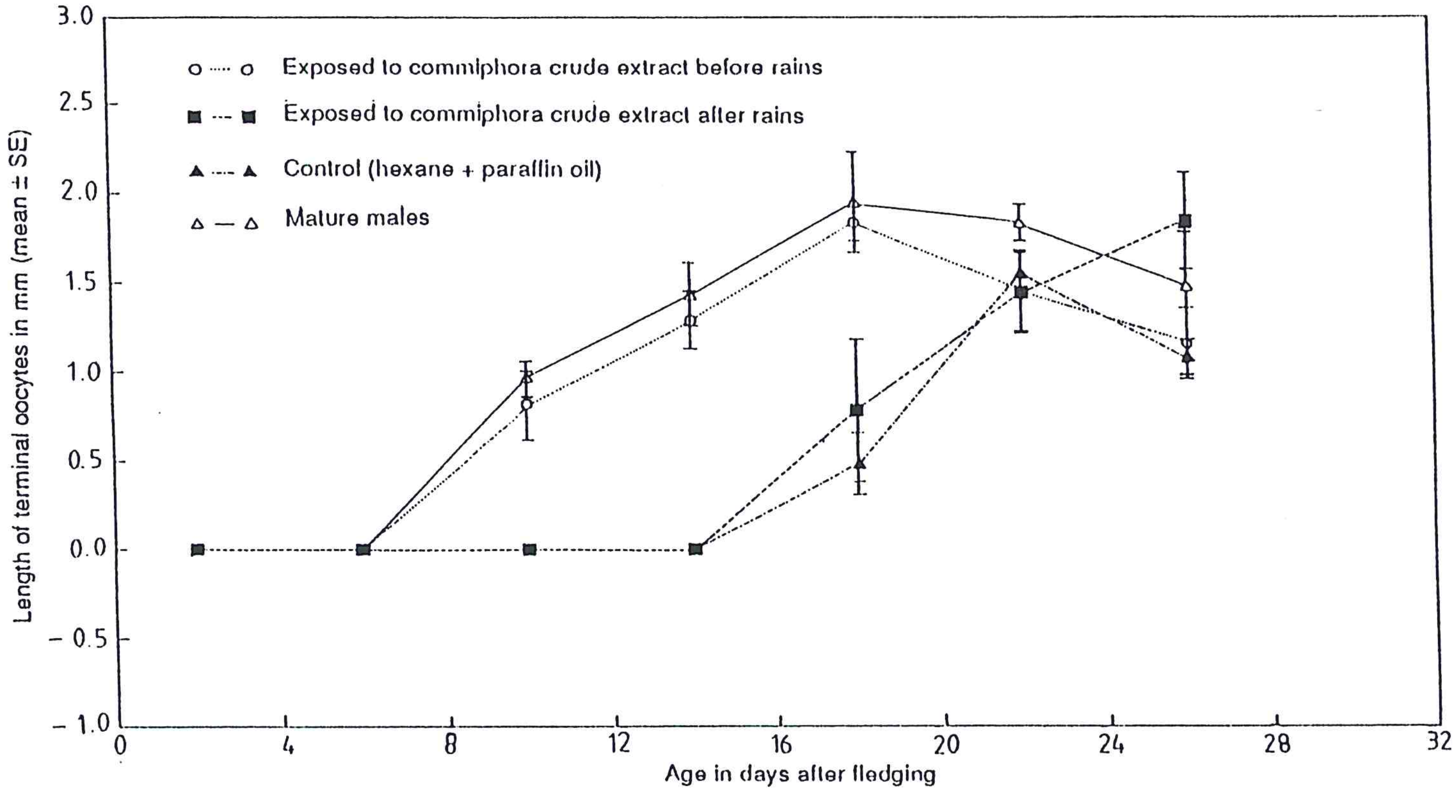


Fig. 22. Phenylacetonitrile produced by immature males exposed to *C. quadricincta* crude extract before and after Winter rains + paraffin oil, mature males, and control (hexane + paraffin oil).

3. 3. Effect on Ovulation and Number of Eggs/pod in Females

The results show that the length of the oocytes of the immature females, exposed to the *C. quadricincta* extract before winter rains, exhibited a shorter gonotrophic period with the first mature oocytes being detected 16 days after fledging compared to the control (hexane + paraffin oil) where the first gonotrophic cycle lasted 22 days after fledging (Fig. 23). On the other hand, in the presence of the mature males the first gonotrophic cycle took significantly shorter time and lasted 16 days after fledging. There was no significant differences between immature females exposed to the *Commiphora* extract and those exposed to the mature males. In the case of the number of eggs per pod, the results (Table 13) showed that there is significant difference ($p \leq 0.05$) between those exposed to extract before the rains and other treatments.

These results confirm maturation-accelerating effect of the *Commiphora* essential oil on the maturation of the immature males and females (Carlisle *et al.*, 1965). These effects are reflected in colour changes, copulation, propensity oviposition, oocytes growth and phenylacetonitrile titres. Furthermore, there is no significant difference of the effect of the *Commiphora*

Table (13). Mean number of eggs per pod of immature females exposed to *Commiphora quadricincta* crude extract before and after winter rains, paraffin oil + hexane (control).

Treatment (test insect/signal source)	Eggs/pod/female±S.E	N
Imm. ♀ / Commiphora extract (BWR)	58.80±2.63 a	15
Imm. ♀ / Mat. ♂	44.63±2.62 b	16
Imm. ♀ / paraffin oil+hexane	44.34±2.12 b	16
Imm. ♀ / Commiphora extract (AWR)	38.94±1.70 b	17

Means with the same letter in column are not significantly different at P=0.05 according to LSD.
N = No. of eggs pod counted for each treatment of the experiment
(BWR)=Before winter rains. (AWR)=After winter rains.

extract on the maturation of immature adults of the two sexes.

Previously, Carlisle *et al.* (1965) had pointed out that locust maturation in Somalia coincided with the bud burst of certain desert shrubs, a week or more before the heavy rains begin and several weeks before the appearance of annual vegetation. The shrubs included many species of *Commiphora* and *Boswellia* which have resinous buds that are the source of the biblical frankincense and myrrh. The air surrounding the shrubs was redolent with the fragrance of the essential oils. The essential oil of *Commiphora spp.* was found to enhance the maturation of the desert locusts. The results of the present study reveal that the crude steam distillate extract does indeed accelerate the maturation of the immature adults of both sexes, confirming the previous work by Carlisle *et al.* (1965). This is reflected in colour change, copulation activity, adult pheromone production, as well as in oviposition of females. However, whether *Commiphora* (or *Boswellia*) are responsible in inducing the maturation of solitarious insects as proposed by Carlisle *et al.* (1965) is a matter of debate. In an area studied by these authors in Somalia, these plants were apparently widespread. On the other hand, in the Red Sea area of the Sudan, these shrubs are quite rare. However, it is possible that the *Commiphora* /*Boswellia* role in other areas is taken up by other plants that are able to produce similar essential oil components. Further studies are needed to throw light on this question.

The present study shows that, overall, the extract before winter rains is more potent as a maturation accelerant than extract after winter rains. This lends further support to Carlisle, *et al.* (1965) speculations on the difference in the composition of the shrubs during two seasons.

4. Identification of *C. quadricincta* Crude Steam Distillate Extracts

C. quadricincta crude extracts were analyzed by GC as shown in (Fig. 24) and by coupled gas chromatography-mass spectrometry (GC-MS). The results are summarised in (Table 14). About 55 compounds were tentatively identified. Eight of the fifty five compounds visible on the GC chromatogram (Fig. 24) were linear compounds: β-myrcene, *trans*, *trans*-nona-2,4-diene, β-ocimene, 4-nonanone, nonanal, hexyl hexoate, 1-octanol and (Z)-β-farnesene. The remaining peaks were cyclic compounds (Table. 14). The mass spectrum obtained for the peaks visible in GC (Fig. 24) gave mass spectra characteristic of the following: camphene, m/z (rel-intensity) at 93(100), 121(62), 79(42), 41, 67 and 91(32), 39 and 107(30), 77(22), 136(18), 53(16); β-pinene, m/z (rel-intensity) at 93(100), 41(50), 69(38) 39 and 91(24), 77

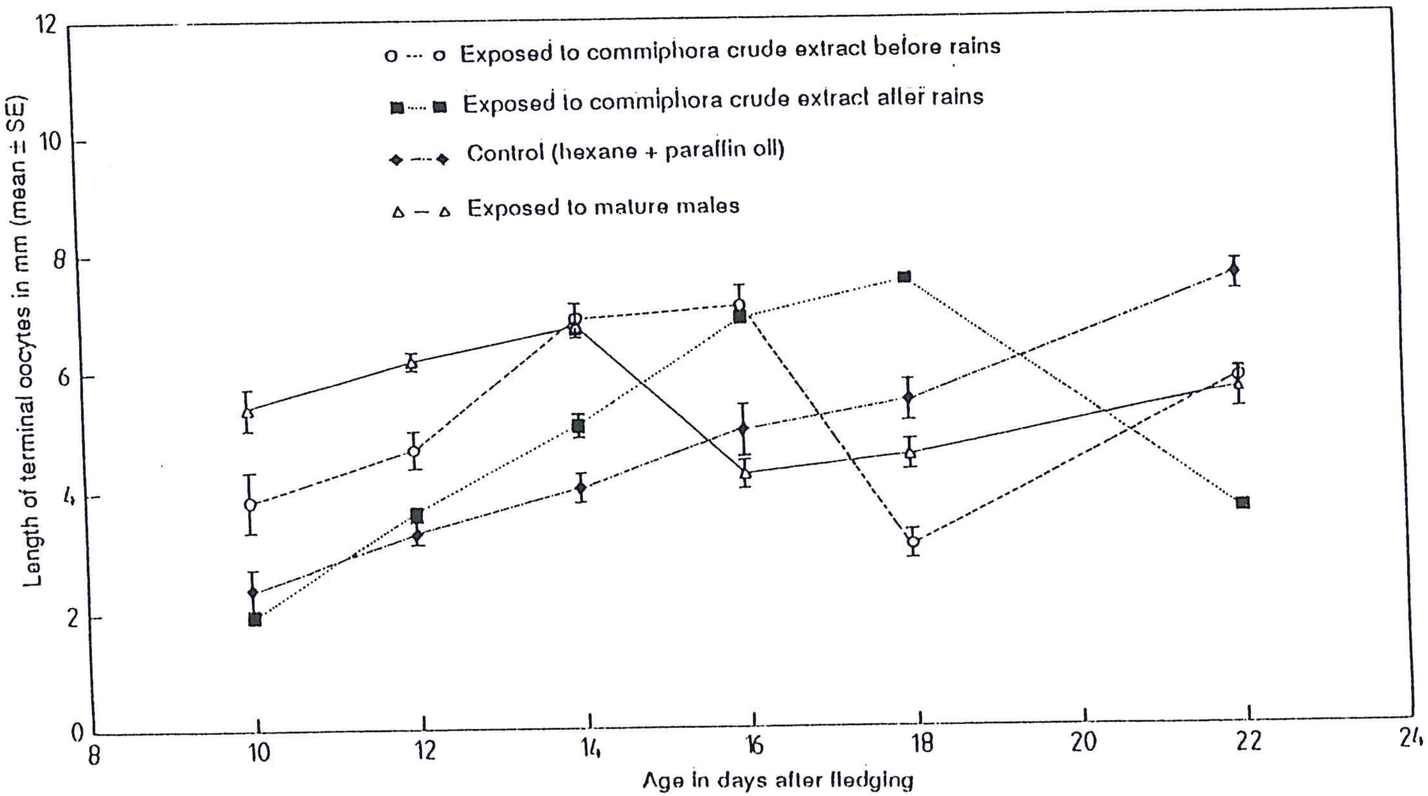


Fig. 23. Length of terminal oocytes of immature females exposed to *C. quadricincta* crude extract before and after Winter rains + paraffin oil, mature males, and control (hexane + paraffin oil).

Table (14). Compounds identified in crude steam distillate extracts from *Commiphora quadricincta*

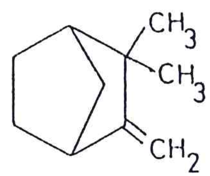
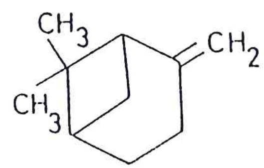
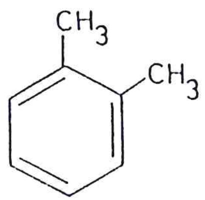
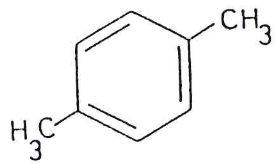
No.	name	structure
1	Camphene	
2	*β*-Pinene	
3	*o*-Xylene	
4	*p*-Xylene	

Table (14). contd.

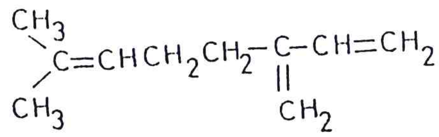
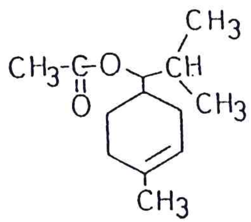
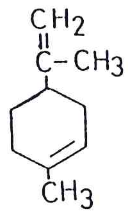
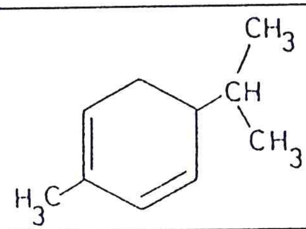
No.	name	structure
5	*β*-Myrcene	
6	4-Terpinenyl acetate	
7	Limonene	
8	*α*-Phellandrene	
9	*trans*,*trans*-nona-2, 4-dienal	$CH_3(CH_2)_3\,CH{=}CH\,CH{=}CH\,CHO$

Table (14). contd.

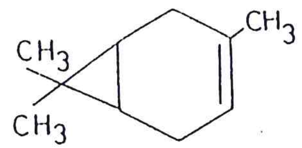
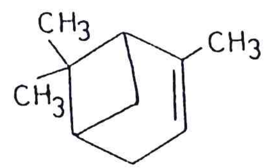
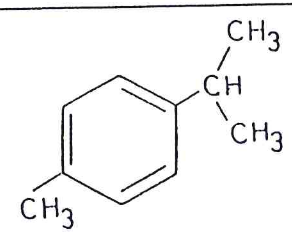
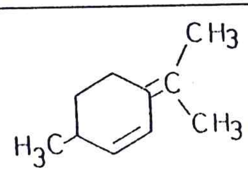
No.	name	structure
10	β-Ocimene	$(CH_3)_2C{=}CHCH_2CH{=}C(CH_3){-}CH{=}CH_2$
11	Δ3-Carene	
12	α-Pinene	
13	*p*-Cymene	
14	Isoterpinolene	

Table (14). contd.

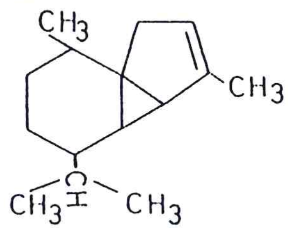
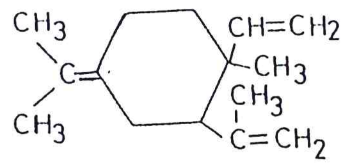
No.	name	Structure
15	4-Nonanone	$CH_3(CH_2)_4-\overset{O}{\overset{\|\|}{C}}-CH_2CH_2CH_3$
16	Nonanal	$CH_3(CH_2)_7CHO$
17	Hexyl hexoate	$CH_3(CH_2)_5-O-\overset{O}{\overset{\|\|}{C}}-(CH_2)_4CH_3$
18	α-Cubebene	
19	γ-Elemene	

Table (14). contd.

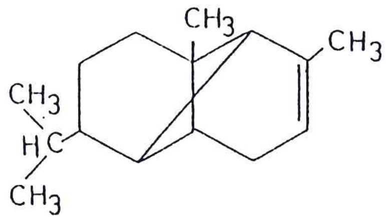
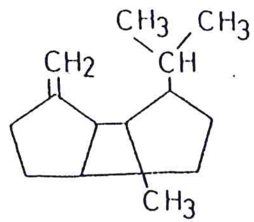
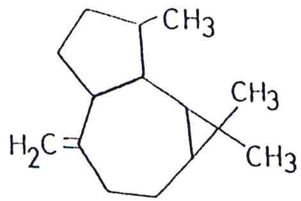
No.	name	Structure
20	α-Copaene	
21	β-Bourbonane	
22	α-Gurjunene	
23	1-Octanol	$CH_3(CH_2)_9OH$

Table (14). contd.

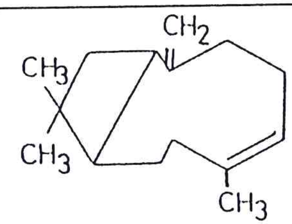
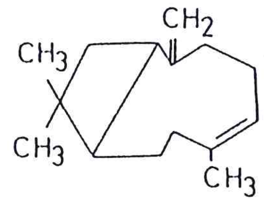
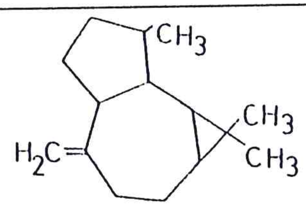
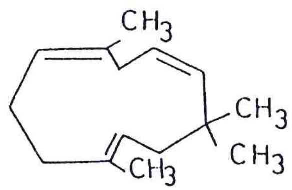
No.	name	Structure
24	*cis*-Caryophyllene	
25	*trans*-Caryophyllene	
26	Alloaromadendrene	
27	α-Humulene	
28	(*Z*)-β-Farnesene	$(H_3C)_2C{=}CH(CH_2)_2\overset{CH_3}{\overset{\vert}{C}}{=}CH(CH_2)_2\overset{CH_2}{\overset{\Vert}{C}}{-}CH{=}CH_2$

Table (14). contd.

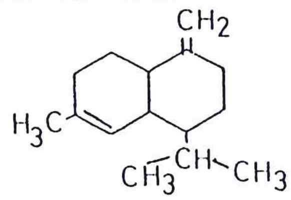
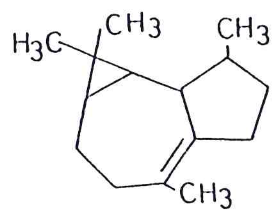
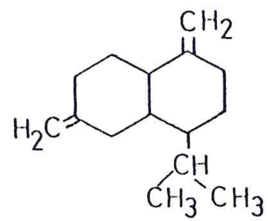
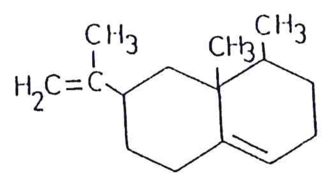
No.	name	Structure
29	γ-Muurolene	
30	Ledene	
31	Decahydro-1,6-bis (methylene)-4-(1-methyl ethenyl)	
32	Eremophilene	

Table (14). contd.

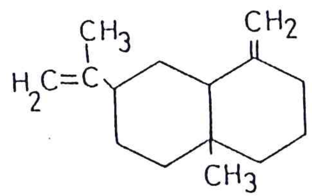
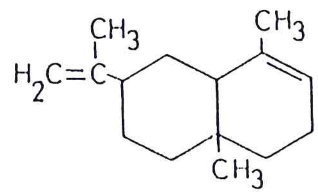
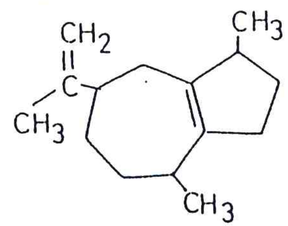
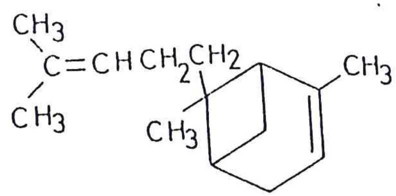
No.	name	Structure
33	β-Selinene	
34	(-)-α-Selinene	
35	α-Guaiene	
36	α-Bergamotene	

Table (14). contd.

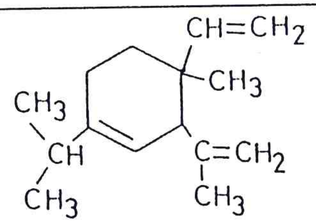
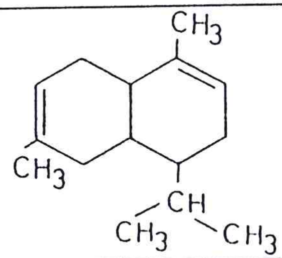
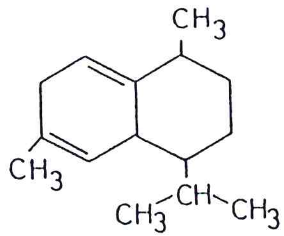
No.	name	Structure
37	δ-Elemene	
38	Cadinene	
39	1,2,3,4,4a,7-hexahydro-1, 6-dimethyl-4-(1-methyl ethenyl) naphthallene	
40	1,2,4a,5,6,8a-hexahydro-4, 7-dimethyl-1-(1-methyl ethenyl) naphthallene	

Table (14). contd.

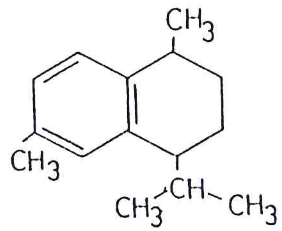
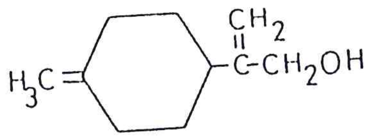
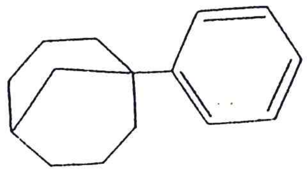
No.	name	Structure
41	Mixture of isopropyl-4,6-dimethyl-1,2,3,4-tetrahydro naphthalene and 4-isopropyl-1,6-dimethyl-1,2,3,3-tetrahydro naphthalene	
42	*p*-mentha-1-(7),18-dien-10-ol	
43	Torreyol	
44	1-Phenyl-bicyclo[3.3.1] nonane	

Table (14). contd.

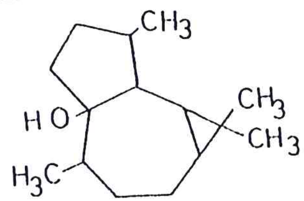
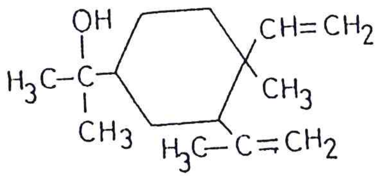
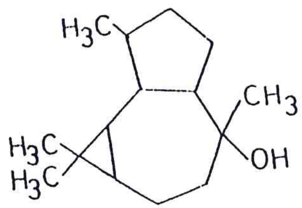
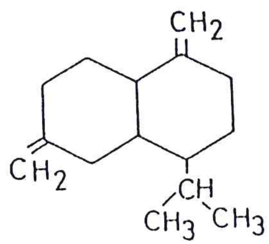
No.	name	Structure
45	Palustrol	
46	Elemol	
47	Ledol	
48	ε-Muurolene	

Table (14). contd.

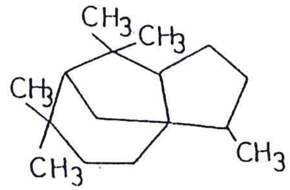
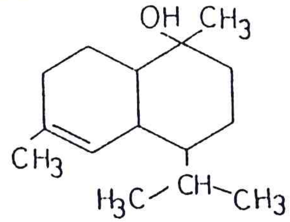
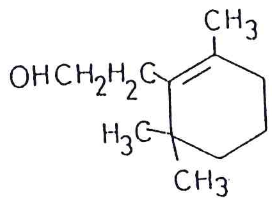
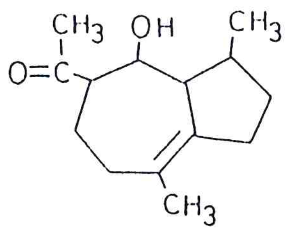
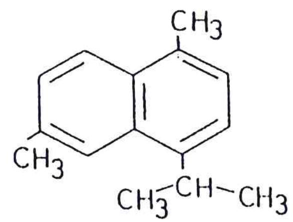
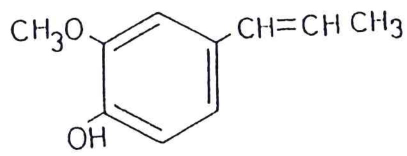
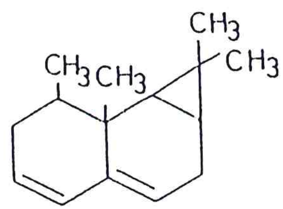
No.	name	Structure
49	α-Cedrol	
50	δ-Cadinol	
51	1-Ethylidene octahydro-7a-methyl-,cis, 1 H indene,	
52	6 Hydroxy-2,8-dimethyl-5-acetyl-bicyclo[5.3.0] deca-1-8-diene	

Table (14). contd.

No.	name	Structure
53	Cadalin	
54	Isoeugenol	
55	1,2,9,10-tetrahydro aristolane	

and 79(22), 121(12), 53 and 136(10);*o*-xylene, m/z (rel-intensity) at 91(100), 106(30), 93(25), 77(19), 39(18), 41, 65 and 79(10); *p*-xylene, m/z (rel-intensity) at 91(100), 106(53), 77(15), 39(10), 51(8), 79 and 103(6); *β*-myrcene, m/z (rel-intensity) at 41(100), 93(84), 69(70), 39(26), 91(20), 79(16), 77(15), 67(14), 53(10); 4-terpinenyl acetate, m/z (rel-intensity) at 93(100), 121(98), 91(60), 136(54), 43(44), 77(39), 79(34), 105(20), 58(18), 107(16), 65 and 119(15), 53(10); limonene, m/z (rel-intensity) at 68(100), 70(67), 93(60), 39 and 79(30), 41(28), 53 and 136(21), 91, 107 and 121(20), 77(18); *α*-phellandrene, m/z (rel-intensity) at 93(100), 91(92), 77(38), 79(22), 39(20), 41 and 95(18), 136(17), 43, 65 and 66(15), 120(10); *trans*, *trans*-nona-2,4-dienal, m/z (rel-intensity) at 81(100), 82(22), 138(20), 53(18), 39(10), 41(8), 95(6); *β*-ocimene, m/z (rel-intensity) at 93(100), 91(44), 79(40), 41(38), 77(36), 43(24), 39(22), 105(18), 58(17), 55(12), 67(11), 53 and 121(10); Δ3-carene, m/z (rel-intensity) at 93(100), 91(50), 77 and 136(38), 121(30), 43 and 79(22), 39 and 41(18), 105(10), 107(9), 65 and 119(8); *α*-pinene, m/z (rel-intensity) at 93(100), 91(49), 79(46), 80(40), 41 and 77(39), 39(36), 105(22), 43, 53, 67 and 121(18), 55(11), 65 and 136(10), 51(9); *p*-cymene, m/z (rel-intensity) at 119(100), 91 and 134(24), 117(20), 34, 41 and 115(12), 65 and 77(10); isoterpinolene, m/z (rel-intensity) at 93(100), 121(80), 136(72), 91(45), 79(43), 77(36), 41(34), 39(30), 105(22), 107(20), 43(18), 53(12), 51, 55 and 67(10), 65(9); 4-nonanone, m/z (rel-intensity) at 43(100), 71(80), 58 and 99(38), 41(28), 86(20), 39(10), 55 and 56(8); nonanal, m/z (rel-intensity) at 57(100), 41(89), 43(76), 56(50), 55(44), 82(42), 70(38), 39(32), 98(30), 68(22), 53, 81 and 95(18), 118(6); hexyl hexoate, m/z (rel-intensity) at 99(100), 43(94), 84(,50), 69(42), 41(39), 71 and 85(25), 55 and 57(16), 39, 60 and 143(10), 115 and 117(6); α-cubebene, m/z (rel-intensity) at 105(100), 119(86), 161(84), 91(41), 41(39), 81(36), 204(22), 55 and 77(20), 69(11), 67 and 133(10), 65 and 115(8), 59(6); γ-elemene, m/z (rel-intensity) at 121(100), 43(92), 105(56), 107(54), 41(46), 97(40), 161(32), 136(26), 67(22), 39(21), 53(18), 189(10), 204(6); α-copaene, m/z (rel-intensity) at 119(100), 105(99), 161(98), 93(53), 44(42), 81(36), 77(22), 55(21), 204(20), 69(18), 133(17), 65(16), 115(12); β-bourbonane, m/z (rel-intensity) at 81(100), 80(70), 123(64), 161(30), 41(28), 77, 91 and 105(20), 55(11), 67 and 119(10); α-gurjunene, m/z (rel-intensity) at 69(100), 41(82), 105(50), 55(49), 84 and 161(44), 204(40), 91, 119 and 189(38), 39(32), 95(24), 133(22), 79(19), 147(18); 1-octanol, m/z (rel-intensity) at 43(100), 56(99), 41(98), 55(82), 70(60), 84(46), 39(24), 68(22), 53(12), 82(8), 79, 93 and 77(6), 120 and 140(4); *cis*-caryophyllene, m/z (rel-intensity) at 41(100), 93(88), 69, 79 and 91(60), 81 and 133(56), 67(50), 105(48), 107(47), 39 and 55(40), 53 and 119(38), 161(37), 147(36), 65 and

189(20), 175(10), 51 and 204(8); *trans*-caryophyllene, m/z (rel-intensity) at 41(100), 93(76), 69(74), 133(62), 91(60), 79(58), 105(45), 39(36), 55(35), 120(30), 161(28), 147(20), 65 and 189(18), 51, 175 and 204(8); alloaromadendrene, m/z (rel-intensity) at 41(100), 91(79), 93(69), 105 and 161(60), 79(56), 69(54), 119, 121 and 133(45), 55(42), 204(36), 147(25), 65 and 189(19), 51, 115 and 175(8); α-humu2lene, m/z (rel-intensity) at 93(100), 80(35), 41(32), 121(27), 91, 92 and 147(19), 79 and 107(17), 39, 67 and 77(15), 53 and 55(13), 204(6); (Z)-β-franesene, m/z (rel-intensity) at 69(100), 41(80), 93(39), 133(26), 67(22), 79 and 120(20), 55 and 81(19); γ-muurolene, m/z (rel-intensity) at 161(100), 105(80), 119(62), 91 and 93(60), 41(56), 79(50), 204(35), 77 and 133(32), 55(25), 67(20), 148 and 189(10), 115(8); ledene, m/z (rel-intensity) at 107(100), 108(86), 93(73), 41(71), 91(70), 119(55), 79(48), 135(42), 55(40), 96(34), 189(33), 204(29), 116(27), 67(25), 147(20), 175(15), 115 and 117(9), 51(8), 103 and 131(6); Decahydro-1,6-bis(methylene)-4-(methylethyl), m/z (rel-intensity) at 161(100), 105(66), 91(59), 41(50), 81(43), 119(40), 79(39), 77(30), 55(25), 133(22), 67 and 204(20), 147(8), 51(6); eremophilene, m/z (rel-intensity) at 161(100), 105(67), 91(53), 41(52), 93(51), 119(49), 79(42), 204(39), 55, 67 and 131(24), 39(22), 147(18), 189(14), 115(8); β-selinene, m/z (rel-intensity) at 41(100), 93(95), 107(88), 105(79), 79(75), 67(67), 55 and 121(58), 133(56), 189(55), 39(46), 204(45), 147(41), 53(40), 175(23), 51(8); (-)-α-selinene, m/z (rel-intensity) at 189(100), 105(71), 93(70), 107(69), 133(55), 41(47), 204(41), 81(40), 55, 147 and 175(33), 121(30), 67 and 77(25), 39(22); α- guaiene, m/z (rel-intensity) at 105(100), 93(48), 94(45), 189(38), 41 and 121(36), 204(37), 81(25), 77 and 133(19), 55 and 147(18), 175(15), 67 and 69(10); α-bergamotene, m/z (rel-intensity) at 93(100), 121(90), 41(80), 107(59), 119(57), 79(42), 69(38), 55(37), 39(25), 136(20), 65(10), 161(8), 204(6); δ-elemene, m/z (rel-intensity) at 121(100), 93(70), 107(50), 41(49), 79(35), 91(30), 67(23), 136(20), 55(19), 161(10), 204(8); cadinene, m/z (rel-intensity) at 161(100), 119(68), 105(64), 134(57), 204(55), 41 and 91(48), 81(31), 77(21), 189(20), 55(19), 69(15), 65, 115 and 117(10), 128(6); 1,2,3,4,4a,7-hexahydro-1,6-dimethyl-4-(1-methylethenyl) naphthallene, m/z (rel-intensity) at 119(100), 105(80), 69(58), 41(54), 161(50), 204(23), 91(22), 55(20), 77 and 133(10), 85 and 115(8), 81(6); 1,2,4a,5,6,8a-hexahydro-4,7-dimethyl-1-(1-methylethenyl) naphthallene, m/z (rel-intensity) at 105(100), 161(45), 41(33), 81(30), 95(28), 91(27), 113(21), 119 and 204(20), 55 and 77(17), 69, 131 and 189(10), 123 and 145(8), 65(6); mixture of isopropyl-4,6-dimethyl-1,2,3,4-tetrahydro naphthallene and 4-isopropyl-1,6-dimethyl-1,2,3,3-tetrahydro naphthallene, m/z (rel-intensity) at 159(100), 43(25), 135 and 202(15), 131(10), 91 and 115(6); *p*-menta-1-(7),18-dien-10-ol, m/z (rel-intensity) at 91(100), 119(50), 41(28), 134(24), 85(18), 79(17), 43(15), 39, 77 and 105(10), 108(9), 55(7); torreyol, m/z (rel-intensity) at 161(100), 43(93), 107(75), 41 and 119(60), 97(51), 93(50), 81(40), 55(34), 67 and 69(27), 77(25), 39 and 133(20), 137(17), 179(12), 65(10), 147 and 151(6); 1-phenyl-bicyclo[3.3.1] nonane, m/z (rel-intensity) at 157(100), 142(50), 200(20), 115(10), 158(8); palustrol, m/z (rel-intensity) at 111(100), 122(89), 41(72), 55(50), 107(49), 95(43), 81(41), 69(38), 147(26), 98 and 161(25), 204(24), 91(20), 133(17), 77 and 165(12), 189(10); elemol, m/z (rel-intensity) at 43(100), 81(54), 109(45), 189(42), 55(38), 93(35), 67(34), 123, 135 and 204(30), 161(29), 105(25), 39 and 77(20), 150(18), 119(10); ledol, m/z (rel-intensity) at 43(100), 41(60), 82(56), 69 and 109(55), 93 and 161(40), 55 and 105(35), 79(27), 123(24), 119(22), 39(18), 133(16), 189 and 204(15), 65 and 149(8), 137(6); ϵ-muurolene, m/z (rel-intensity) at 81(100), 43(59), 91(53), 161(40), 119(39), 105(38), 55(20), 123(17), 67, 71 and 77(15), 39, 134 and 204(14), 109(10); α-cedrol, m/z (rel-intensity) at 119(100), 161(60), 105(45), 41(39), 204(33), 82(31), 55(30), 95(27), 69(22), 79, 91 and 179(15), 109(12), 65(5); δ-cadinol, m/z (rel-intensity) at 43(100), 41 and 109(69), 69(61), 161(43), 55, 81 and 93(40), 105(39), 122(33), 189(25), 77, 133 and 147(22), 39 and 204(20), 139(11), 65(10); 1-ethylidene octahydro-7a-methyl-, cis, 1 H indene, m/z (rel-intensity) at 149(100), 59(80), 91(50), 81 and 108(35), 164(30), 95(22), 41 and 119(18), 55 and 77(12), 67(10), 134(6); 6 hydroxy-2,8-dimethyl-5-acetyl-bicyclo [5.3.0] deca-1-8-diene, m/z (rel-intensity) at 159(100), 41(69), 43(65), 79(44), 91(40), 55, 97 and 105(38), 109(37), 121(30), 69(28), 202(24), 131(23), 177(21), 117(20), 65 and 145(12); cadalin, m/z (rel-intensity) at 183(100), 198(43), 165(38), 153(20), 83 and 141(10), 115 and 128(8); isoeugenol, m/z (rel-intensity) at 164(100), 149(40), 77(38), 103(33), 91(30), 55(29), 131(28), 121(18), 39(17), 51 and 65(16), 137(6); 1,2,9,10-tetrahydroaristolane, m/z (rel-intensity) at 159(100), 202(21), 145(20), 57 and 187(10), 117 and 131(6) (Appen. L). However, comparison with authentic samples is needed to confirm these identifications.

The results of the GC-MS of this study shows that the essential oil of *Commiphora* contains many terpenoids and other compounds. A number of monoterpenes (β-pinene, α-pinene, limonene and eugenol) were found effective in promoting and synchronizing maturation (Carlisle, *et al.*, 1965). However, it is clear that a wide profile of terpenoids from a wider profile of desert plants need to be assayed to provide a more comprehensive picture of the role of desert plants in locust maturation. Thus, of 55 tentatively identified compounds in the *Commiphora* crude extract, 10 were electrophysiologically active. These were identified as isoterpinolene, 4-nonanone, hexeyl hexoate, decahydro-1,6- bis (methylene)-4-(1-methylethyl), α–bergamotene, isoeugenol, and four other unknown compounds (Fig. 24).

A comparison of the compositions of the steam volatiles of *C. quadricincta* before and after the rains (Fig. 25 and 26) show that the GC–EAG active compounds were present in higher amounts in the volatiles of the shrub before the rain than in those after the rain (end of the rainy season). This lends further support to Carlisle, *et al.* (1965) speculations on the difference in the composition of the shrubs during two seasons and suggests that further studies are warranted in this area.

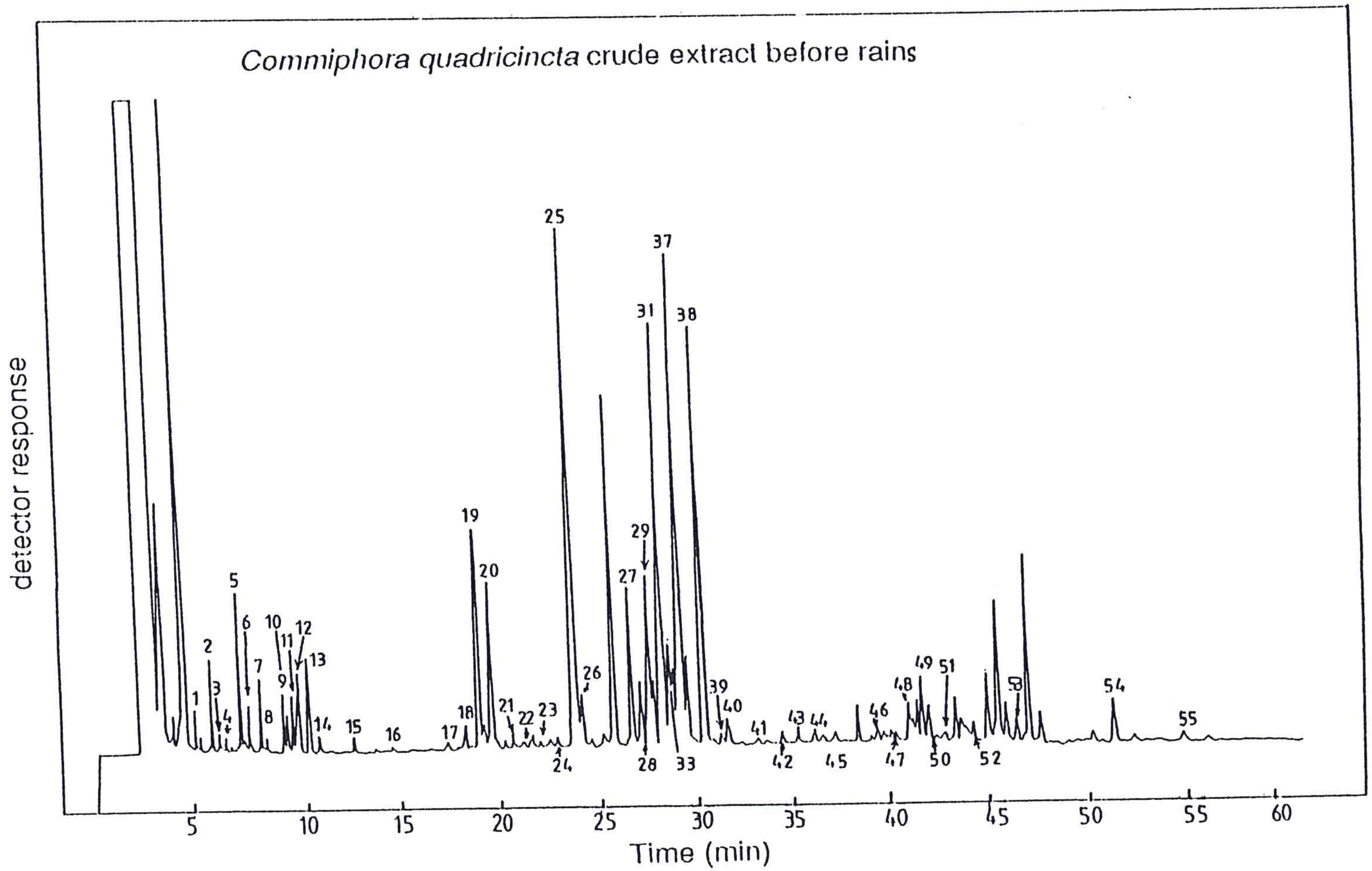


Fig. 24. Gas chromatogram of crude extract from desert shrub *Commiphora quadricincta* injected onto a 50-m Carbowax 20 M capillary column. Collected in October two weeks before Winter rains at Winter breeding areas of the desert locust at Red Sea Coast, Sudan.

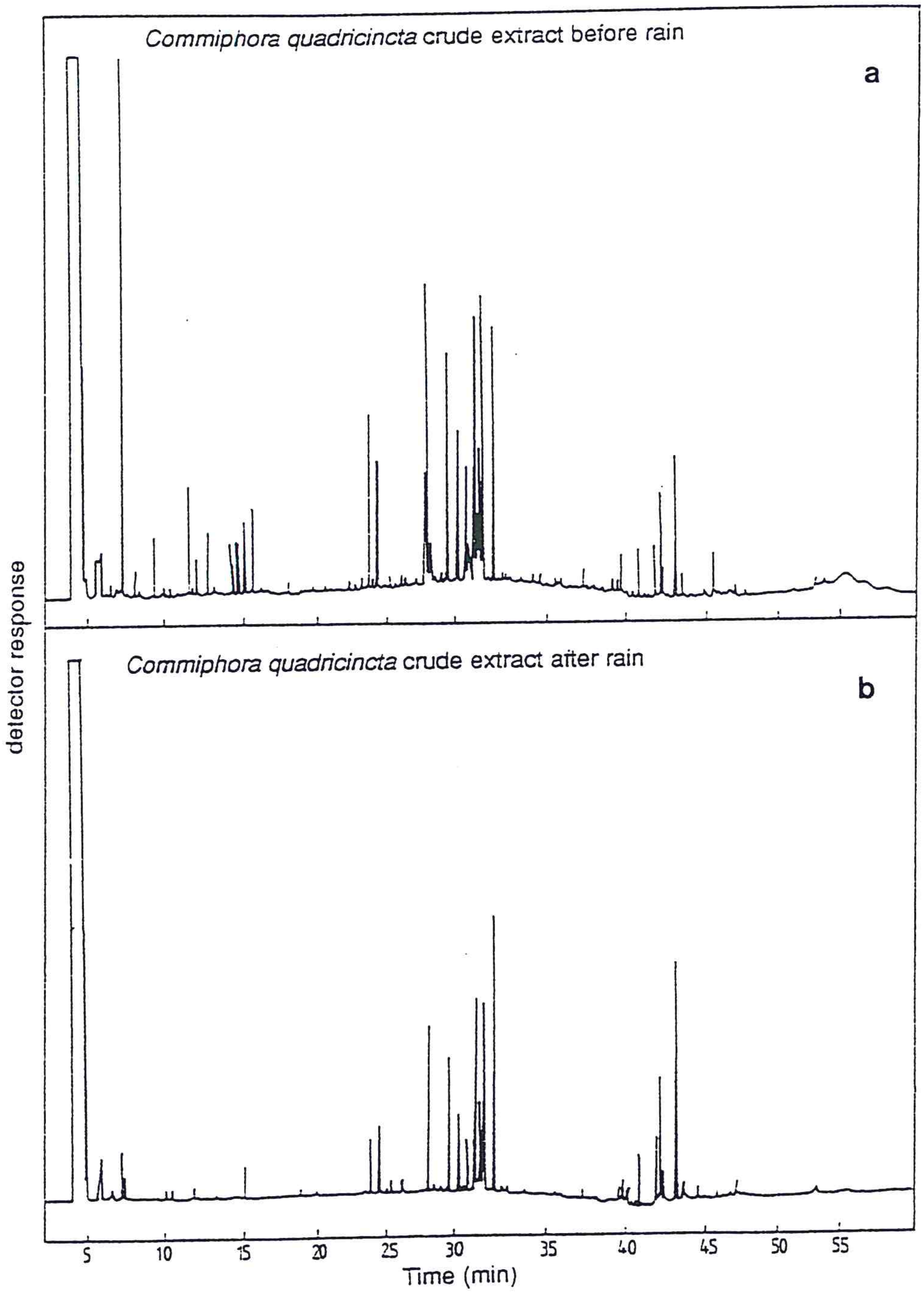


Fig. 25. Gas chromatogram of crude extract from desert shrub *Commiphora quadricincta* injected onto a 50-m Carbowax 20 M capillary column. (A) Collected in October two weeks before Winter rains (B) Collected in March after Winter rains at Winter breeding areas of the desert locust at Red Sea Coast, Sudan.

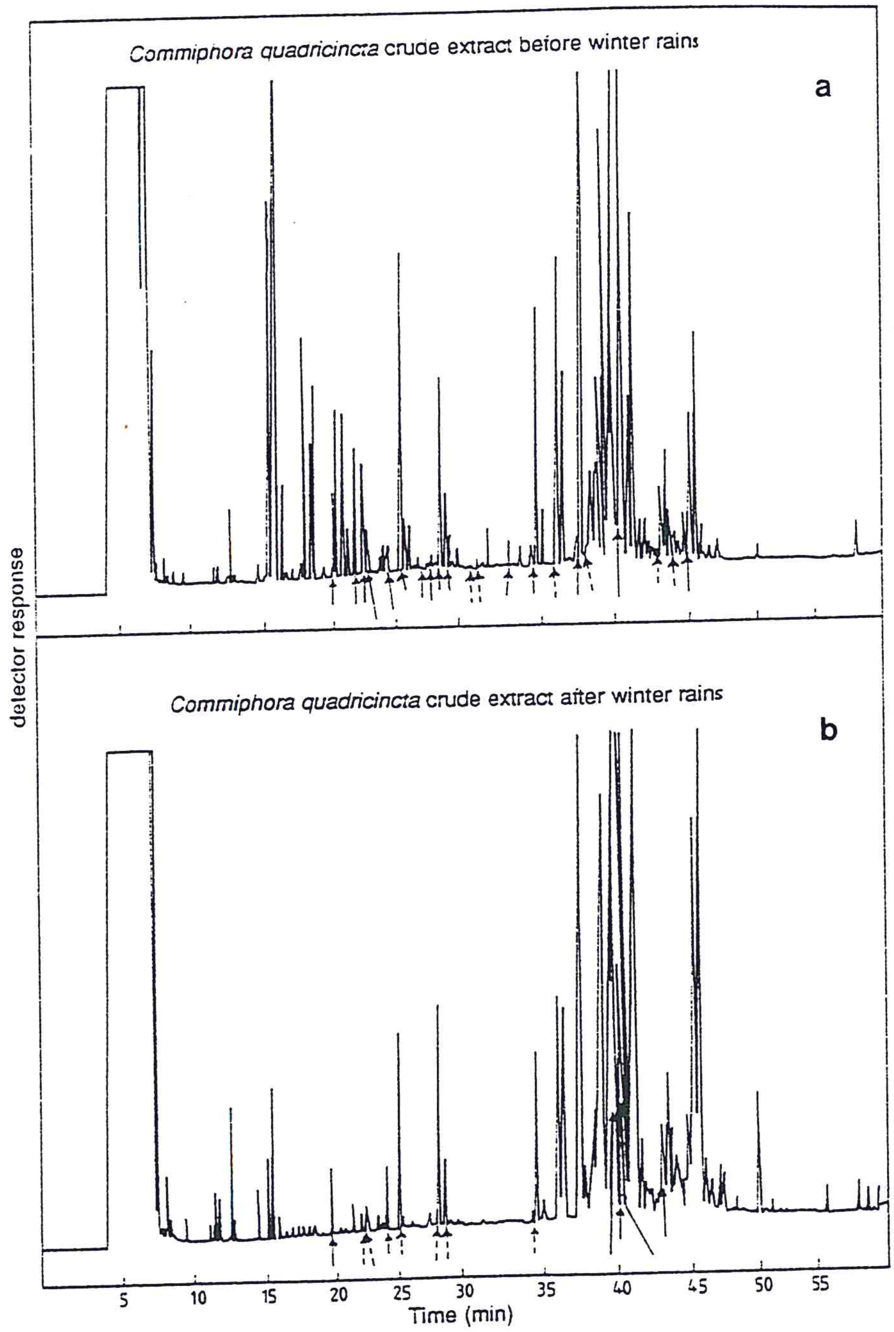


Fig. 26. Gas chromatogram of crude extract from desert shrub *Commiphora quadricincta* injected onto a 50-m Methyl silicone 20 M capillary column. (A) Collected in October two weeks before Winter rains (B) Collected in March after Winter rains at Winter breeding areas of the desert locust at Red Sea Coast, Sudan.

CONCLUSIONS

Maturation time, in immature adult males and females, in the presence of the fifth instar nymphs and their trapped volatiles, tends to take longer than that of immature adults kept on their own (control). On the other hand, immature adult males and females, kept with mature males, tend to take shorter time to mature than immature insects on their own or those reared in the presence of fifth instar nymphs. Thus, in the presence of nymphs, copulation and pheromone production in males, copulation and oviposition in females are postponed. Exposure to nymphs also affects maturation of the males which failed to become bright yellow, even after maturation and copulation. Accordingly, nymphal volatiles and older adult male volatiles act as primer pheromones; the former retarding maturation, whereas the latter accelerating maturation of young adults.

The results also show that both nymphal sexes are equally effective in inducing retardation of maturation and there is no sex differentiation in the production of nymphal pheromone, unlike in the adults where the pheromone is produced by the males.

Moreover, the results of the present study show that nymphal faeces have no measurable influence on the

for their communication system. Both interspecific (environmental cues) and intraspecific (pheromone) are deployed. Five different pheromone systems, in various stages of the life of the gregarious desert locust, are known to be operating. Figure 27 summarises the relationship between the stages producing pheromones and those affected by it. In the solitaria allelochemicals may be important in hastening maturation after a period of drought and the mediation of a long range pheromone has been demonstrated by other workers.

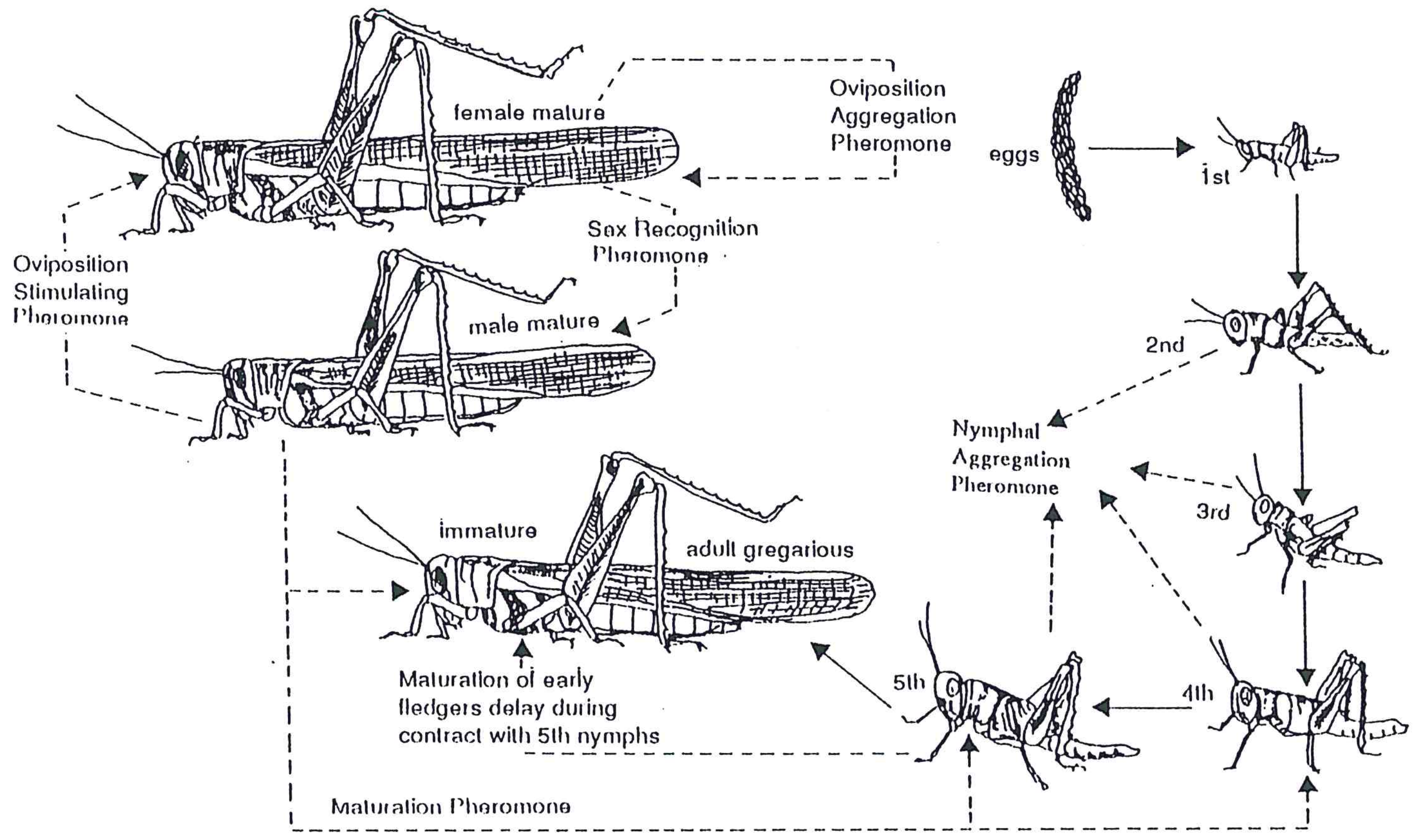


Fig. 27. The pheromonal system of the desert locust which controls gregarization, oviposition, sex recognition and maturation synchrony.

REFERENCES CITED

Andrewartha, H. G. (1952). Diapause in relation to the ecology of insect. *Biol. Rev.* 27: 50-107.

Amerasinghe, F. P. (1978a). Effect of JHI and JHIII on yellowing, sexual activity and pheromone production in allatectomized male *Schistocerca gregaria*. *J. Insect Physiol.*, V. 24: 603-611.

Amerasinghe, F. P. (1978b). Pheromonal effect on sexual maturation, yellowing, and the vibration reaction in immature male desert locust *Schistocerca gregaria*. *J. Insect Physiol.* V. 24: 309-314.

Bernays, E. A.; J., Horsey, and E. M., Leather (1974). The inhibitory effect of seedling grasses on feeding and survival of Acrididae. *Bull. Entomol. Res.* 64:413-420.

Bernays, E. A.; D.J., Chaberlain, and P., Mc Carthy (1980). The differential effects of ingested tannic acid on different species of Acridoidea. *Entomol. Exp. Appl.* 28: 158-166.

Bradow, Judith M. (1991). Relationships between chemical structure and inhibitory activity of C_6 through C_9 volatiles emitted by plant residues. *J. Chem. Ecol. V.* 17: *No.* (11) 2193-2212.

Brown, E.S. (1965). Notes on the migration and direction of flight of *Eurygaster integriceps* Put. and Aelia species (Hemiptera, Pentatomoidea) and their possible bearing on invasions of cereal crops. *J. Anim. Ecol.* 34: 93-107.

Byers, J.A. (1991). Pheromones and chemical ecology of locusts. *Biol. Rev.* 66: 347-378.

Caldwell, R.L. (1974). A comparison of migratory strategies of two milkweed bugs. In Experimental Analysis of insect behaviour. Barton Browne, L. (ed.) Berlin-Heidelberg- New York: *Springer*.

Cantacuzene, A. M.; S., Lauverjat, and M., Papillon (1972). Influence of the temperature on *Schistocerca gregaria*. *J. Insect Physiol.* 18: 2077-93.

Carlisle, D. B.; P. E., Ellis, and E., Betts (1965) The influence of aromatic shrubs on sexual maturation in the desert locust *Schistocerca gregaria* .*J. Insect Physiol. V*. 11: 1541-1558.

Carlisle, D. B., and P. E., Ellis (1967). Synchronization of sexual maturation in desert locust swarms. *5e Un. int. Etude Insects SOC., Toulouse* (1965): 63-67.

Chapman, R. F.; W. W., Page, and A. G., Cook (1979). A study of the population changes in the grasshopper, *Zonocerus variegatus*, in Southern Nigeria. *J. Anim. Ecol*. 48: 247-270.

COPR, (1982). The Locust and Grasshopper Agricultural Manual.(Center for Overseas Pest Research).

Danks, H. V. (1987). *Insect Dormancy: and Ecological Perspective. Biological Survey of Canada*, Ottawa.

Danilevskii, A. S. (1965). *Photoperiodism and the seasonal development of insects*; Oliver & Boyd, Lond, pp 36-124.

De Wilde, J. (1954). Aspects of diapause in adult insect with special regard to the Colorado beetle, *Leptinotarsa decemlincata* Say. *Arch. neerl. Zol*. 10: 375-385.

De Wilde, J. (1962). Photoperiodism in insects and mites. *Ann. Rev. Entomol*. 7: 1-26.

De Wilde, J.; C. S., Dulntfer, and L., Mook (1959). Physiology of diapause in adult Colorado beetle *Leptinotarsa decemlincata* Say. the photoperiod as a controlling factor. *J. Ins. Physiol*. 3: 75-85.

De Wilde, J.; W., Bongers, and H., Schooneveld (1969). Effect of the host plant age on phytophagous insects. *Ent. Exp. Appl*. 12: 714-720.

Dingle, H. (1968). The influence of environment and heredity on flight activity in the milkweed bug *Oncopeltus*. *J. Exp. Biol*. 48: 175-184.

Dingle, H. (1974). Diapause in a migrant insect, the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae). *Oecologia* 17: 1-10 .

Dingle, H. (1978). Migration and diapause in tropical, temperate, and island milkweed bugs. In Evolution of Insect Migration and Diapause. *Springer-Verlag New, York, Heidelberg, Berlin*: 254-276.

Dingle, H. (1980). Ecology and evolution of migration. *Animal migration, orientation and navigation* (ed. by S. A. Gauthreaux), pp. 1-101. Academic press, New York.

Dingle, H. (1985). Migration. Compreh. *Insect Physiol. Biochem. and Pharmacol. V. 9: Behaviour,* 375-415.

Dingle, H.; B. A., Alden; N. R., Blakley; D., Kopec, and E. R., Muler (1980). Variation in photoperiodic response within and among species of milkwood bugs (*Oncopeltus*). *Evolution* 34, 356-370.

Dingle, H.; and J. D., Baldwin (1983) Geographic variation in life histories: Acomparison of tropical and temperate milkweed bugs (*Oncopeltus*). *In Geographic Variation in Insect Life Cycle Strategies.*

Ellis, P. E.; D. B., Carlisle, and O. P., Osborne (1965). Desert locust: Sexual maturation delayed by feeding on senescent vegetation. *Science, N. Y.* 149: 546-547.

Elsey, KD (1988). Reproductive diapause in the spotted cucumber beetle. *Florida-Entomologist.* 71: 1: 78-83.

Evans, L. D.; E. S., Krafsur (1990). Light intensity, photoperiod, and diapause induction in face flies (Diptera: Muscidae). *Environmental Entomology.* 19: 5: 1217-1222.

FAO (1993). *A guide to migrant pest management in Africa.* (edt. W. F. Meinzingen) pp. 183.

Farrow, R.A. (1990). Flight and migration in acridoids. *Biology of Grasshopper* (edt. chapman and Anthony) pp. 277-314.

Ferenz, H. J.; K., Luber, and J., Wieting (1994). Pheromones as a means of controlling migratory locusts. pp. 81-89.

Finke, MD.; and JM., Scriber (1988). Influence on larval growth of the eastern black swallowtail butterfly *Papilio polyxenes* (Lepidoptera: Papilionidae) of seasonal changes in nutritional parameters of Umbelliferae species. *American Midland Naturalist.* 119: 1: 45-62.

Fisher, R. C. (1971). Aspects of the physiology of endoparasitic Hymenoptera. *Biol. Rev.* 46: 243-278.

Gara, RI; and JO., Wood (1989). Termination of reproductive diapause in the Sitka spruce weevil, *Pissodes strobi* (Peck) (Col., Curculionidae) in western Washington. *Journal of Applied Entomology*. 108: 2: 156-163.

Gillett, J. B. ; M. A., Cantab, and F. L. S. (1991). *Flora of tropical east Africa Burseraceae*. PP, 93.

Goryshin, NI.; TA., Volkovich; AK., Saulich; M., Vagner, and IA., Borisenko (1988). The role of temperature and photoperiod in the control of development and diapause of the predatory bug *Podisus maculiventris* (Hemiptera, pentatomidae). *Zoolgicheskii-Zhuranl*. 67: 8: 1149-1161.

Hagen, K. S. (1962). Biology and ecology of predaceous Coccinellidae. *Ann. Rev. Ent.* 7: 289-326.

Hakomori, T.; and S., Tanaka (1992). Genetic control of diapause and other developmental traits in Japanese strains of the migratory locust, *Locusta migratoria* L.: univoltine vs. bivoltine. *Jap. J. Ent.* 60: 319-328.

Hill, L. (1965). The incorporation of C_{14} glycine into the proteins of the fat body of the desert locust during ovarian development. *J. Insect Physiol*. 11: 1605-1615.

Jackson, G. J. ; G. B., Popov; A. O., Ibrahim; S. A., Al Ghamedi, and A. M., Khan (1978). Effect of natural food plants on the development, maturation, fecundity and phase of desert locust *Schistocerca gregaria* (Forskal). *COPR (London) and LRS/ARC (Jeddah)*, PP 1-17.

Javahery, M. (1990). Biology and ecological adaptation of the green stick bug (Hemiptera: Pentatomidae) in Quebec and Ontario. *Ann. Entomol. Soc. Am.* 83: 2: 201-206.

Johnson, C. G. (1969). *Migration and dispersal of insects by flight*. Methuen, London.

Keay, R. W. J. (1959). *Vegetation map of Africa South of the tropic of cancer*. Oxford University press 427-431.

Lance, DR.; and JR., Fisher (1987). Food quality of various plant tissues for adults of the northern corn rootworm (Coleoptera: Chrysomelidae). *J. Kan. Entomol. Soc.* 60: 3: 462-466.

Loher, W. J. (1960). The chemical acceleration of the maturation process and its hormonal control in the male of the desert locust. *Proc. Roy. Soc. B,* 153: 381- 397.

Loher, W. J. (1990) Pheromone and phase transformation in locust "*Biology of grasshoppers*" 337-355.

Mahamat, H.; A., Hassanali; E. O., Osir; D., Ogoyi; H., Odongo; and S., El Bashir (1991). Molecular markers for augmenting morphomtric characterization of the phase status of desert locust. *Nineteenth Annual Report ICIPE* PP. 88-89.

Mahamat, H.; A., Hassanali; H., Odongo; B., Torto and S., El Bashir (1993). Studies on the maturation-accelerating pheromone of the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae). *Chemoecology* 4: 159-164.

Marshall, A. J.; and M. J. De S., Disney (1957).Experimental induction of the breeding season in axerophilous bird. *Nature Lond.* 180: 647.

Masaki, S. (1956). The effect of temperature on the termination of diapause in the egg of *Lymantria dispar* Linne (Lepidoptera: Lymantriidae). *J. Appl. Zool.* 21: 148-157.

Masaki, S. (1980). Summer diapause. *Ann. Rev. Ent.* 25:1-25.

Mc Ginnis, A. J.; and R., Kasting (1966). Comparison of tissues from solid- and hollow-stemmed spring wheats during growth. IV. Apparent dry matter utilization and nitrogen balance in the two-striped grasshopper, *Melanoplus bivittatus* (Say). *J. Insect Physiol.* 12: 671-678.

Morden, R. P.; and G. P., Waldbauer (1980). Diapause and its termination in the psychid moth *Thyridopteryx ephemeraeformis*. *Ent. Exp. App.* 28: 322-333.

Mulkern, G. B. (1967). Food selection by grasshoppers, *Ann. Rev. Entomol.* 12: 59-78.

Mulkern, G. B.; and D. R., Toczek (1972). Effect of plant extracts on survival and development of *Melanoplus differentialis* and *Melanoplus sanguinipes* (Orthoptera: Acrididae). *Ann. Entomol. Soc. Am.* 65: 662-671.

Muller, H. J. (1957). Uber die Diapause von *Stenocranus minutus* Fabr. (Homoptera : Auchenorrhvacha). *Beitr. Ent.* 7: 203-226.

Naranjo, SE.; and AJ., Sawyer (1987). Reproductive biology and survival of *Diabrotica barberi* (Coleoptera: Chrysomelidae): effect of temperature, food, and seasonal time of emergence. *Ann. Entomol. Soc. Am.* 80: (6) 841-848.

Norris, M. J. (1954). Sexual maturation in the desert locust *Schistocerca gregaria* (Forskal) with special reference to the effect of grouping. *Anti. Locust Bulletin.* 18: 1-14.

Norris, M. J.(1957). Factors affecting the rate of sexual maturation of the desert locust, *Schistocerca gregaria* (Forskal) in the laboratory. *Anti. locust Bull.* 28: 26pp.

Norris, M. J. (1959). The influence of day length on imaginal diapause in the red locust, *Nomadacris septemfasciata* (Serv.). *Entomol. Exp. Appl.* 2; 154-68.

Norris, M. J. (1961). Group effects on feeding in adult males of the desert locust, *Schistocerca gregaria* (Forskal) in relation to sexual maturation. *Bull. Ent. Res.* 51: 731-753.

Norris, M. J. (1962). Group effects on the activity and behaviour of adult males of the desert locust, *Schistocerca gregaria* (Forsk.) in relation to sexual maturation. *Anim. Behav.* 10: 275-291.

Norris, M. J. (1963). Laboratory experiments on gregarious behaviour in ovipositing females of the desert locust, *Schistocerca gregaria* (Forsk.) in relation to sexual maturation. *Entomol. Exp. Appl.* 6:269-363.

Norris, M. J. (1964a). Accelerating and inhibiting effects of crowding on sexual maturation in two species of locusts. *Nature Lond.* 203: 784-785.

Norris, M. J.(1964b). Environmental control of sexual maturation in insect. *Symp. R. Ent. Soc. Lond.* 2: 56-65.

Norris, M. J. (1965a). The influence of constant and changing photoperiod on imaginal diapause in the red locust *Nomadacris septemfasciata* Serv. *J. Insect Physiol*. 11: 1105-1119.

Norris, M. J. (1965b). Reproduction of the grasshopper *Anacridium aegyptium* L. in the laboratory. *Proc. R. ent. Soc. Lond. (A)* 40: 19-29.

Norris, M. J.; and M. P., Pener (1965). An inhibitory effect of allatectomized males and females on the sexual maturation of young males adults of *Schistocerca gregaria* (Forsk.) (Orthoptera: Acrididae). *Nature V*. 208: 1122.

Obeng-Ofori, D. ; B., Torto, and A., Hassanali (1993). Evidence for mediation of two releaser pheromones in the aggregation behaviour of the gregarious desert locust, *Schistocerca gregaria* (Forskal) (Orthoptera: Acrididae). *J. Chem. Ecol. V*. 19: No.(8) 1665-1670.

Obeng-Ofori, D.; B. Torto; P.G.N., Njagi; A., Hassanali; and H., Amiani (1994a). Fecal volatiles as part of the aggregation pheromone complex of the desert locust, *Schistocerca gregaria* (Forskal) (ORTHOPTERA:ACRIDIDAE). *J. Chem. Ecol. V*. 20: No.(8) 2077-2087.

Obeng-Ofori, D.; P.G.N., Njagi; B., Torto; A., Hassanali, and H., Amiani (1994b). Sex differentiation studies relating to releaser aggregation pheromones of the gregarious desert locust *Schistocerca gregaria* (Orthoptera: Acrididae). *Entomol. exp. appl*. 85-91.

Okay, S. (1953). Formation of green pigment and colour changes in Orthoptera. *Bull. Ent. Res. Lond*. 44: 299-315.

Pener, M. P. (1967). Effects of allatectomy and sectioning of the nerves of the corpora allata on Oocyte growth male sexual behaviour and colour change in adult of *Schistocerca gregaria*. *J. Insect Physiol*. 13: 665-684.

Perring, F. H.; and K., Mellanby (1981). *ECOLOGICAL EFFECTS OF PESTICIDE* Linnean Society symposium series NO.5. Published by Academic press.

Popov, G. B. (1958). Ecological studies on oviposition by swarms of the desert locust (*Schistocerca gregaria* Forskal). Entomol. Exp. Appl. 6:279-303.

Rankin, M.A.; and H. M., Riddiford (1977). Hormonal control of migratory flight in *Oncopeltus fasciatus*: The effects of the corpus cardiacum, corpus allatum, and starvation on migration and reproduction, *Gen. Comp. Endocr.* 33; 309-321.

Richards, M. J.; and M. A., El Mangoury (1968). Further experimental on the effect of social factor on the rate of sexual maturation in the desert locust. *Nature V.* 219: 865-866.

Ruberson, J.R. ; L., Bush; and T.J., Kring (1991). Photoperiodic effect on diapause induction and development in the predator *Orius insidiosus* (Heteroptera: Anthocoridae). *Environmental Entomology V.* 20: (3) P. 786-789.

Saunders, DS; VC, Henrich and LI., Gilbert (1989). Induction of diapause in Drosophila melanogaster: photoperiodic regulation and the impact of arrhythmic clock mutation on time measurement. *Proceeding of the national academy of sciences of the United States of America.* 86: (10) 3748-3752.

Solbreck, C. (1971). Displacement of marked *Lygaeus equestris* (L.) (Heteroptera: Lygaeidae) during pre-and posthibernation migrations. *Acta. Ent. Fenn.* 28: 74-83.

Solbreck, C. (1972). Sexual cycle, and changes in feeding activity and fat body size in relation to migration in *Lygaeus equestris* (L.) (Heteroptera: Lygaeidae). *Ent. Scand.* 3: 267-274.

Solbreck, C. (1976). Flight patterns of *Lygaeus equestris* (L.) (Heteroptera) in spring and autumn with special reference to the influence of weather. *Oikos* 27: 134-143.

Solbreck, C. (1978). Migration, diapause, and direct development as alternative life histories in a seed bug, *Neacoryphus bicrucis* (Say). In: *Evolution of insect migration and diapause. Springer* 195-217.

Solbreck, C.(1979). Induction of diapause in a migratory seed bug, *Neacoryphus bicrucis* (Say) (Heteroptera: Lygaeidae). *Oecologia* 43: 41-49.

Steedman, A. (1988). *LOCUST HANDBOOK* Over seas. Developmental natural Resources Institute LONDON.

Stein, W. Bie; B., Herstad; H., Olafsson, and L., Somme (1989). *LOCUST AND GRASSHOPPER CONTROL*. pp 64.

Stevenson, A. B.; G., Boivin (1990). Interaction of temperature and photoperiod in control of reproductive diapause in the carrot weevil (Coleoptera: Curculionidae). *Environmental Entomology*. 19: (4) 836-841.

Tanaka, H. (1982). Diapause in Locusta migratoria: III. Geographic variation. *Ann. Congr. Jap. Soc. Ent. Zool.* 26: 2 Abstract (in Japanese).

Tanaka, S.; T., Hakomori; and E., Hasegawa (1993). Effects of day length and hopper density on reproductive traits in a Japanese population of the migratory locust, *Locusta migratoria* L., *J. Insect Physiol. V*. 39: No. (7) 571-580.

Tauber, M. J.; C. A., Tauber; and S., Masaki (1986). *Seasonal Adaptation of insects*. Oxford University Press, London.

Torto, B.; D., Obeng-Ofori; P. G. N., Njagi; A., Hassanali; and H., Amiani (1994). Aggregation pheromone system of the adult gregarious desert locust *Schistocerca gregaria* (Forskal). *J. Chem. Ecol*. 20: 7: 1749-1762.

Tracy,-JL; and JR, Nechols (1988). Comparison of thermal responses, reproductive biologies, and population growth potentials of the squash bug egg parasitoids *Ooencyrtus anasae* and *Ooencyrtus sp.* (Hymenoptera: Encyrtidae). *Environmental Entomology* 17: (4) 636-643.

Uvarov, B. (1966). *Grasshopper and locusts A HANDBOOK OF GENERAL ACRIDIOLOGY V*. I. Cambridge University press.

Uvarov, B. (1977). *Grasshopper and locusts A HANDBOOK OF GENERAL ACRIDIOLOGY V*. II. Cambridge University press.

Vinogradova, E. B. (1969). Experimental investigation of the ecological factors causing diapause of the adults of blood-sucking mosquitoes (Diptera,Culicidae). (In Russian with English summary) *Ent. Obozr.* 39: 327-340.

Waloff, N.; and O. W., Richards (1958). The biology of the chrysomelid beetle, *Phytodecta olivaceae* (Forster) (Coleoptera: Chrysomelida). *Trans. R. ent. Soc. Lond.* 110: 99-116.

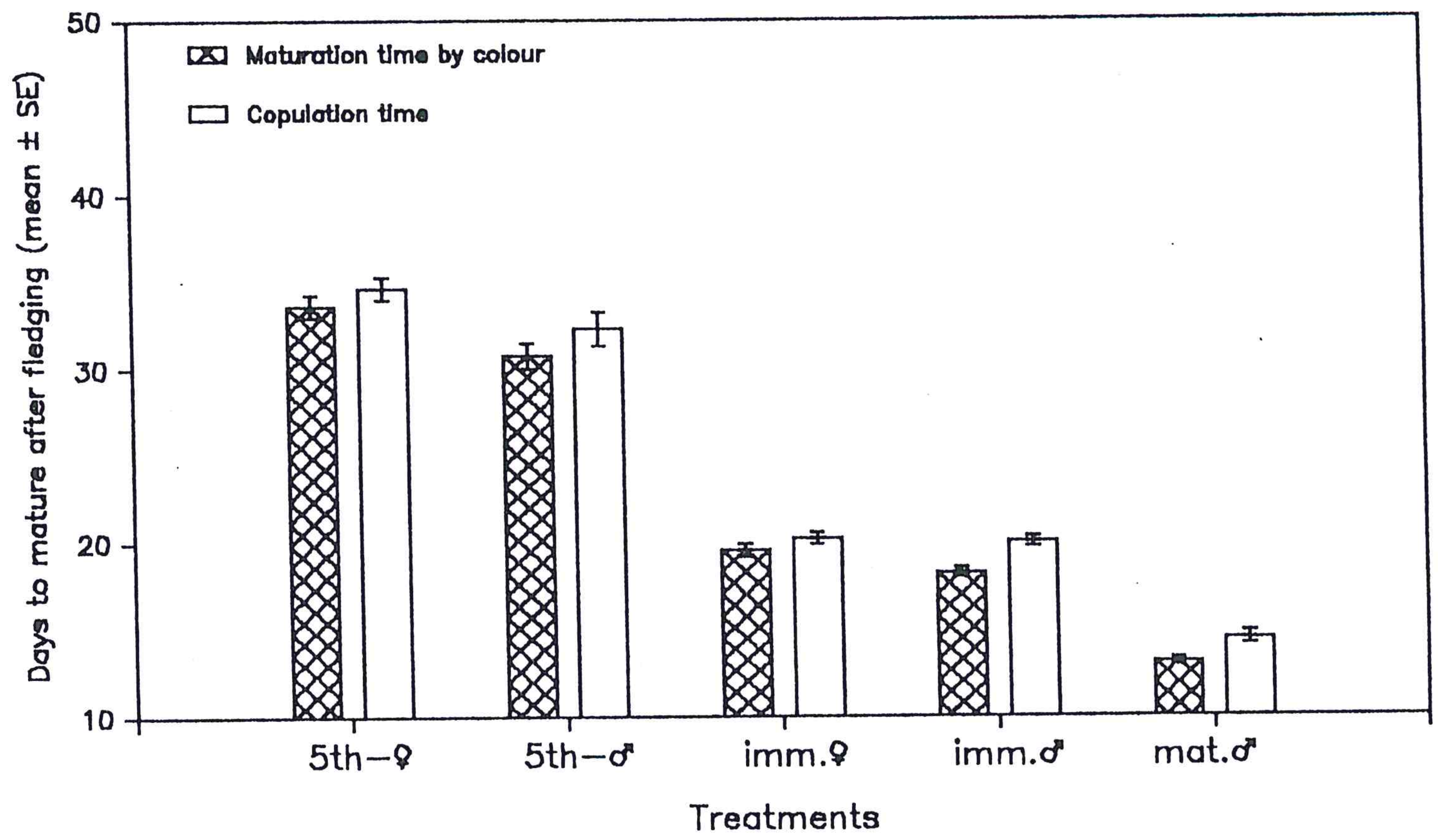
Wardhaugh, KG (1986). Diapause strategies in the Australian plague locust (*Chortoicetes terminifera* Walker). *Evolution of insect life cycles*. New York, USA; *Springer* 89-104.

Watabe, HA (1988). Photoperiodic response of domestic *Drosophila funebris* (Diptera, Drosophilidae), with reference to its adaptive significance. *Kontyu*. 56: 3: 667-673.

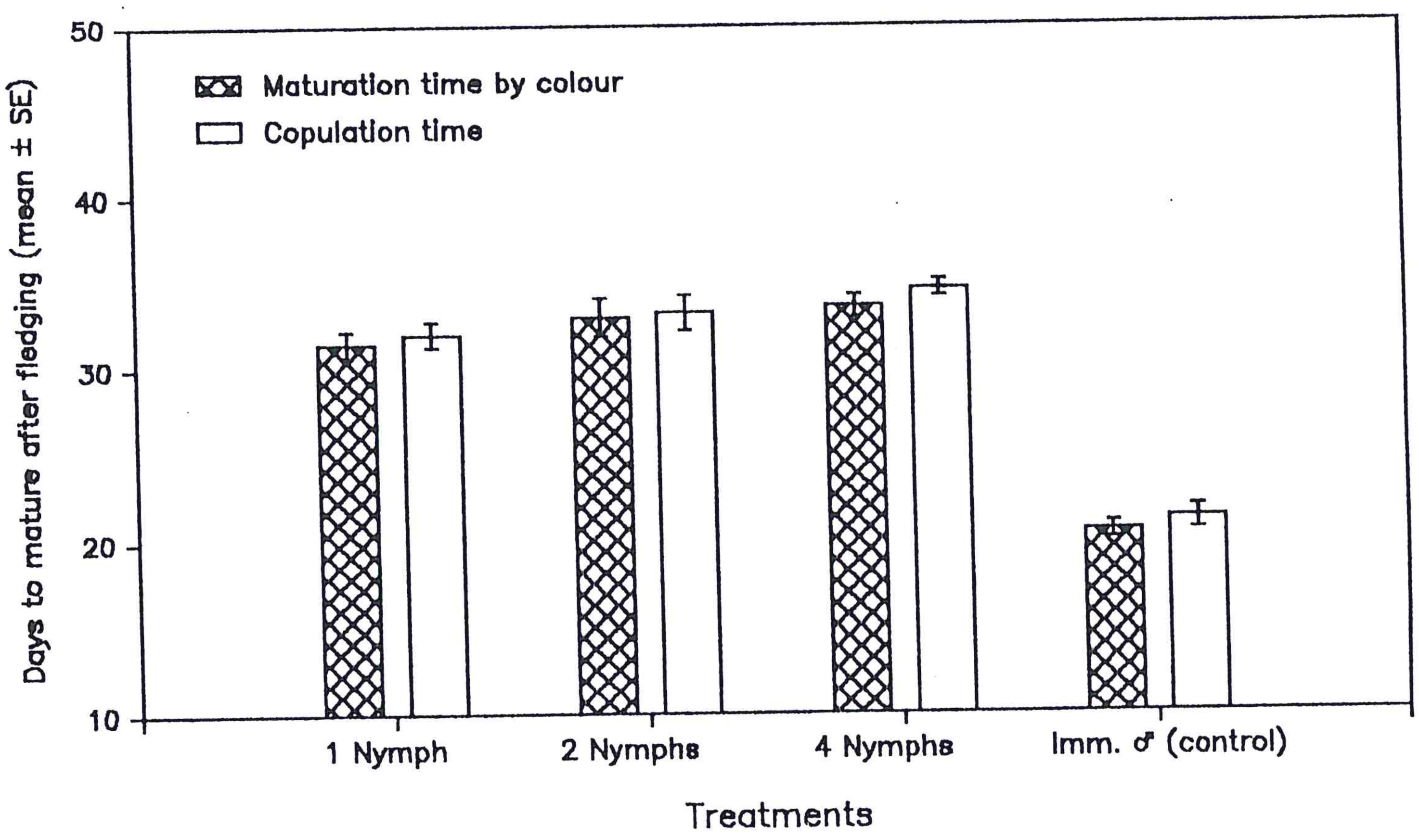
Woodward, T. E. (1952). Studies on the reproductive cycle of three species of British Heteroptera with special reference to the over wintering stages. *Trans. R. Ent. Soc. Lond*. 103: 171-218.

Woude, H.; and HA, Verhoef (1988). Reproductive diapause and cold hardiness, in temperate *Collembola Orchesella cincta* and *Tomocerus miner*. *J. Insect Physiol*. V. 34: (5) 387-392.

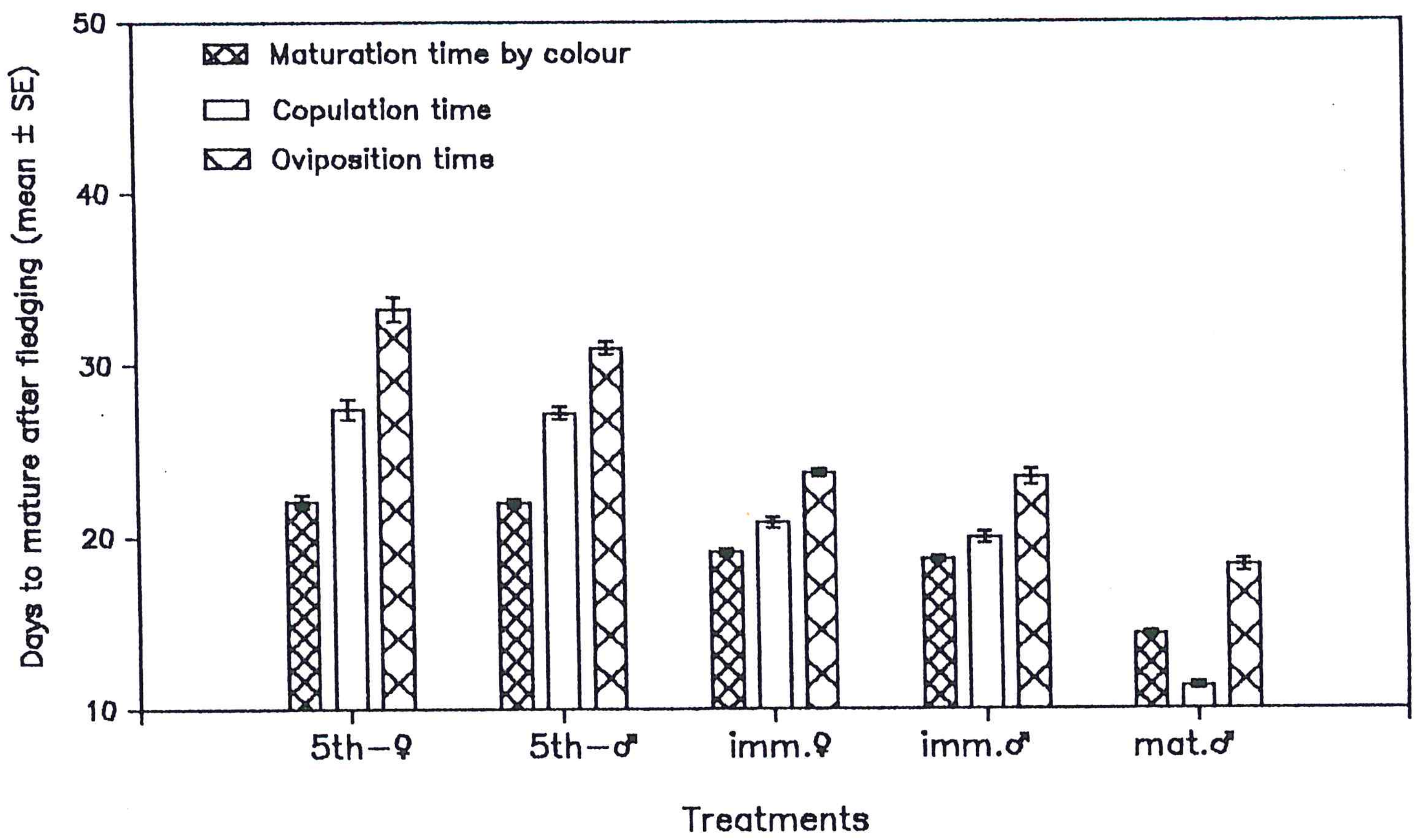
APPENDICES



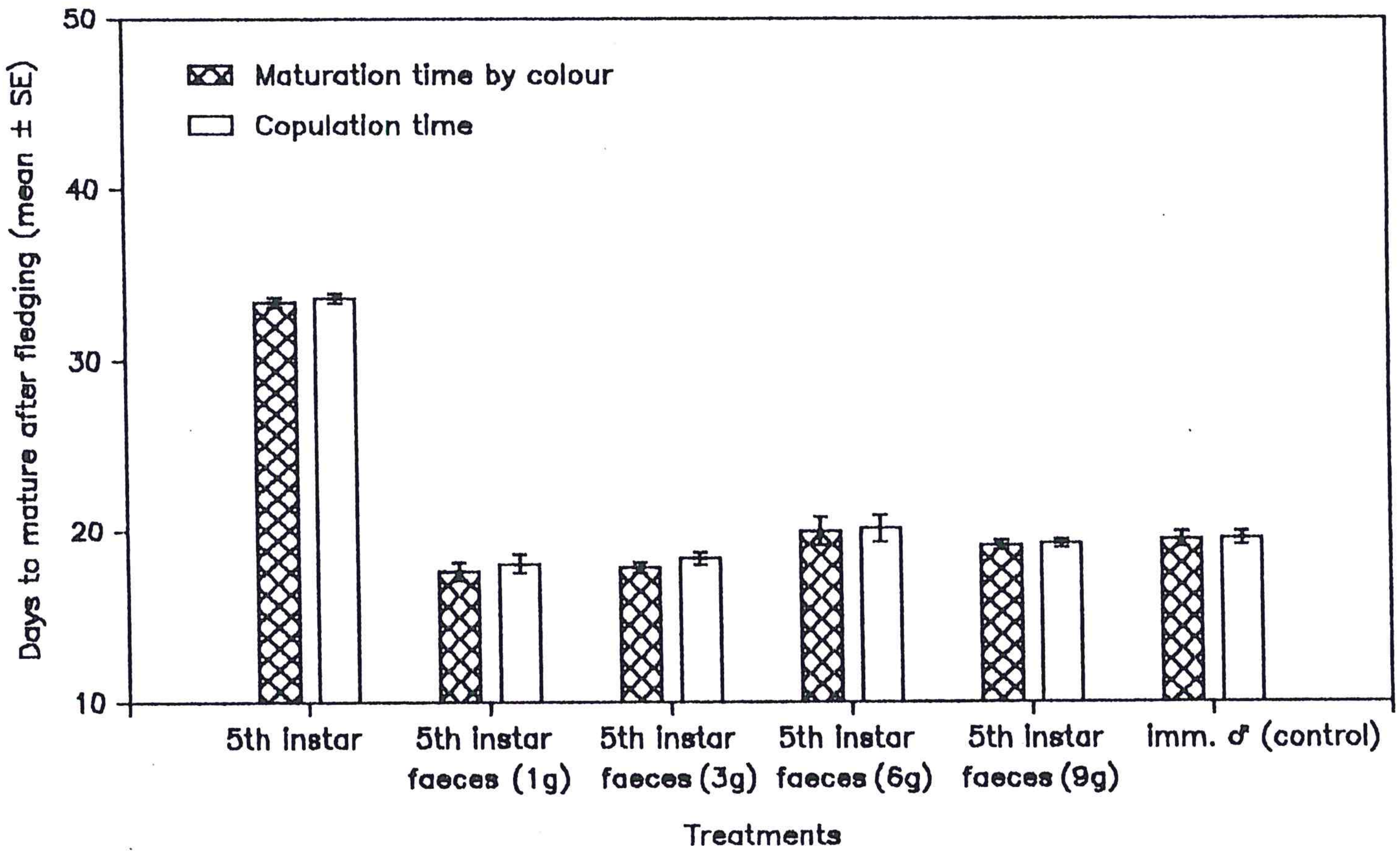
Appen. A. Maturation time of immature males in the presence of female and male 5th instar nymphs, immature females (control), immature males (control) and mature males.



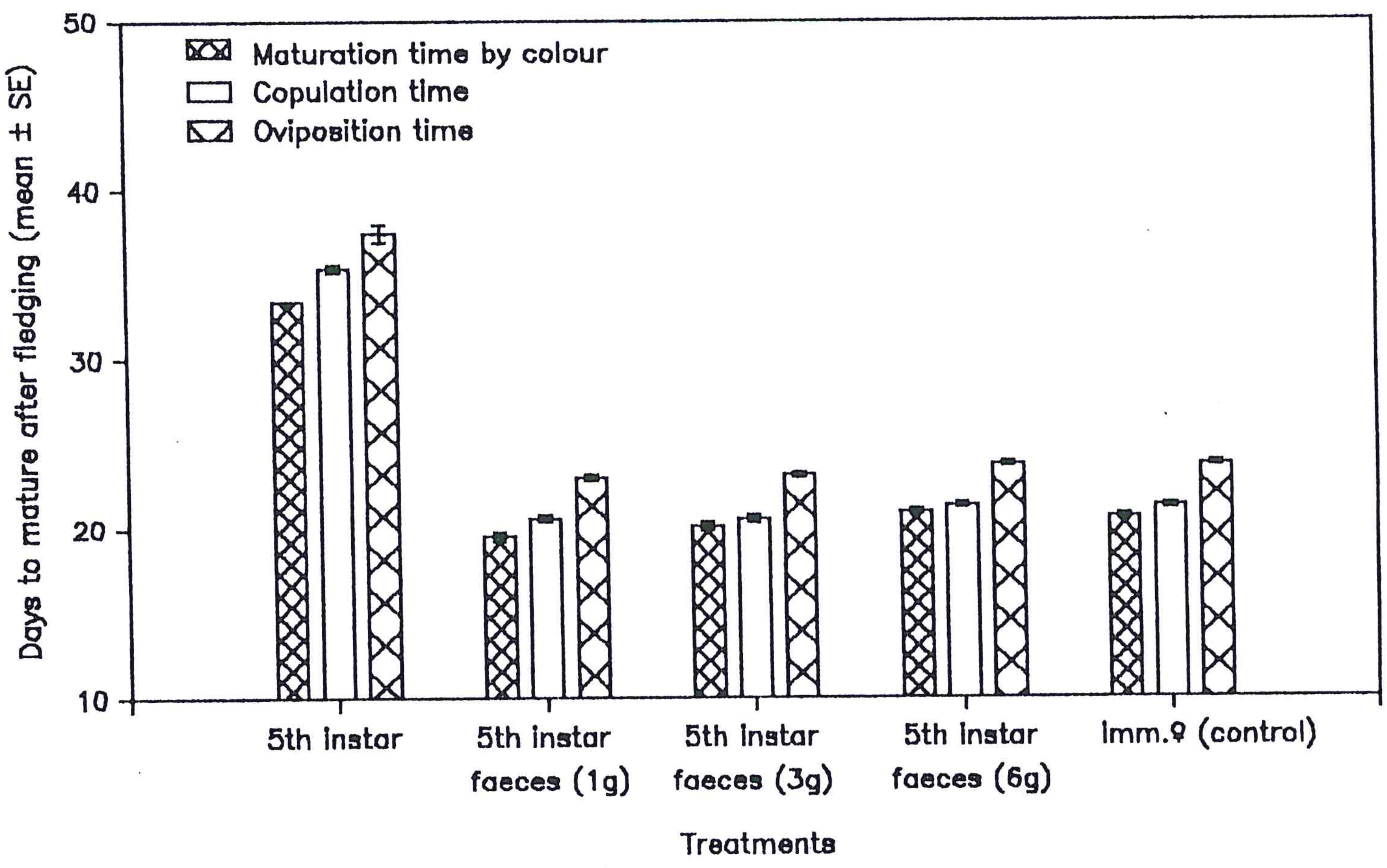
Appen. B. Maturation time of immature males in the presence of one, two and four 5th instar nymphs, and immature males (control).



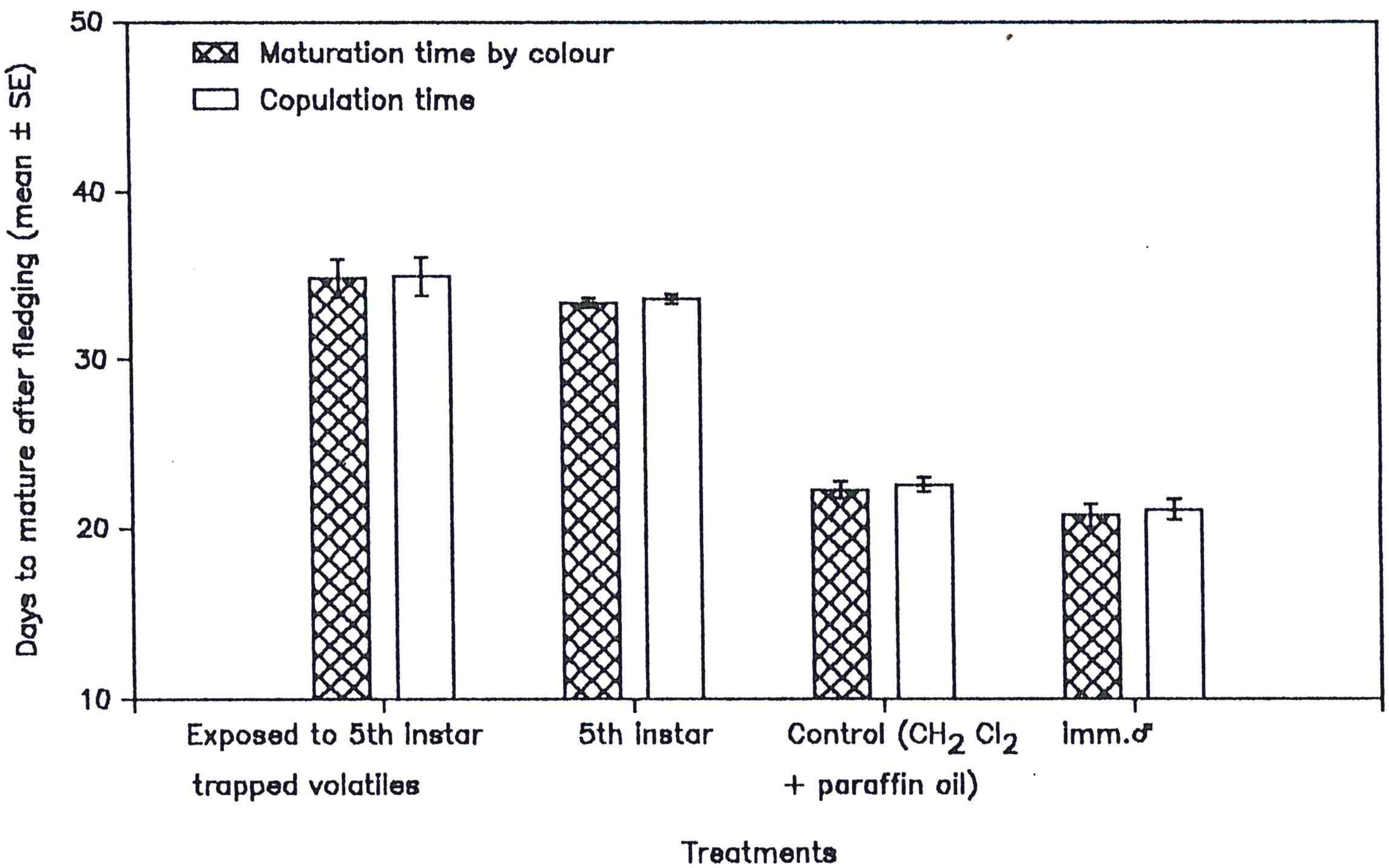
Appen. c. Maturation time of immature females in the presence of female and male 5th instar nymphs, immature females (control), immature males (control) and mature males.



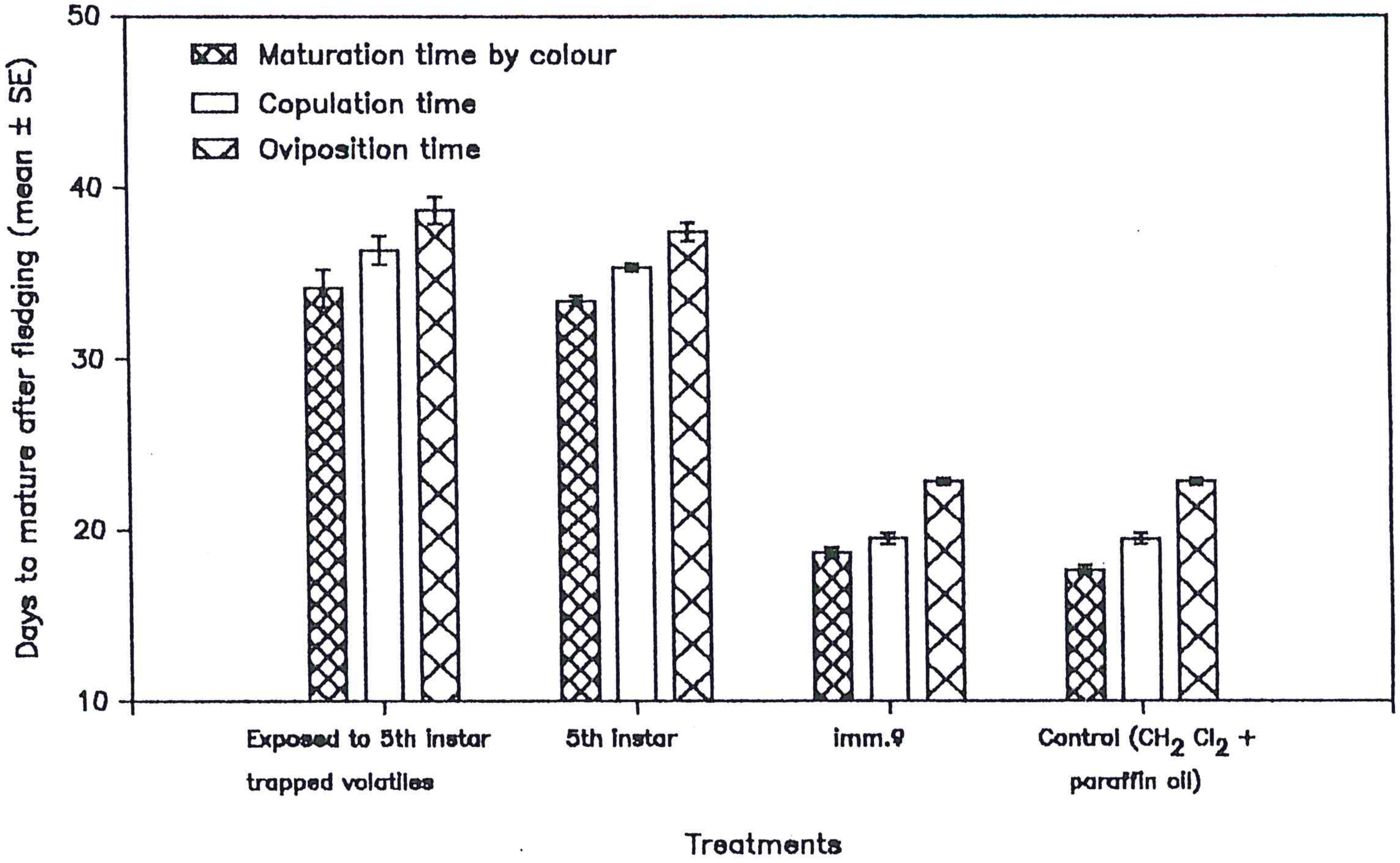
Appen. D. Maturation time of immature males exposed to 5th instar nymphs, 5th instar faeces (1, 3, 6 and 9g) and control (immature males).



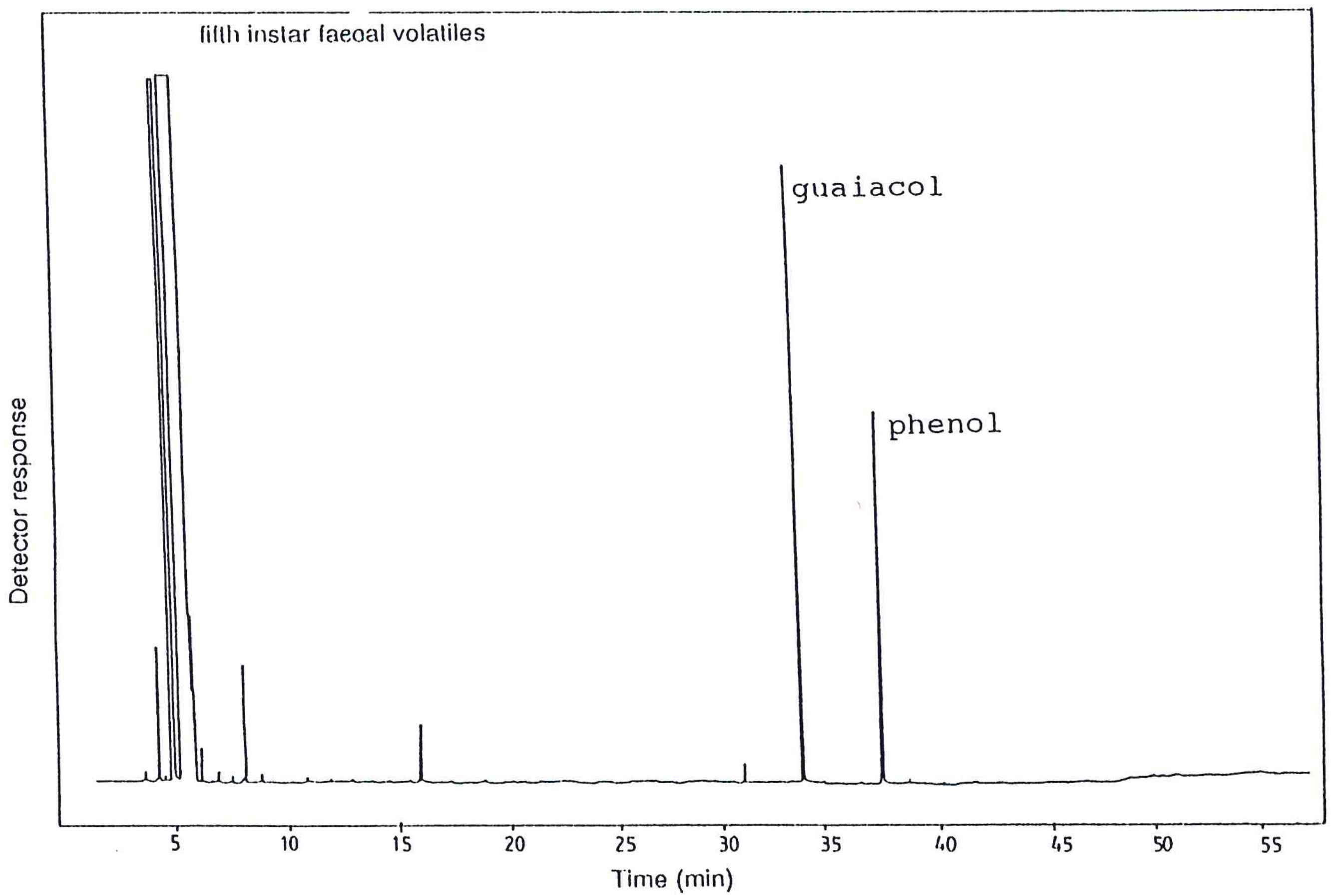
Appen. E. Maturation time of immature females exposed to 5th instar nymphs, 5th instar faeces (1, 3 and 6g), and control (immature females).



Appen. F. Maturation time of immature males exposed to 5th instar nymphs trapped volatiles and control (CH_2 Cl_2 + paraffin oil).

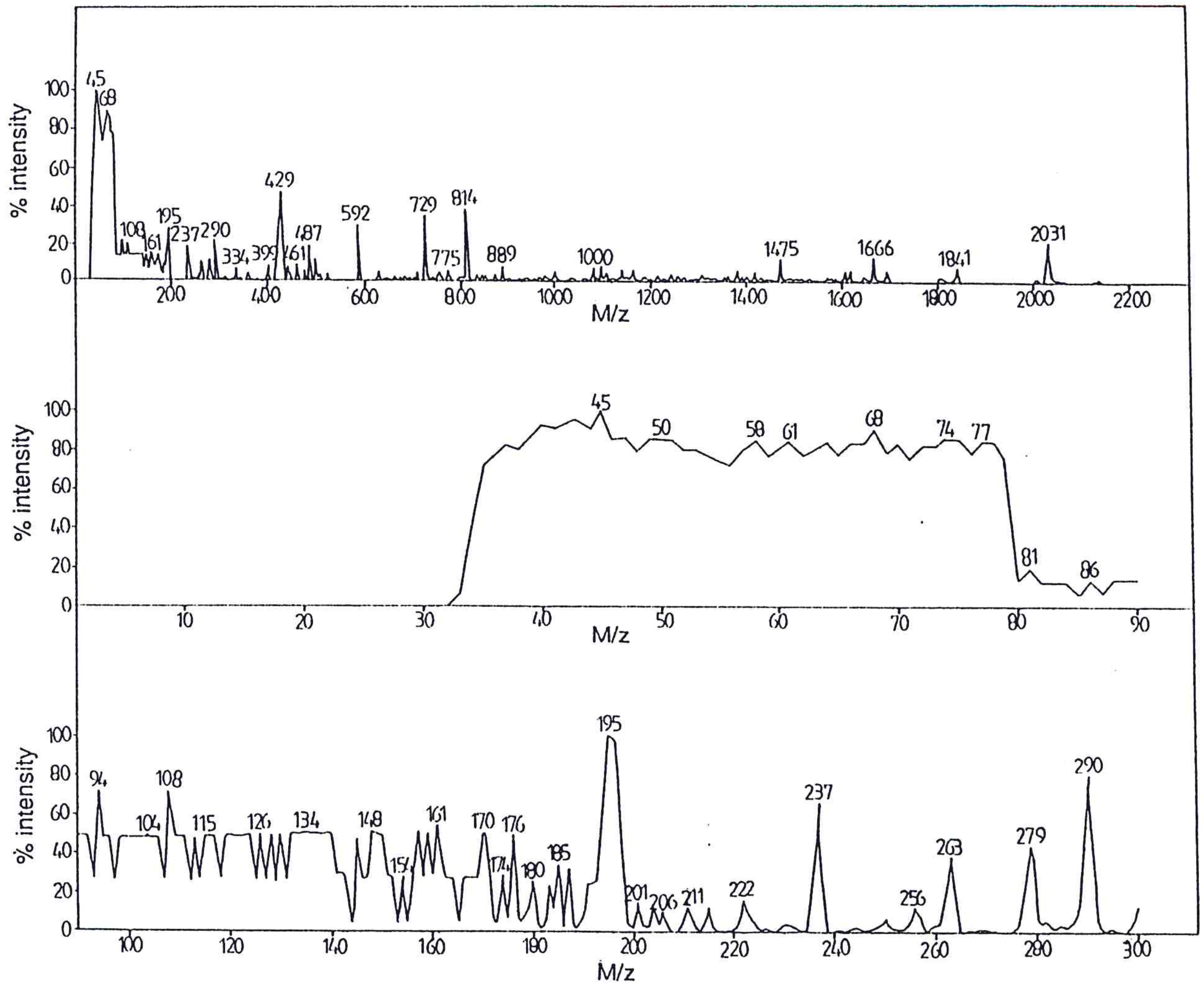


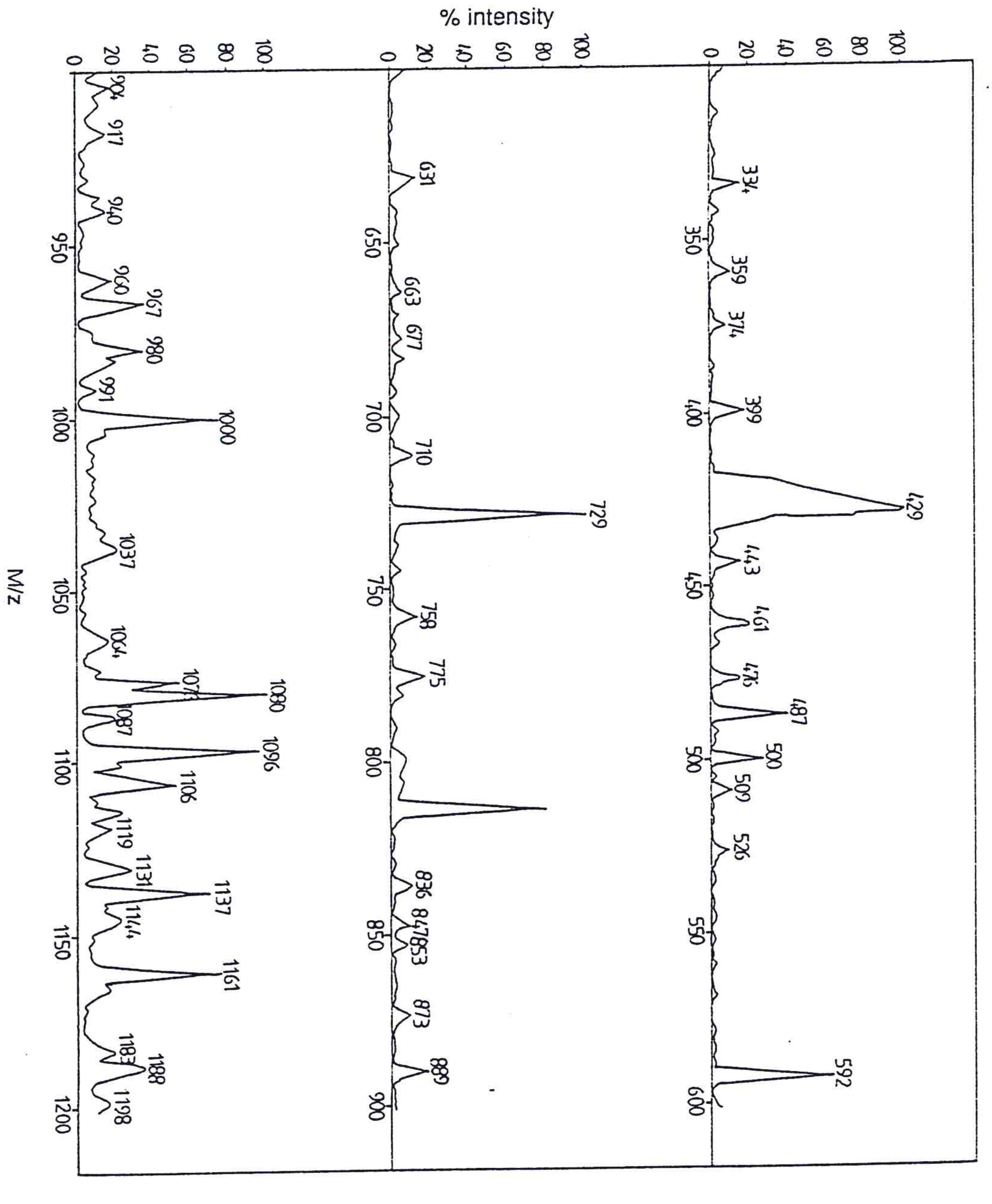
Appen. G. Maturation time of immature females exposed to 5th instar nymphs, 5th instar nymphs trapped volatiles and control (CH_2 Cl_2 + paraffin oil).

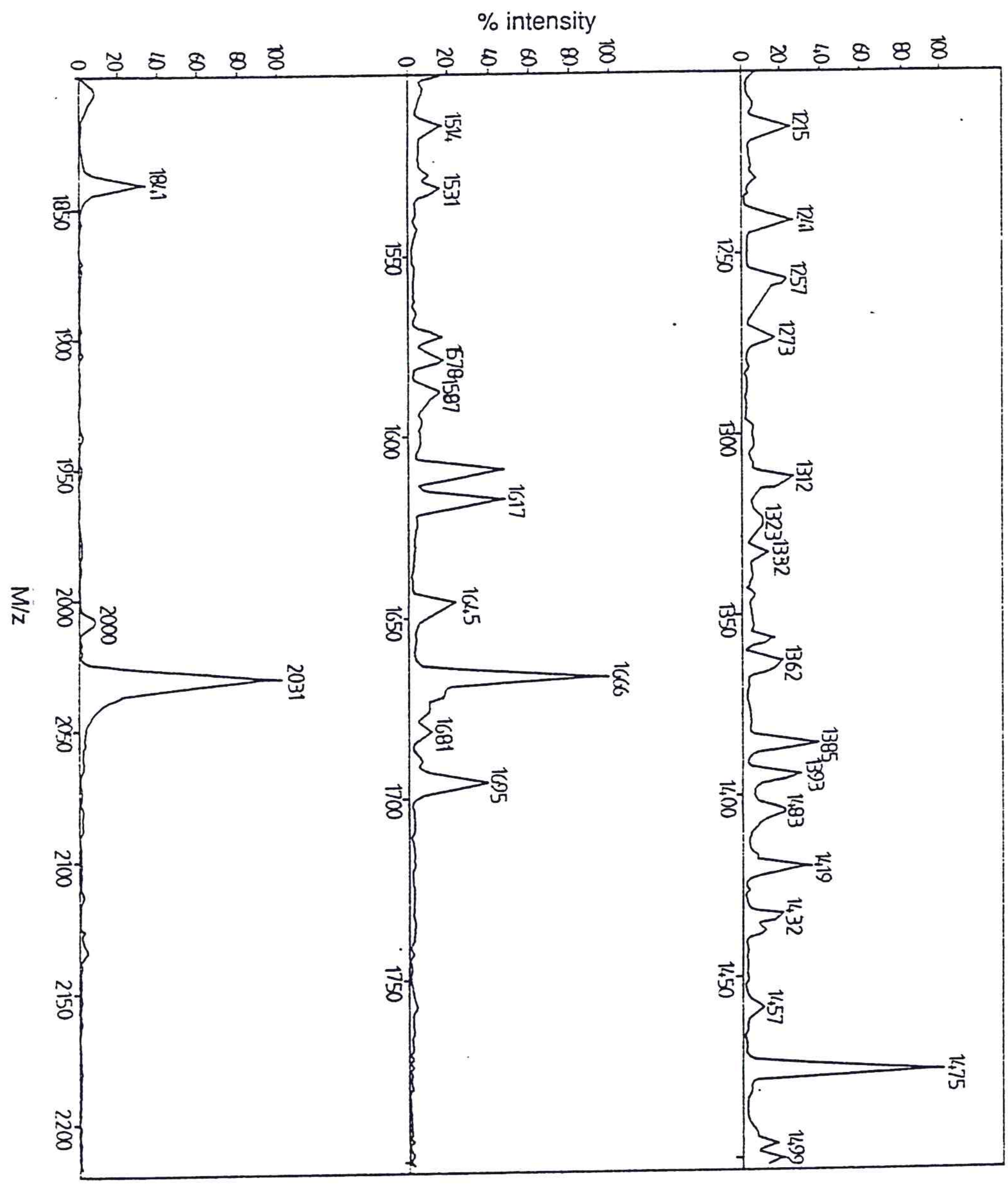


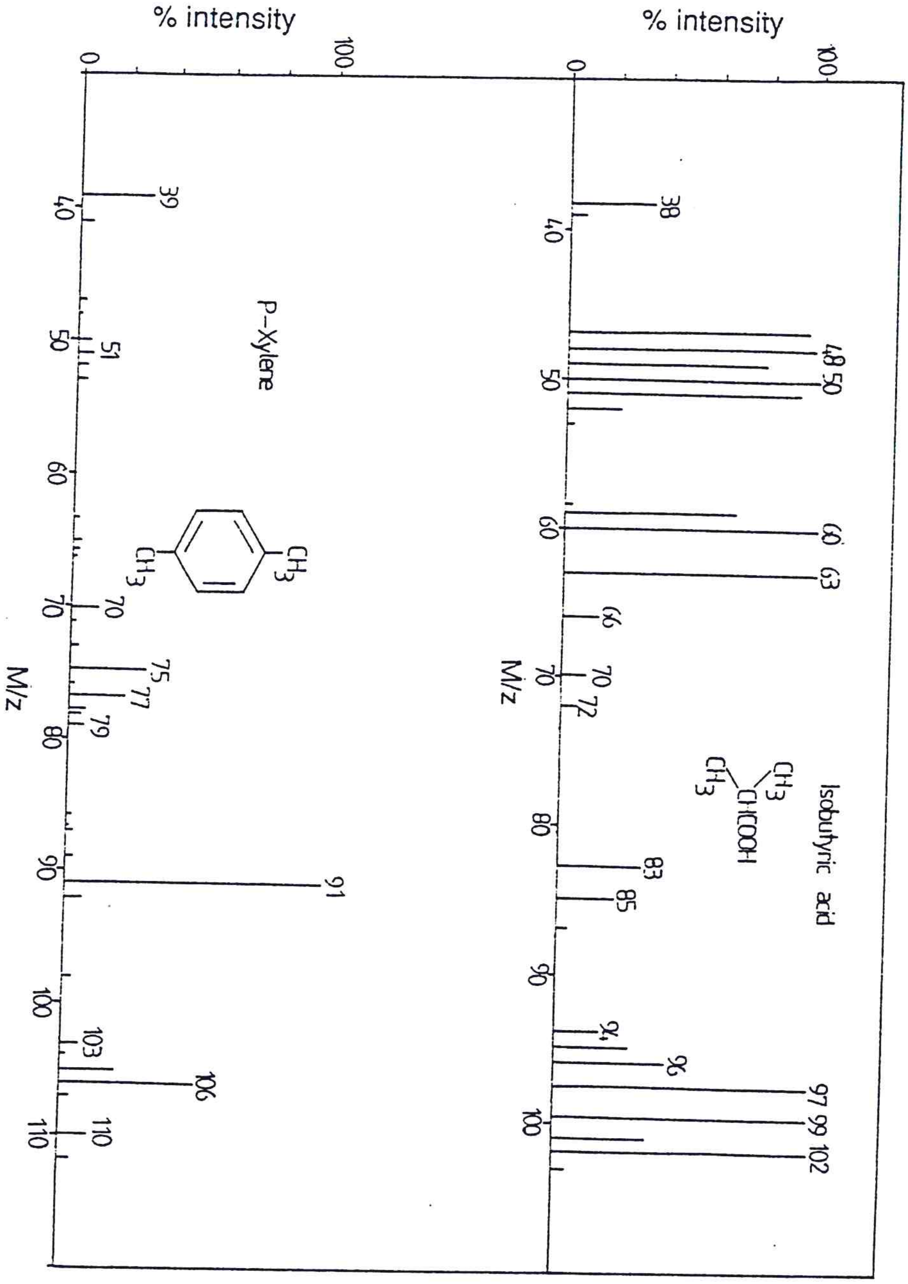
Appen. H. Gas chromatogram of volatiles collected from gregarious fifth instar faeces of *S. gregaria*. injected onto a 50-m Carbowax 20 M capillary column.

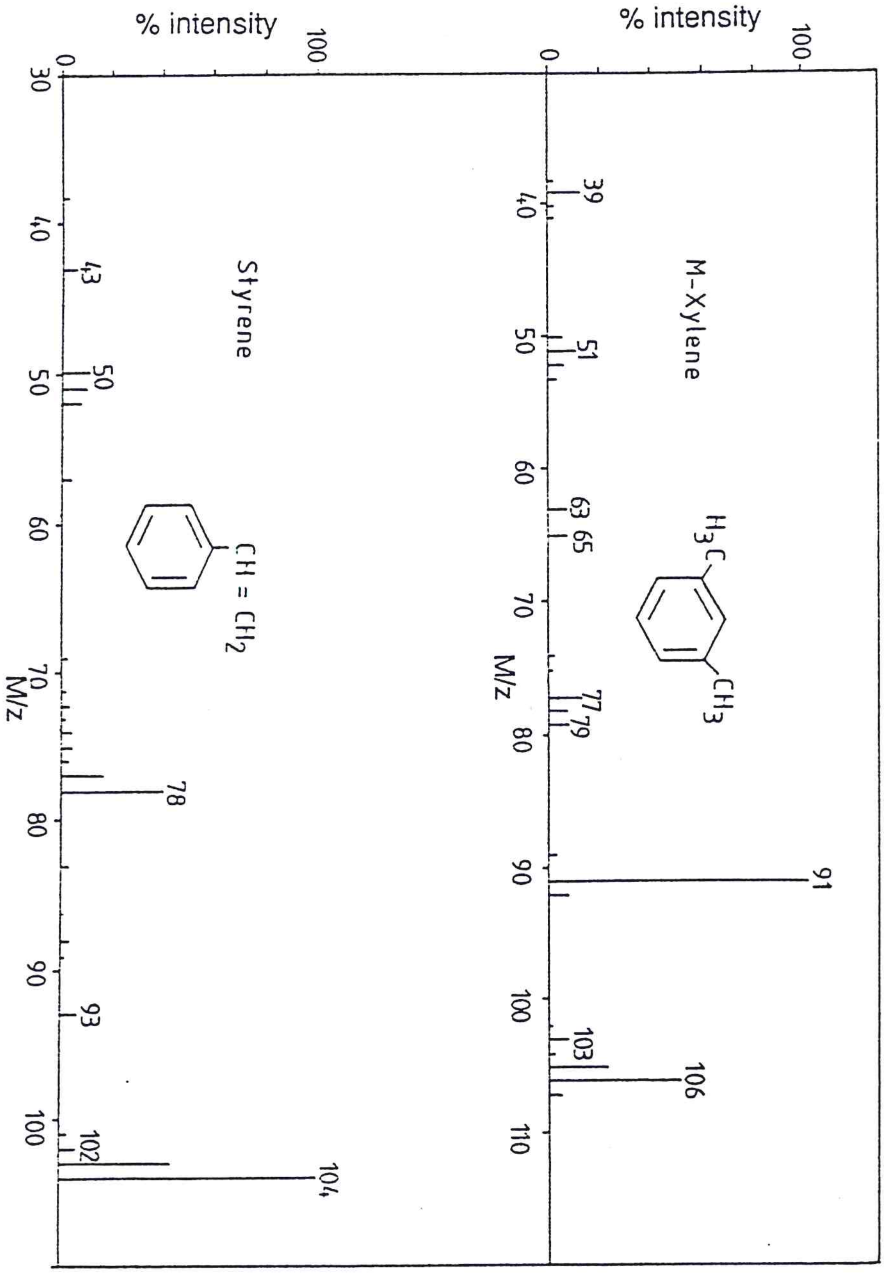
APPENDIX (1) MASS SPECTRUM OF FIFTH NYMPHAL VOLATILES

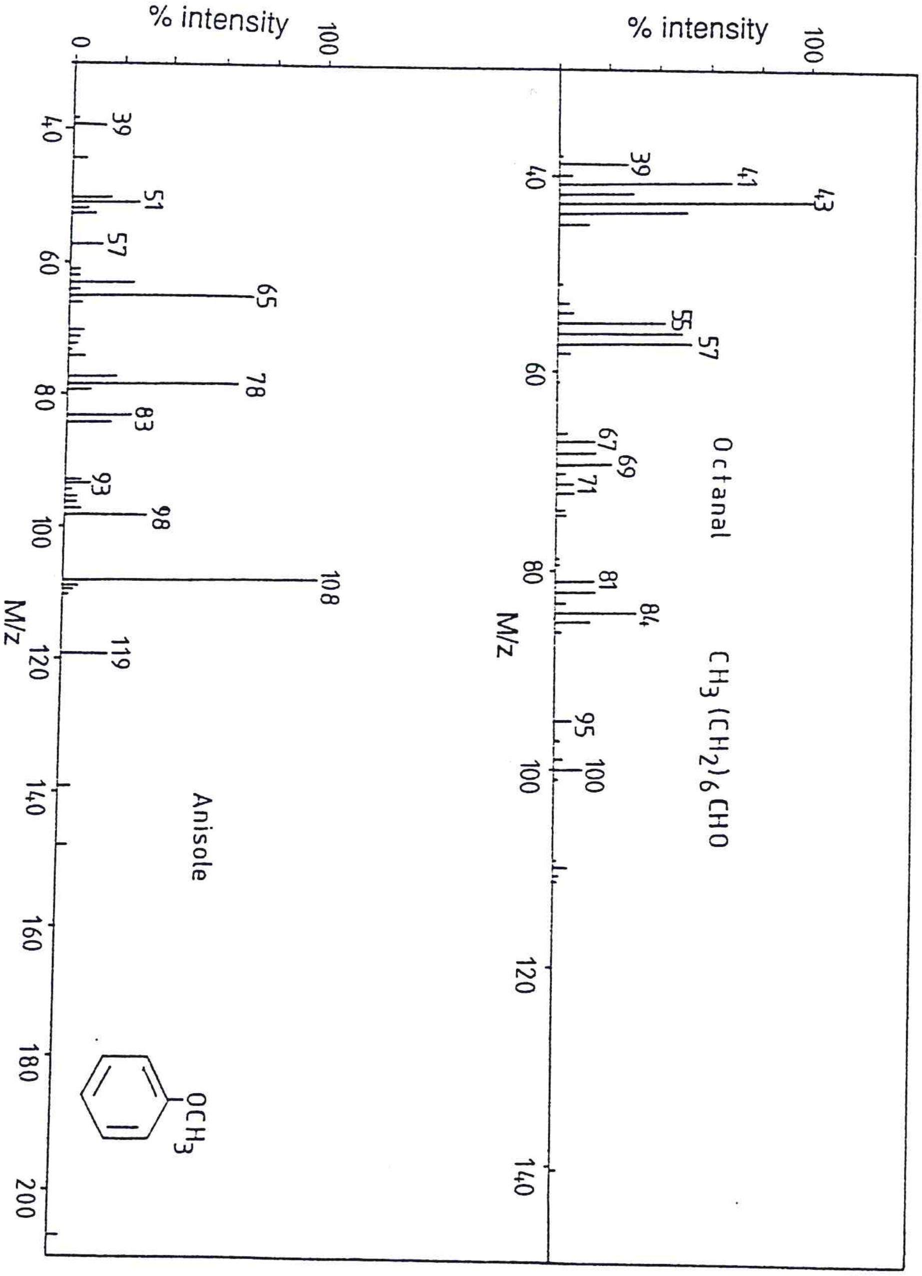



% intensity
M/z
334
359
374
399
429
443
461
475
487
500
509
526
592
631
663
677
710
729
758
775
836
847
853
873
889
904
917
940
960
967
980
991
1000
1037
1064
1080
1087
1096
1106
1119
1131
1137
1144
1161
1183
1188
1198

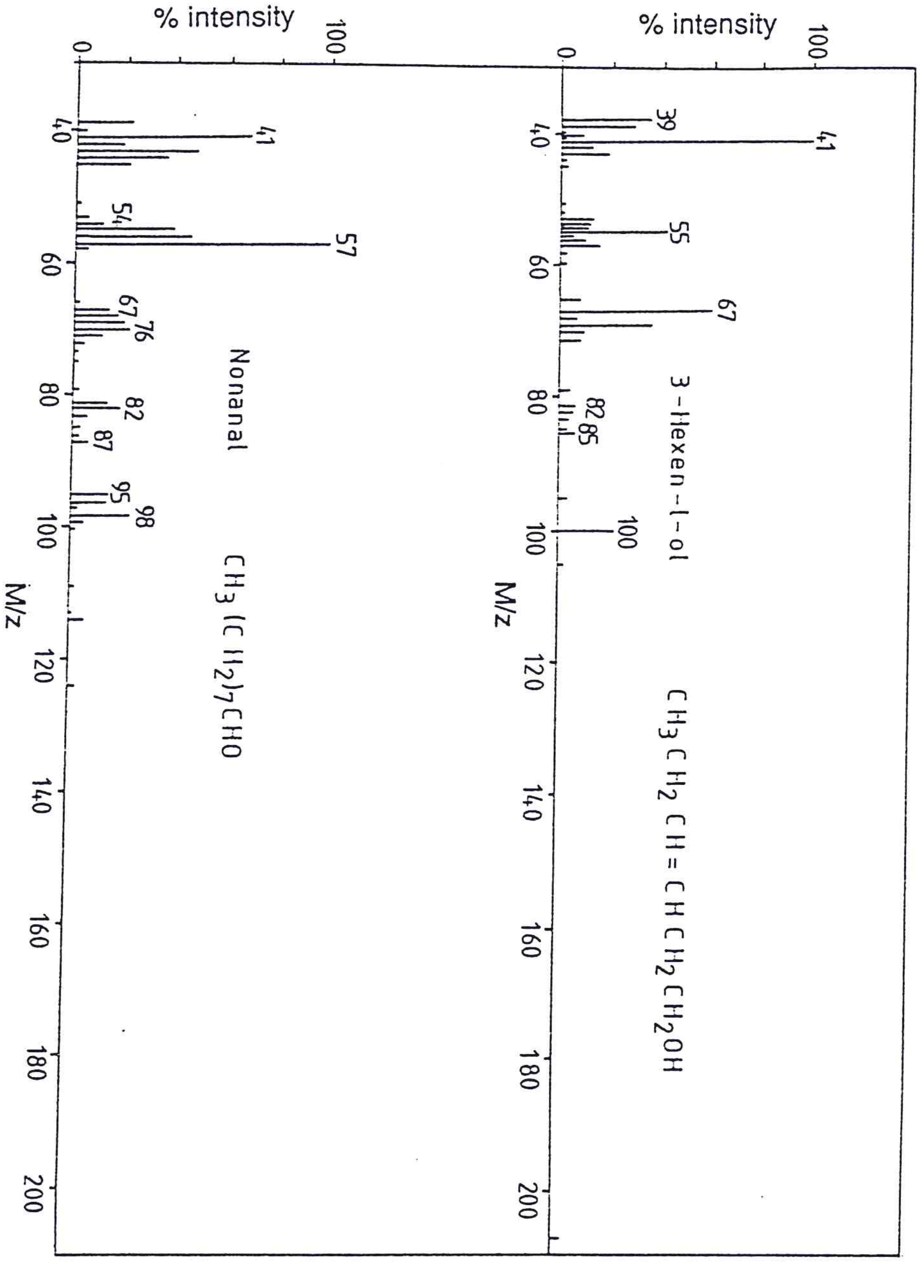

% intensity
M/z
1215
1241
1257
1273
1312
1323
1332
1362
1385
1393
1403
1419
1432
1457
1475
1499
1514
1531
1579
1587
1617
1645
1666
1681
1695
1841
2000
2031


% intensity
% intensity
Isobutyric acid
P-Xylene
M/z
M/z

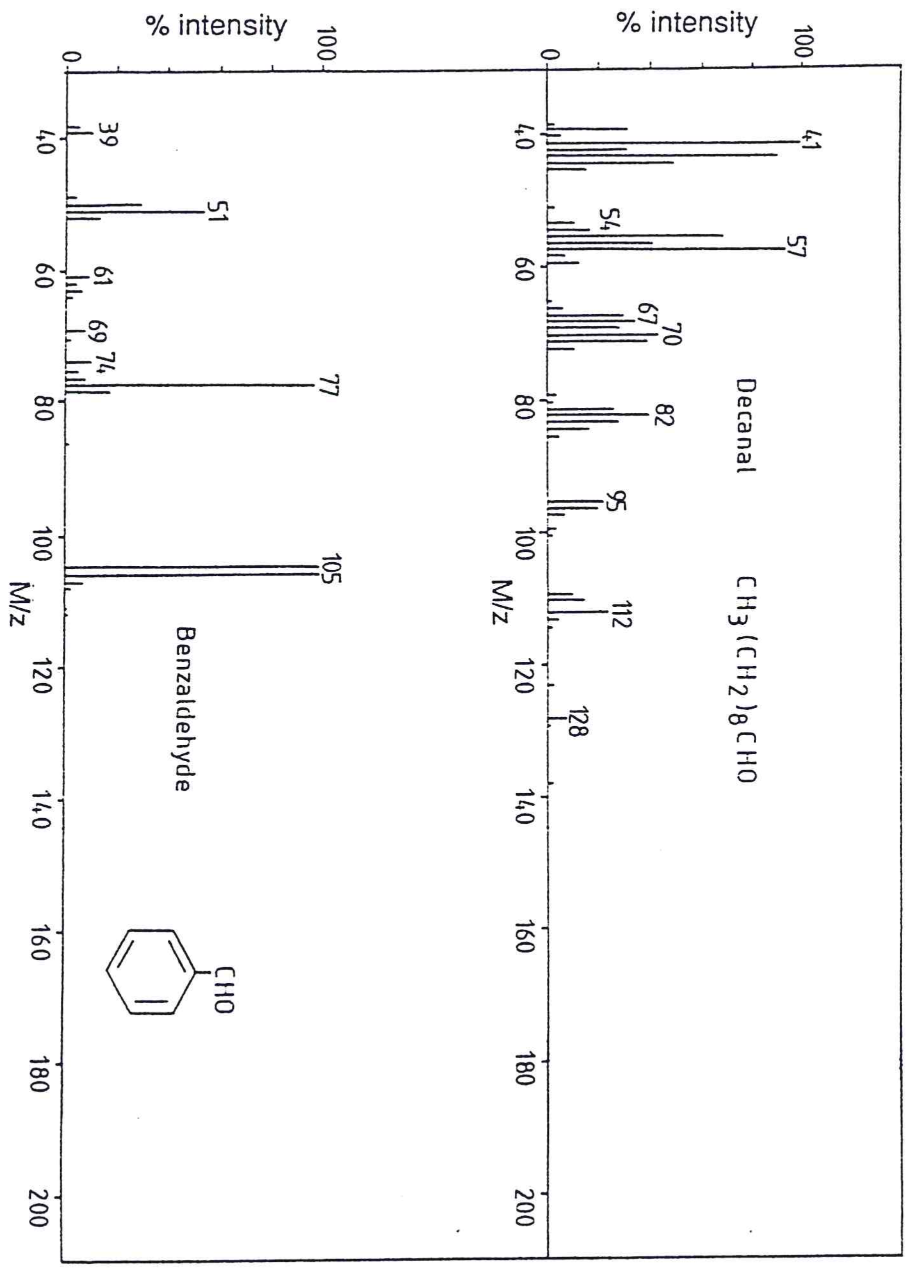

M-Xylene
Styrene
% intensity
% intensity
M/z
M/z
H3C
CH3
CH = CH2
39
51
63 65
77 79
91
103
106
43
50
78
93
102
104

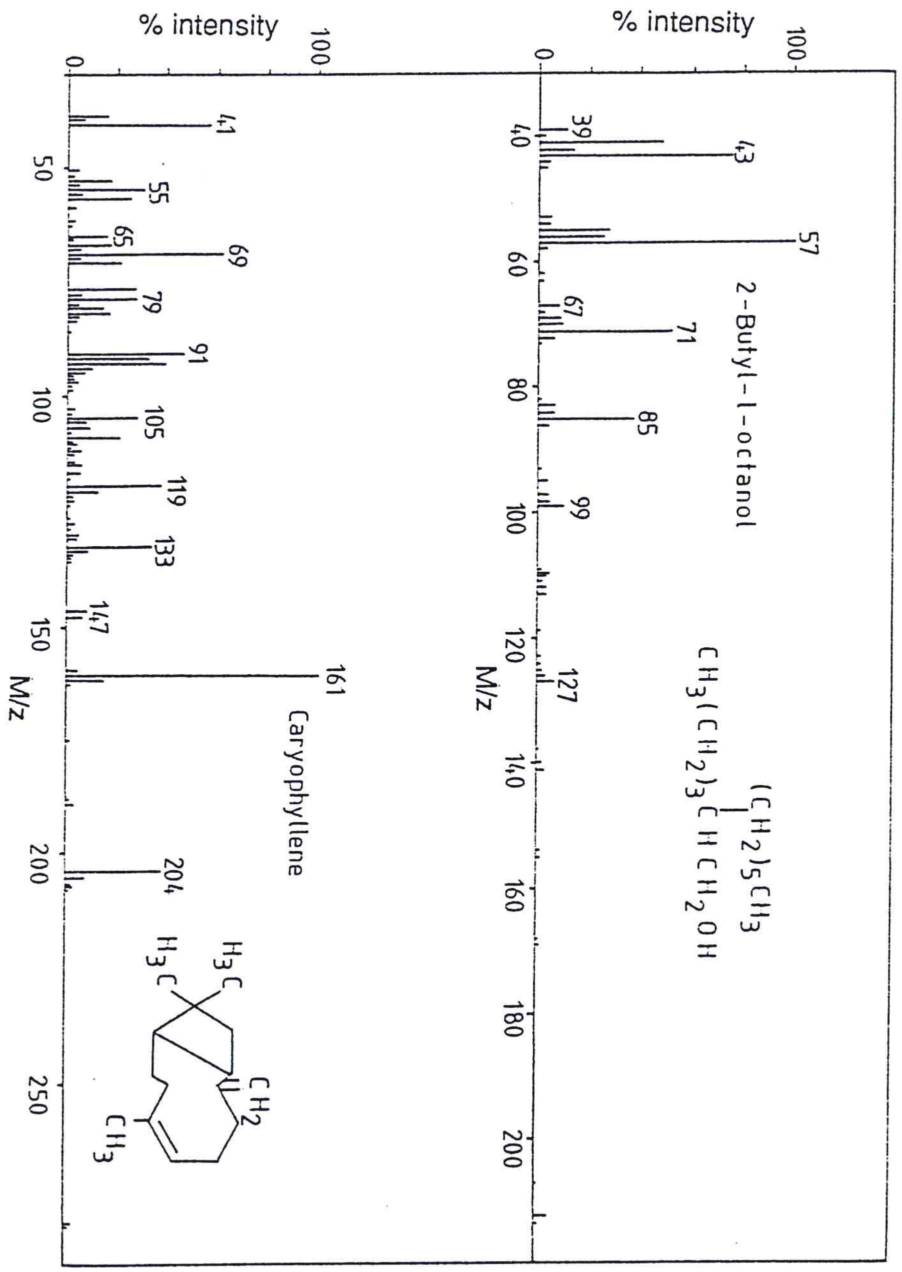


% intensity
100
Octanal
CH3 (CH2)6 CHO
M/z
% intensity
0
100
Anisole
OCH3
M/z

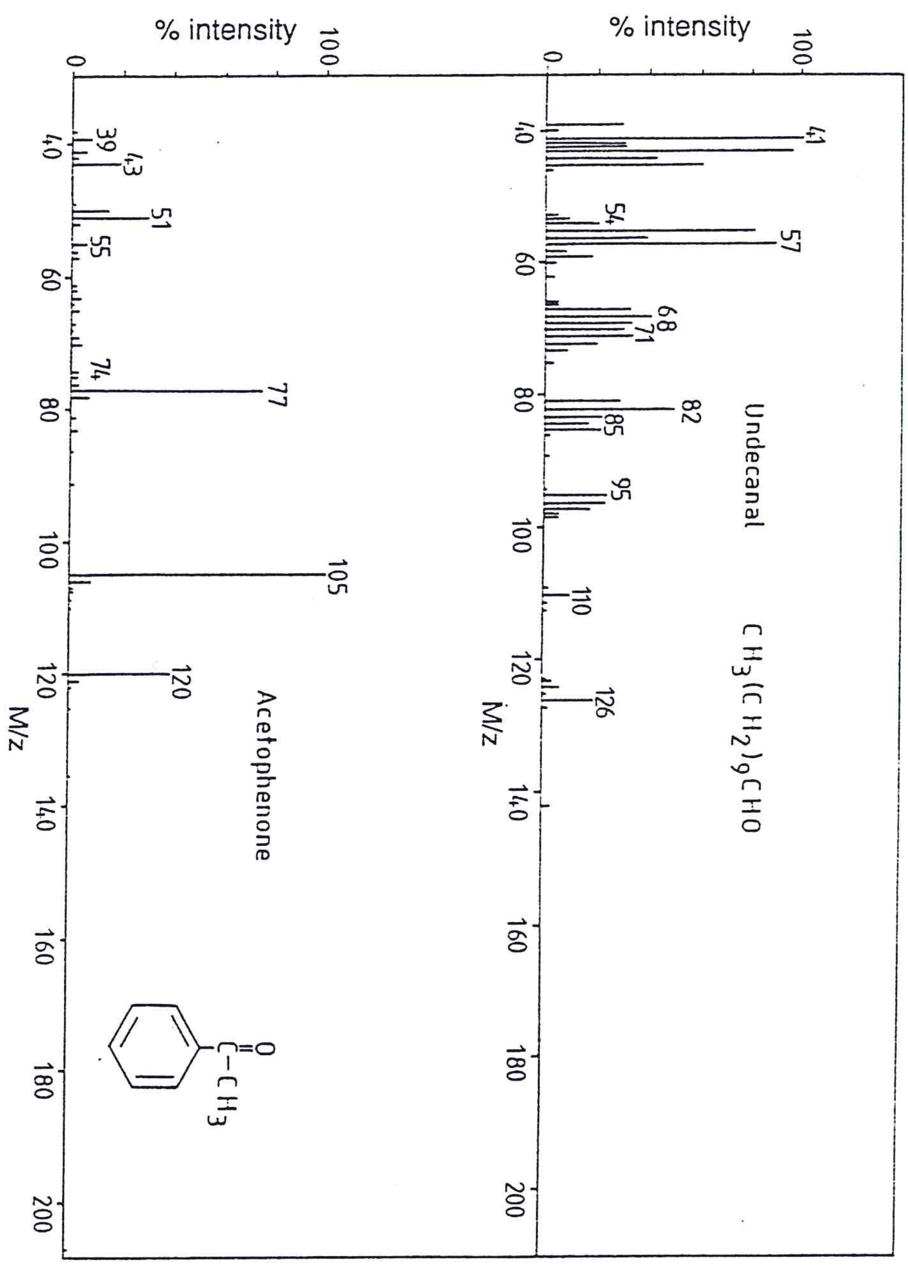


% intensity
3-Hexen-1-ol
$CH_3CH_2CH=CHCH_2CH_2OH$
% intensity
Nonanal
$CH_3(CH_2)_7CHO$
M/z

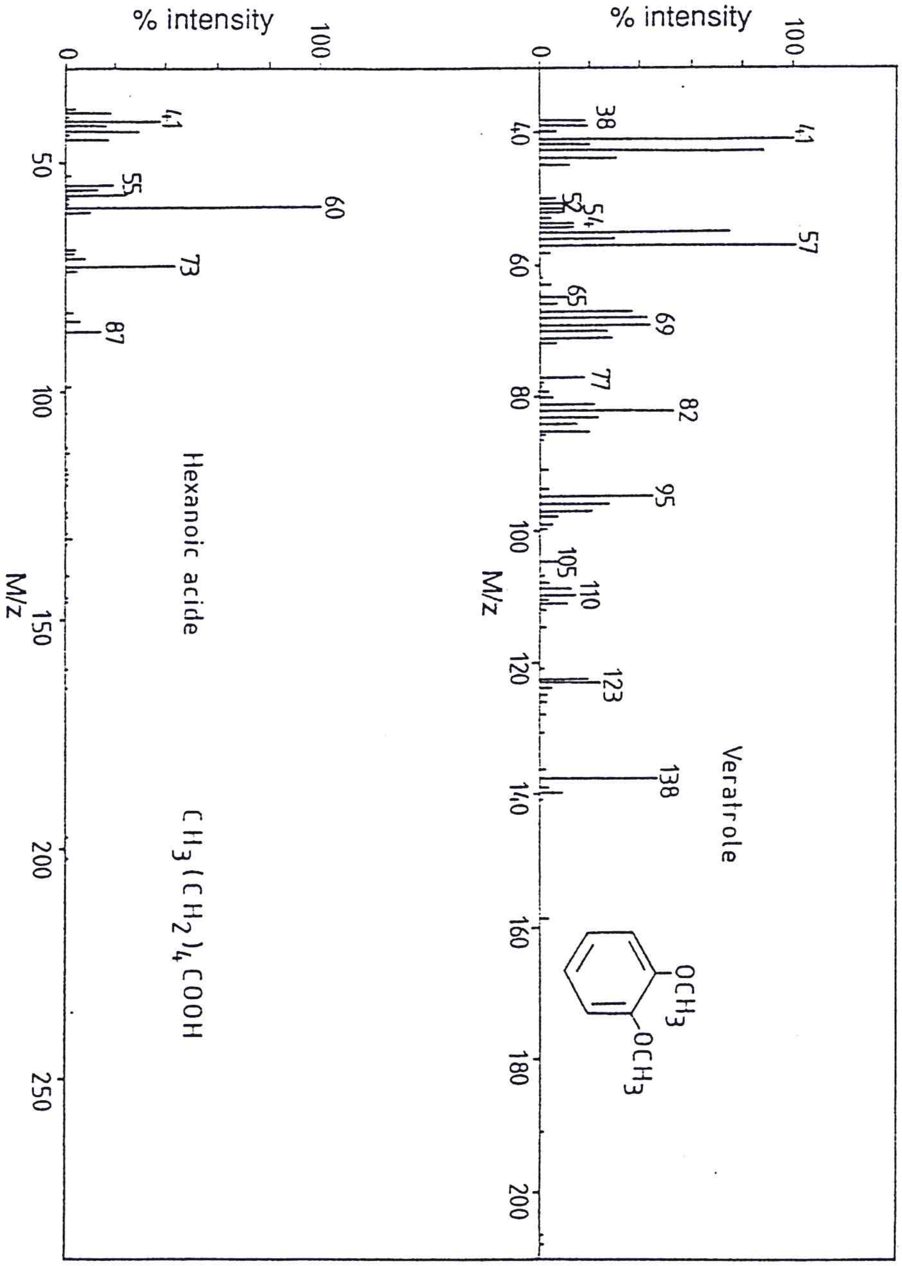

% intensity
% intensity
Decanal
CH3(CH2)8CHO
Benzaldehyde
CHO
M/z
M/z
41
54
57
67
70
82
95
112
128
39
51
61
69
74
77
105

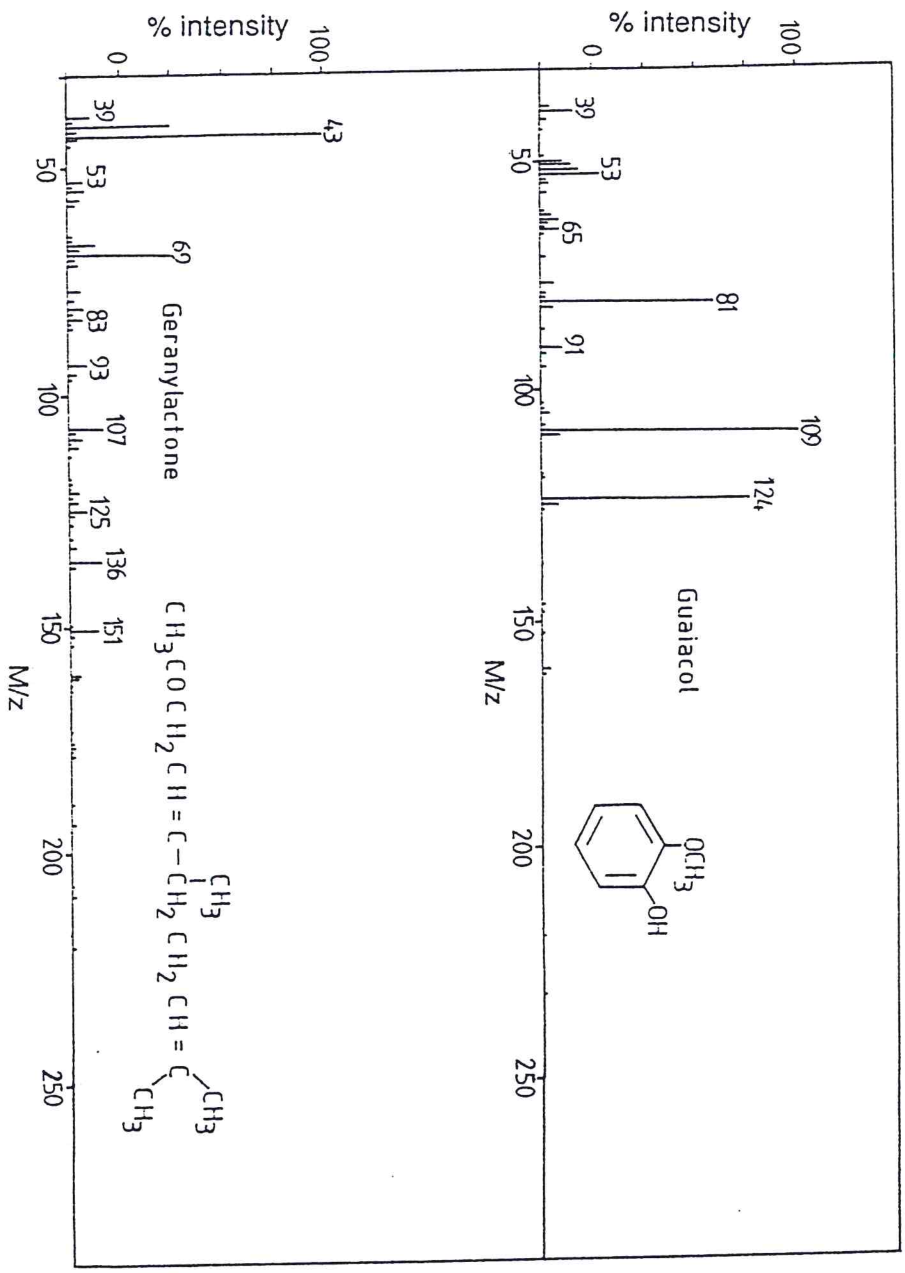


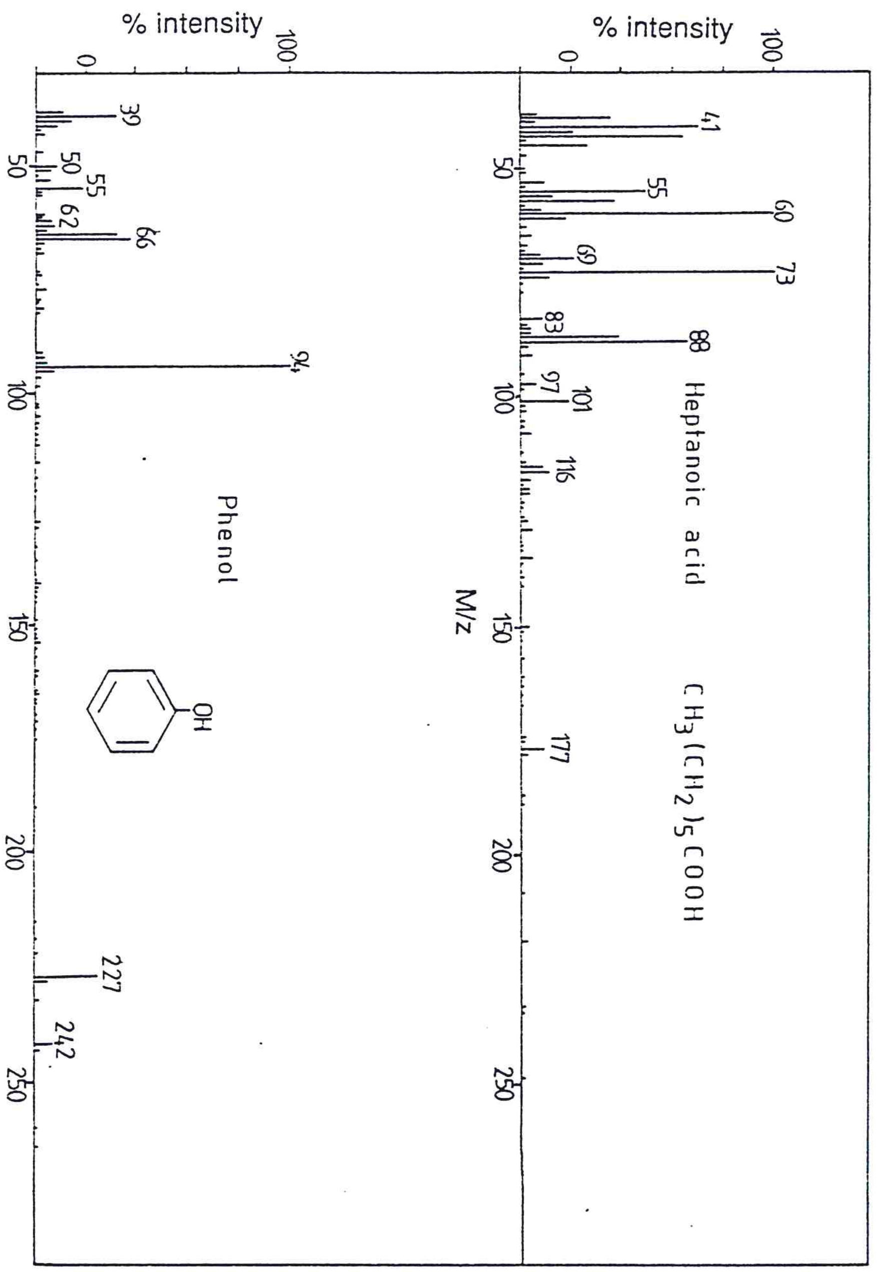
% intensity
2-Butyl-1-octanol
(CH2)5CH3
CH3(CH2)3CHCH2OH
39
43
57
67
71
85
99
127
M/z
% intensity
41
55
65
69
79
91
105
119
133
147
161
204
Caryophyllene
H3C
H3C
CH2
CH3
M/z

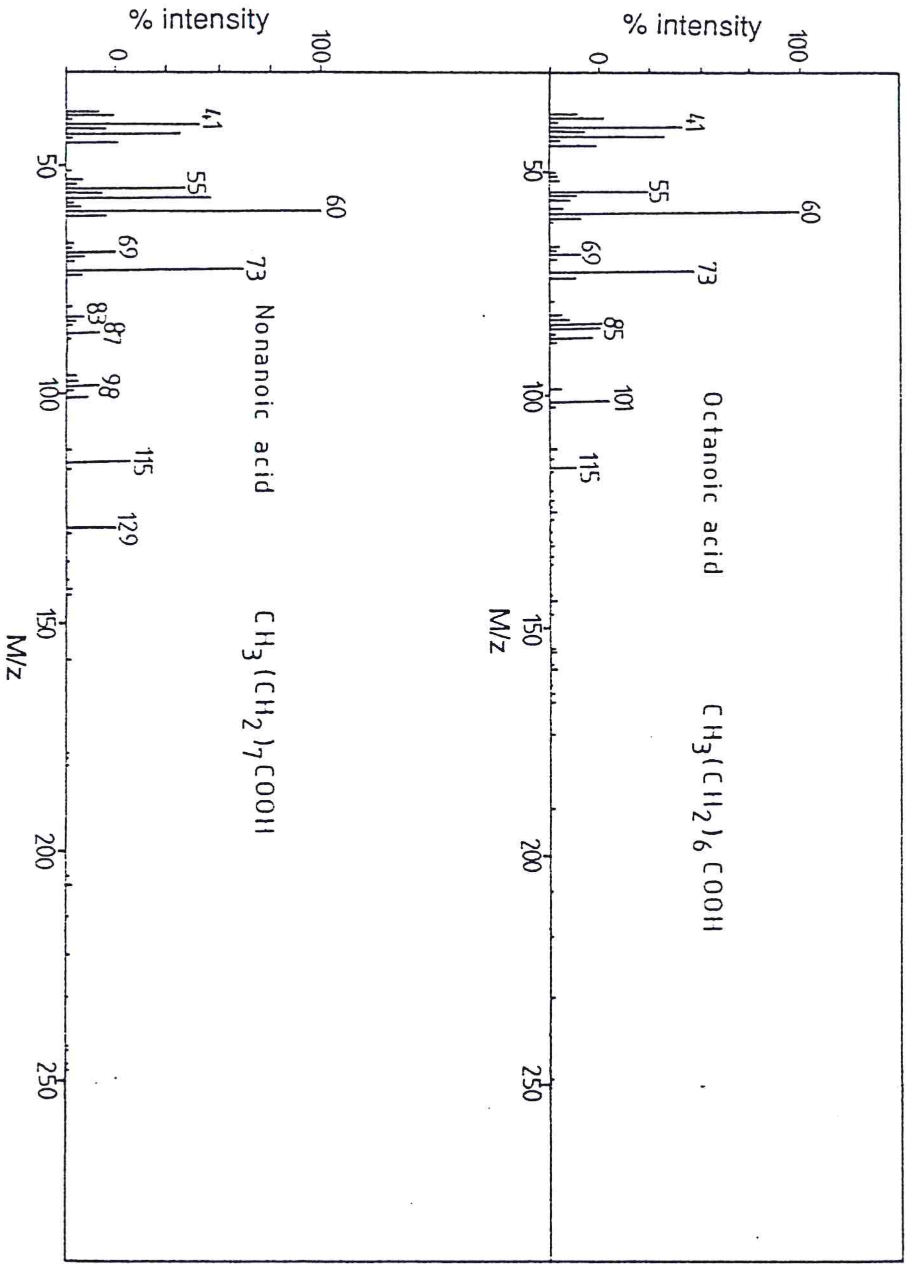


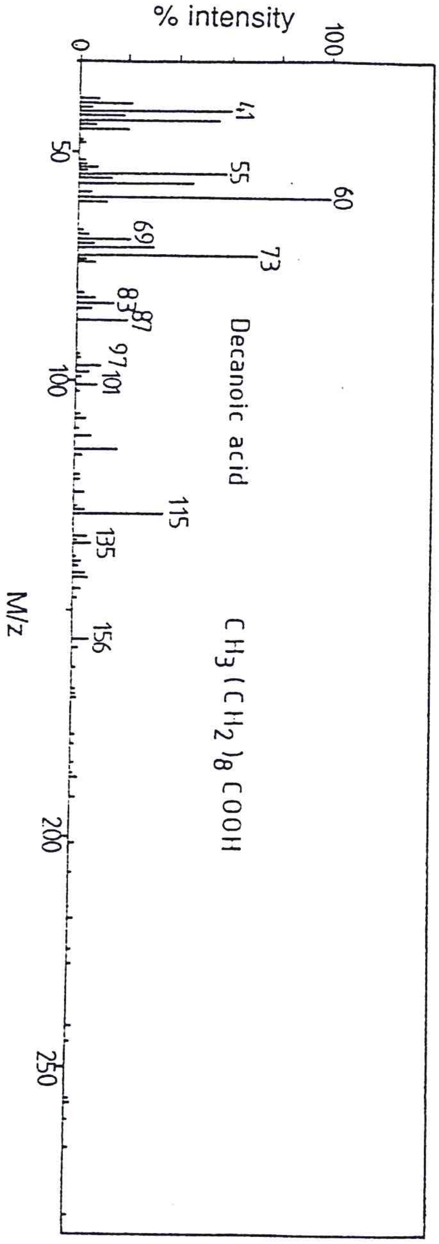
% intensity
100
0
41
54
57
68
71
82
85
95
110
126
Undecanal
CH3(CH2)9CHO
40
60
80
100
120
140
160
180
200
M/z
% intensity
100
0
39
43
51
55
74
77
105
120
Acetophenone
40
60
80
100
120
140
160
180
200
M/z

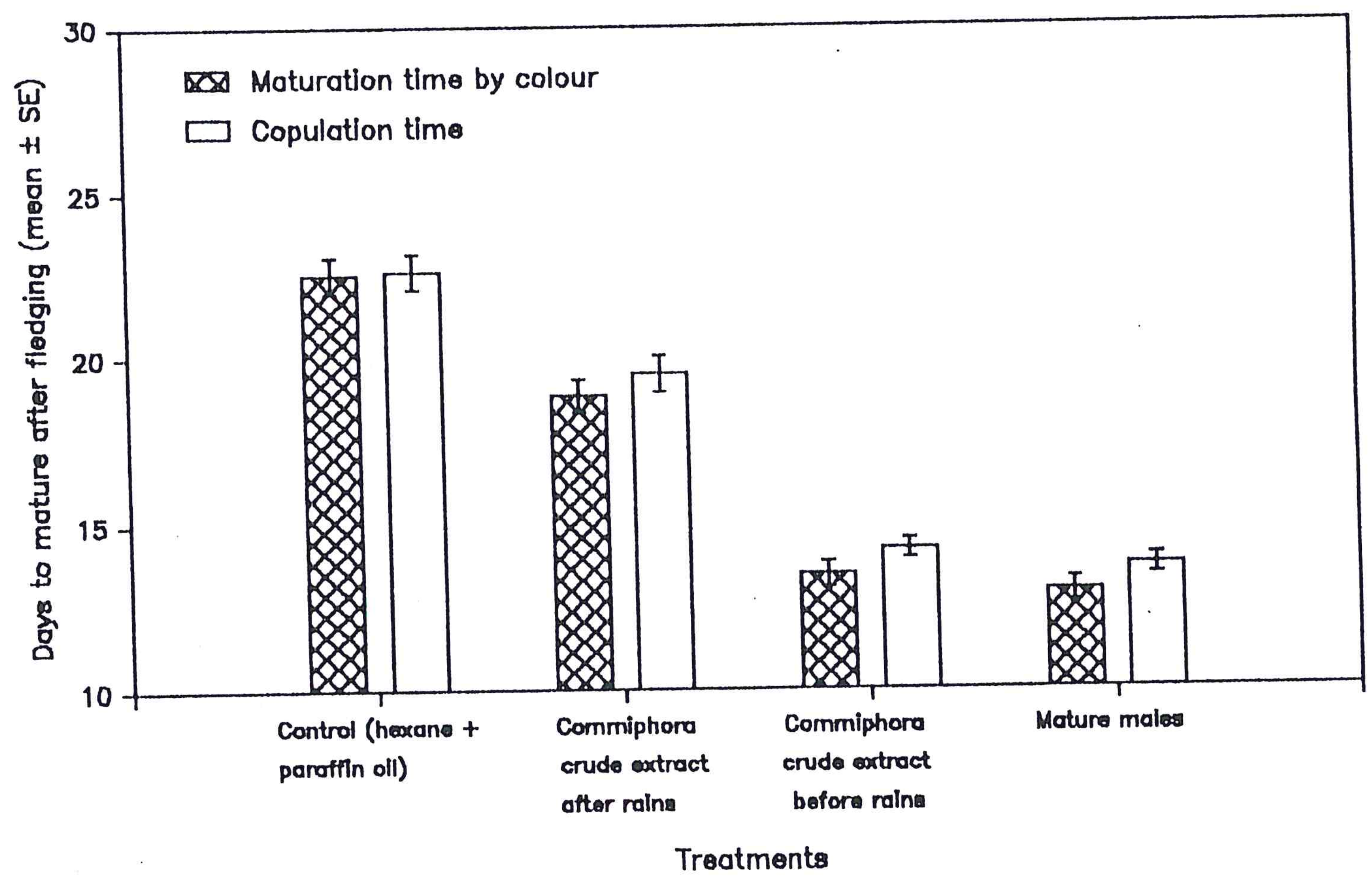

% intensity
% intensity
Veratrole
OCH3
OCH3
Hexanoic acide
CH3(CH2)4COOH
M/z
M/z


% intensity
100
0
39
53
65
81
91
109
124
50
100
150
200
250
M/z
Guaiacol
OCH3
OH
% intensity
100
0
39
43
53
69
83
93
107
125
136
151
Geranylactone
M/z
CH3COCH2CH=C–CH2CH2CH=C
CH3
CH3
CH3

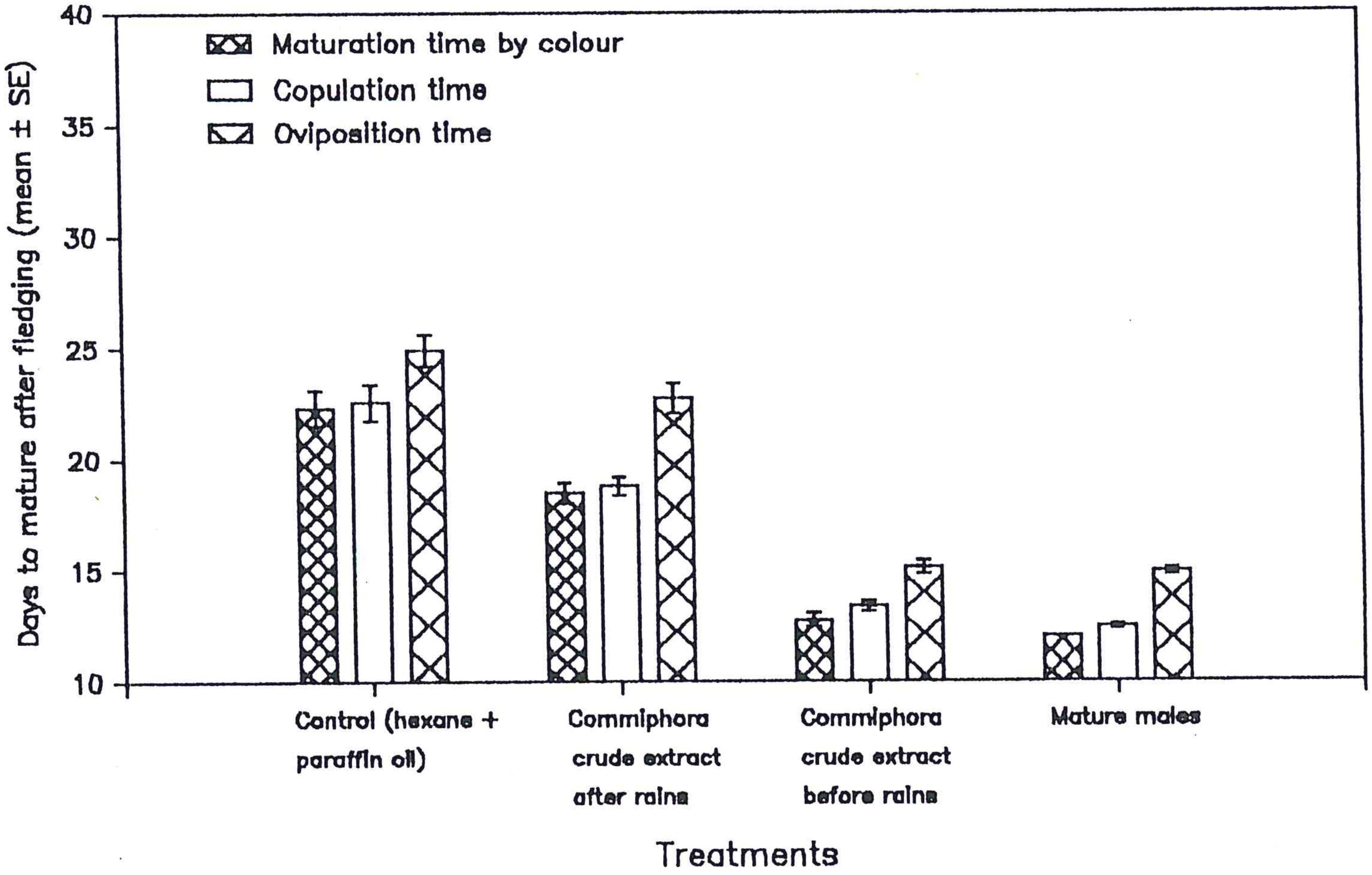

% intensity
100
0
41
55
60
69
73
83
88
97
101
116
177
50
100
150
200
250
Heptanoic acid
$CH_3(CH_2)_5COOH$
M/z
% intensity
100
0
39
50
55
62
66
94
227
242
Phenol
OH


% intensity
Octanoic acid
$CH_3(CH_2)_6COOH$
Nonanoic acid
$CH_3(CH_2)_7COOH$
M/z


% intensity
0
100
41
50
55
60
69
73
83
87
97
101
100
115
135
156
200
250
M/z
Decanoic acid
$CH_3(CH_2)_8COOH$

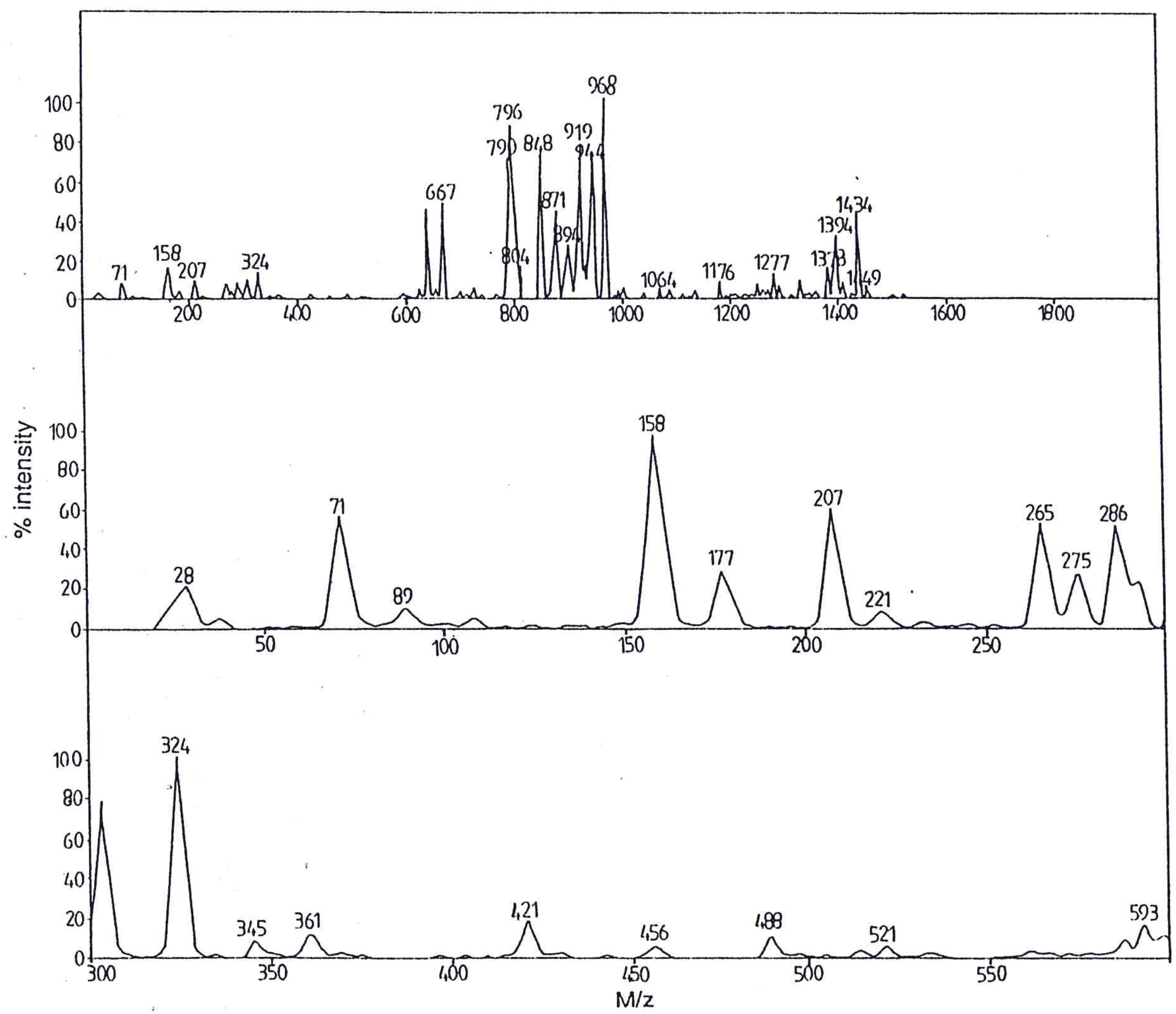


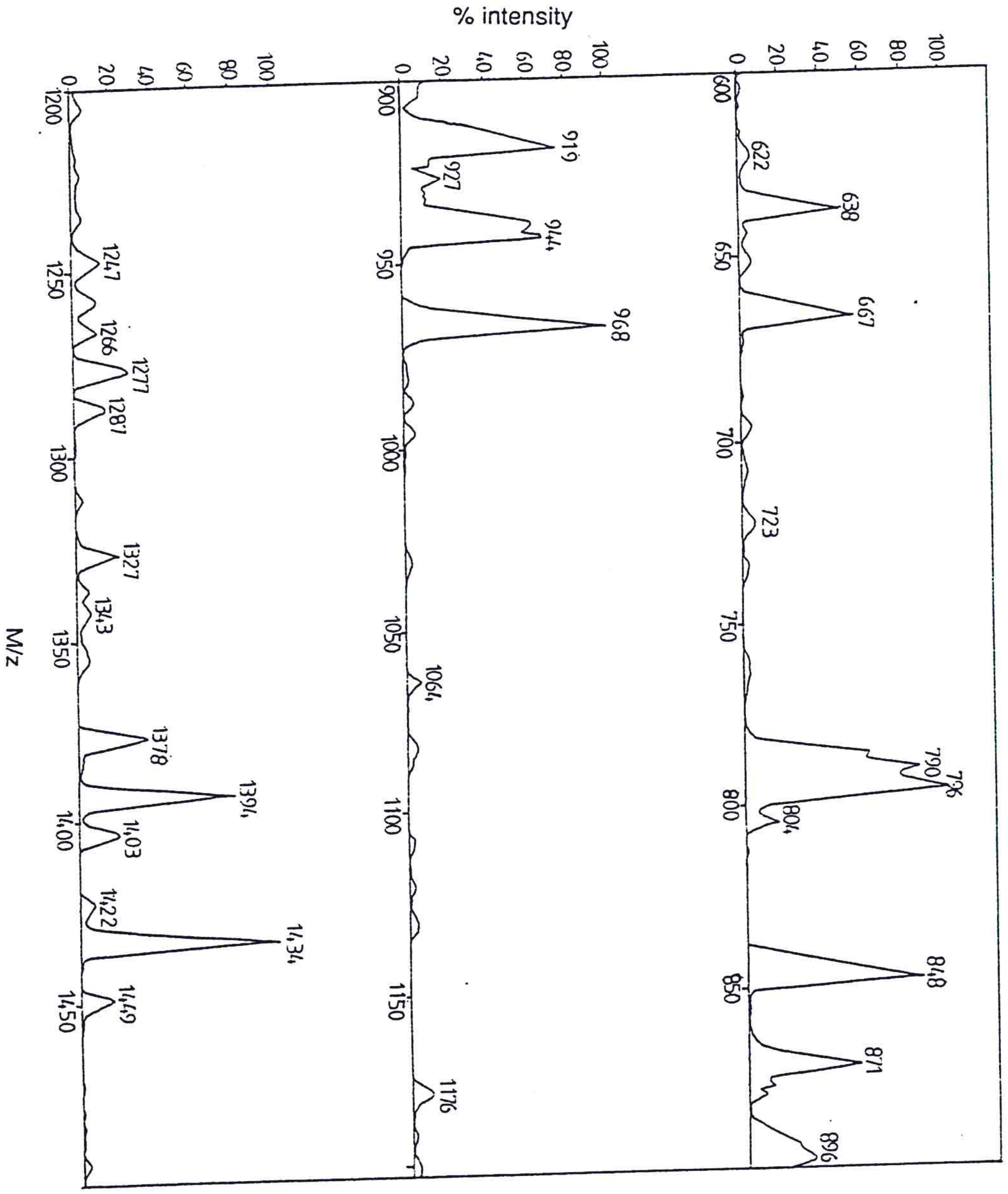
Appen. J. Maturation time of immature males exposed to *C. quadricincta* crude extract before and after Winter rains, mature males and control (hexane + paraffin oil).

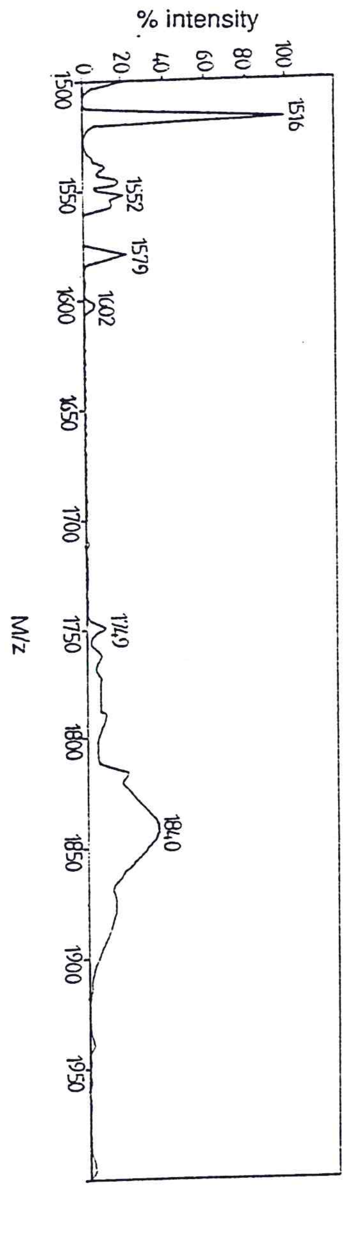


Appen. K. Maturation time of immature females exposed to *C. quadricincta* crude extract before and after Winter rains, mature males and control (hexane + paraffin oil).

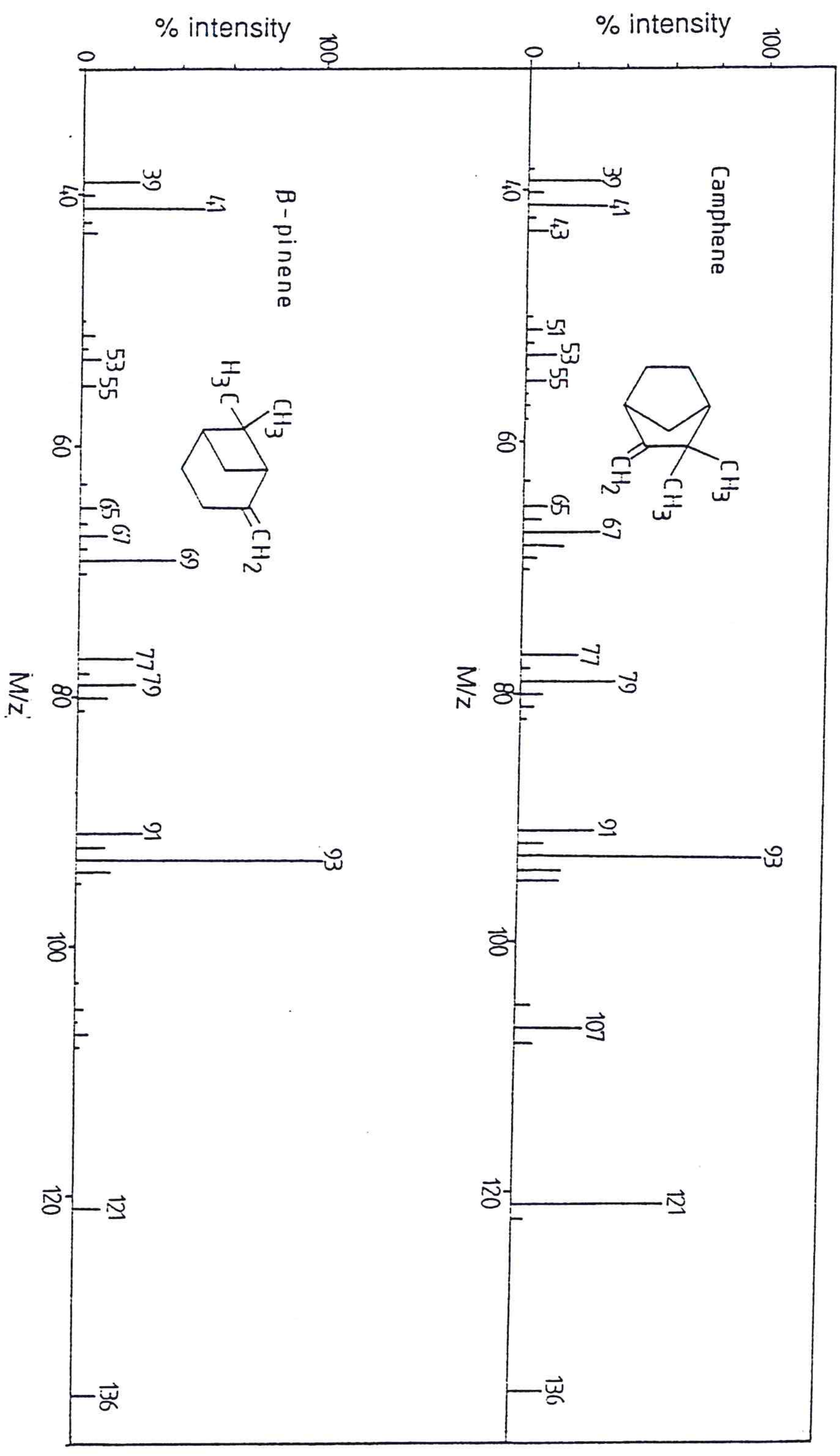
APPENDIX (L) MASS SPECTRUM OF COMMIPHORA CRUDE EXTRACT

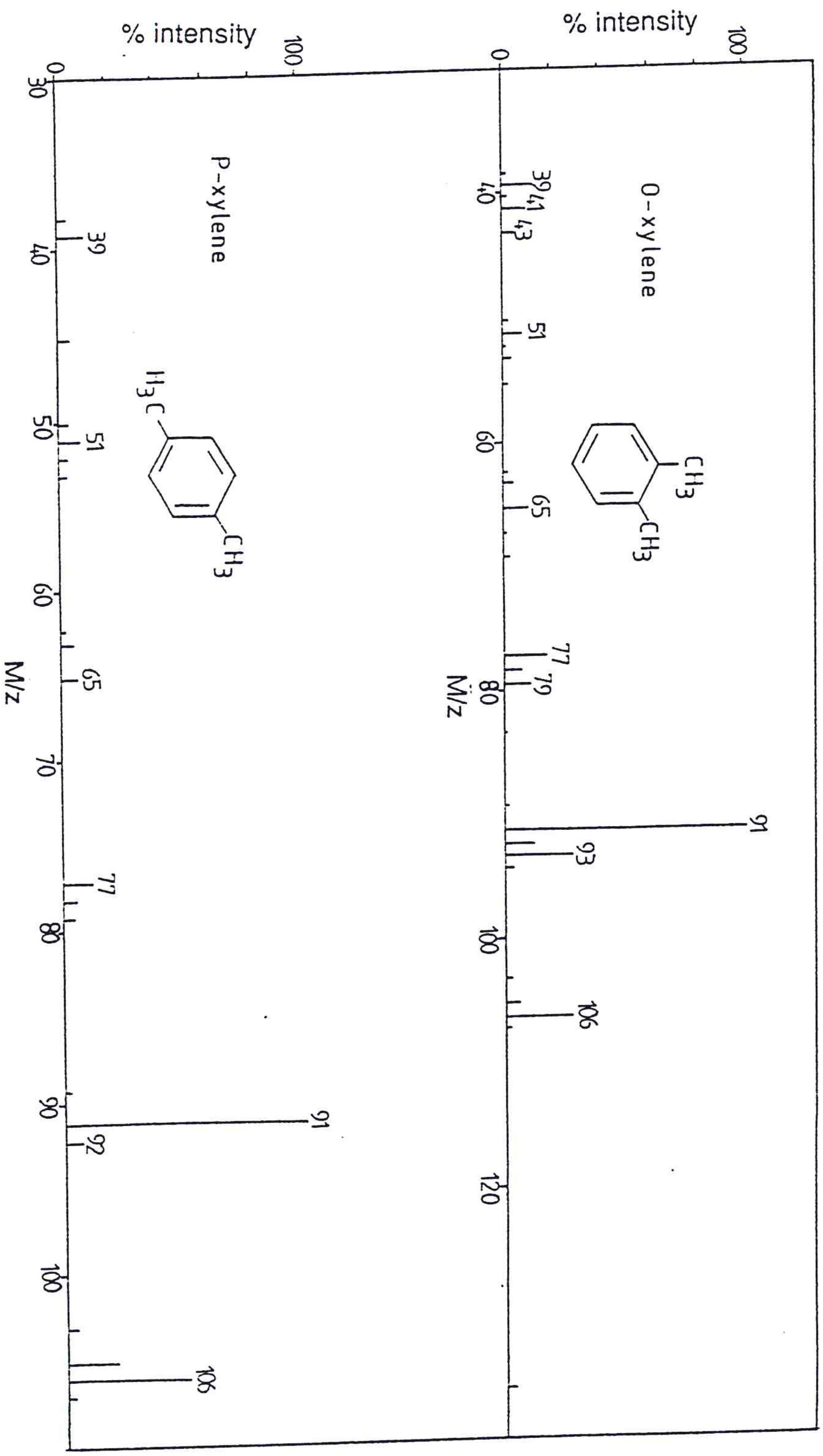


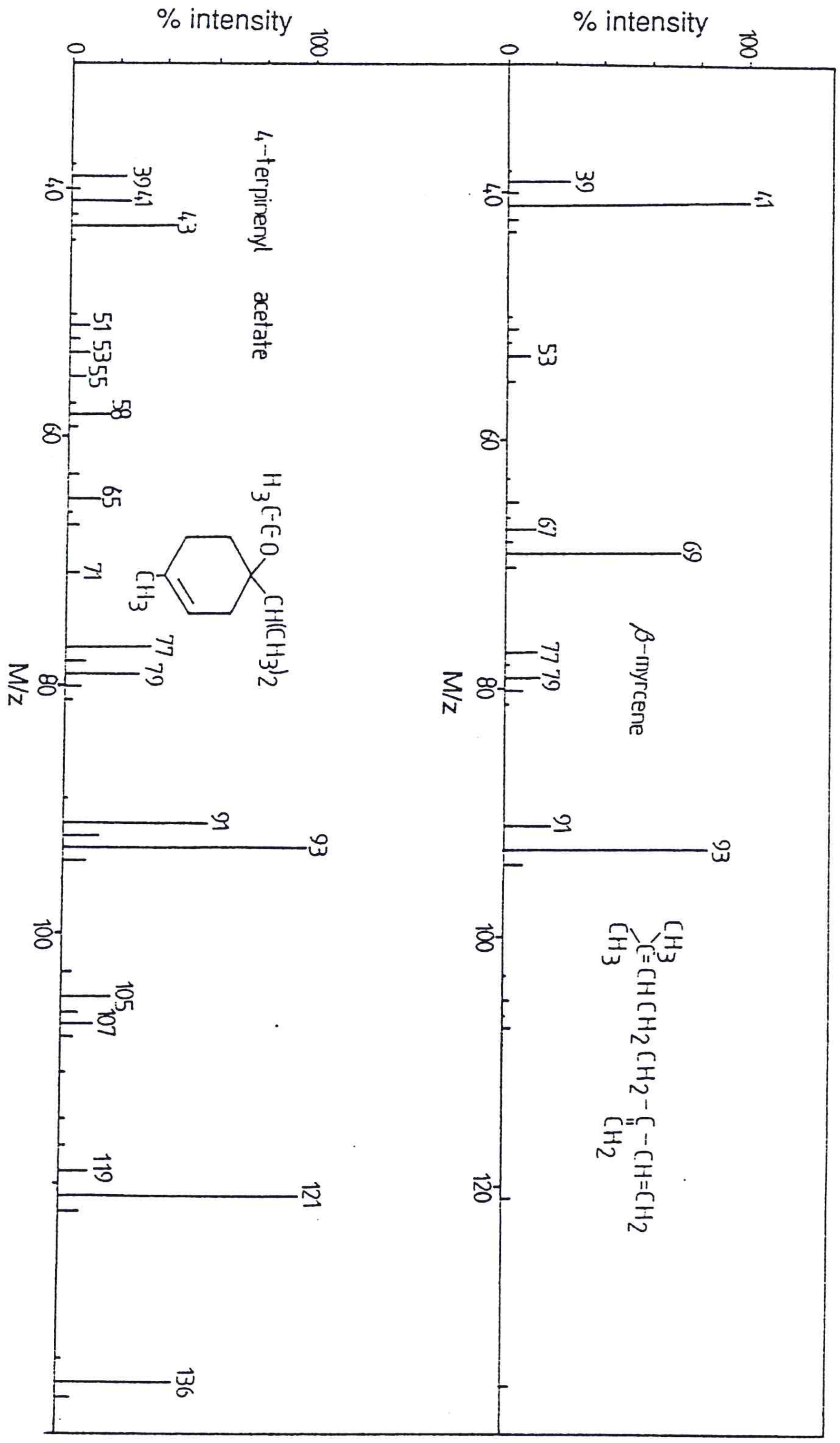

% intensity
M/z
622
638
667
723
790
796
804
848
871
896
919
927
944
968
1064
1176
1247
1266
1277
1281
1327
1343
1378
1394
1403
1422
1434
1449

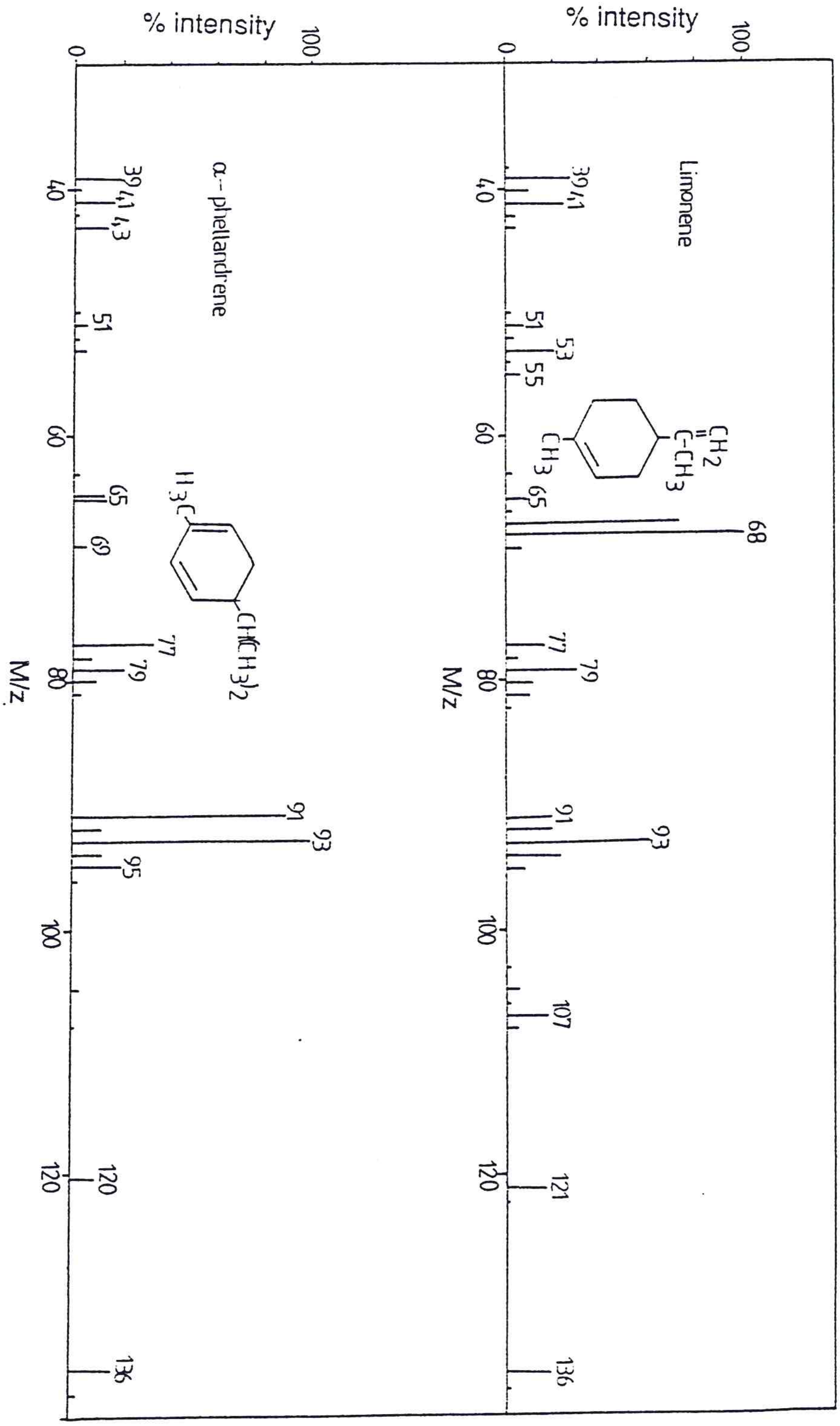


% intensity
0
20
40
60
80
100
1516
1552
1579
1602
1749
1840
1500
1550
1600
1650
1700
1750
1800
1850
1900
1950
M/z

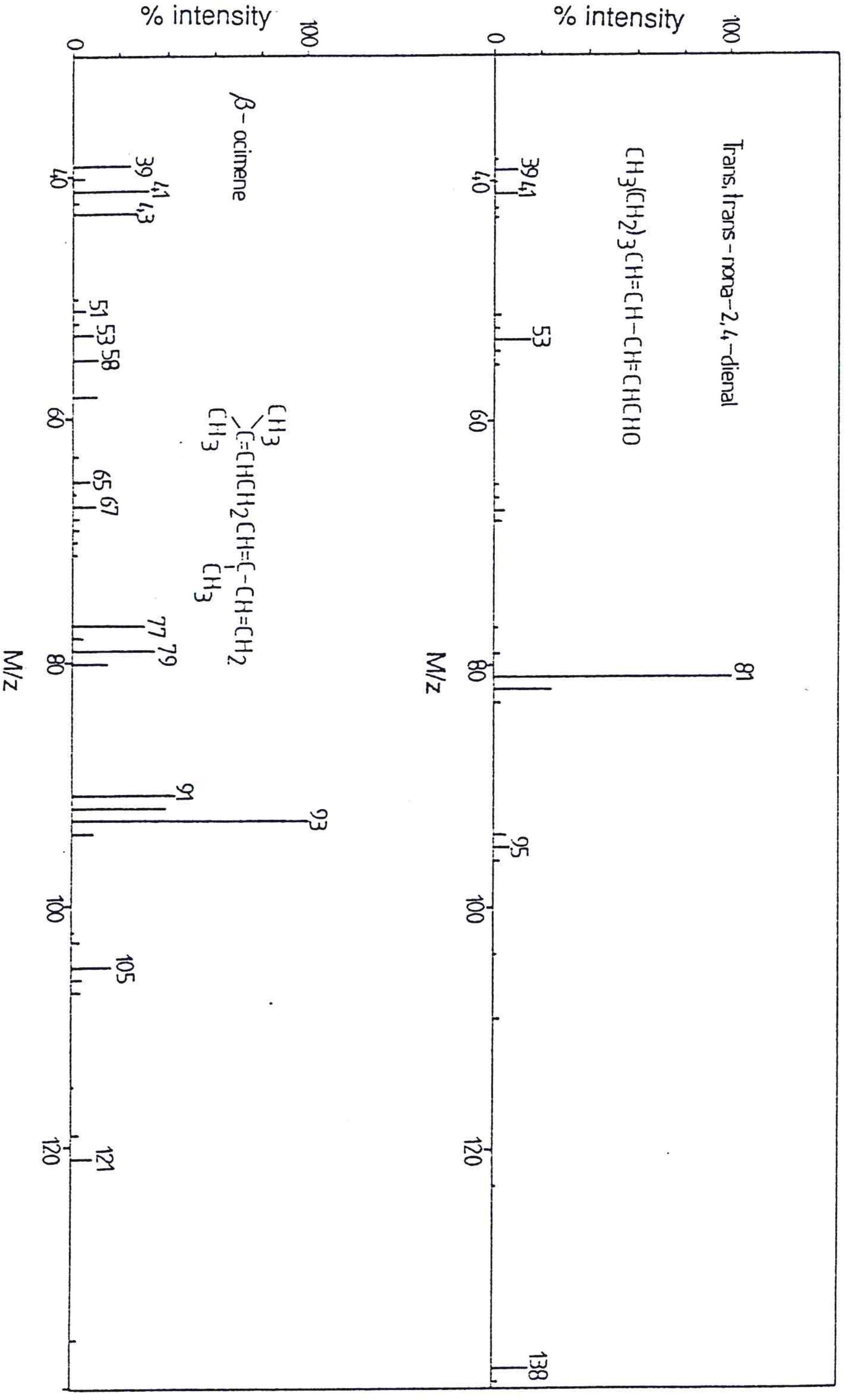

Camphene
β-pinene
% intensity
% intensity
M/z
M/z
39
41
43
51
53
55
65
67
69
77
79
91
93
107
121
136
0
100
40
60
80
100
120


% intensity
O-xylene
P-xylene
M/z
91
93
106
92
77
79
65
51
39
41
43
40

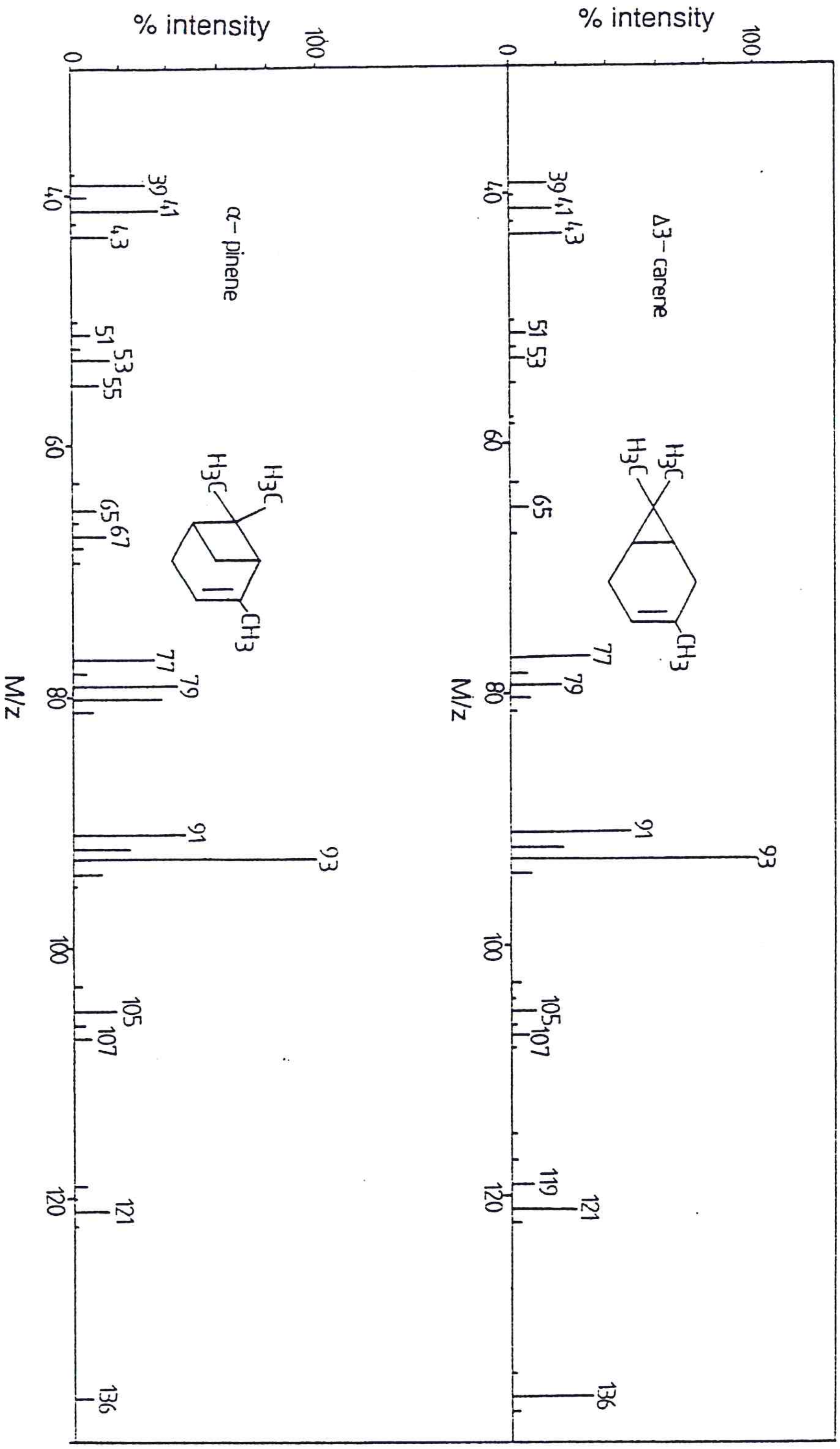

% intensity
% intensity
β-myrcene
4-terpinenyl acetate
M/z
M/z

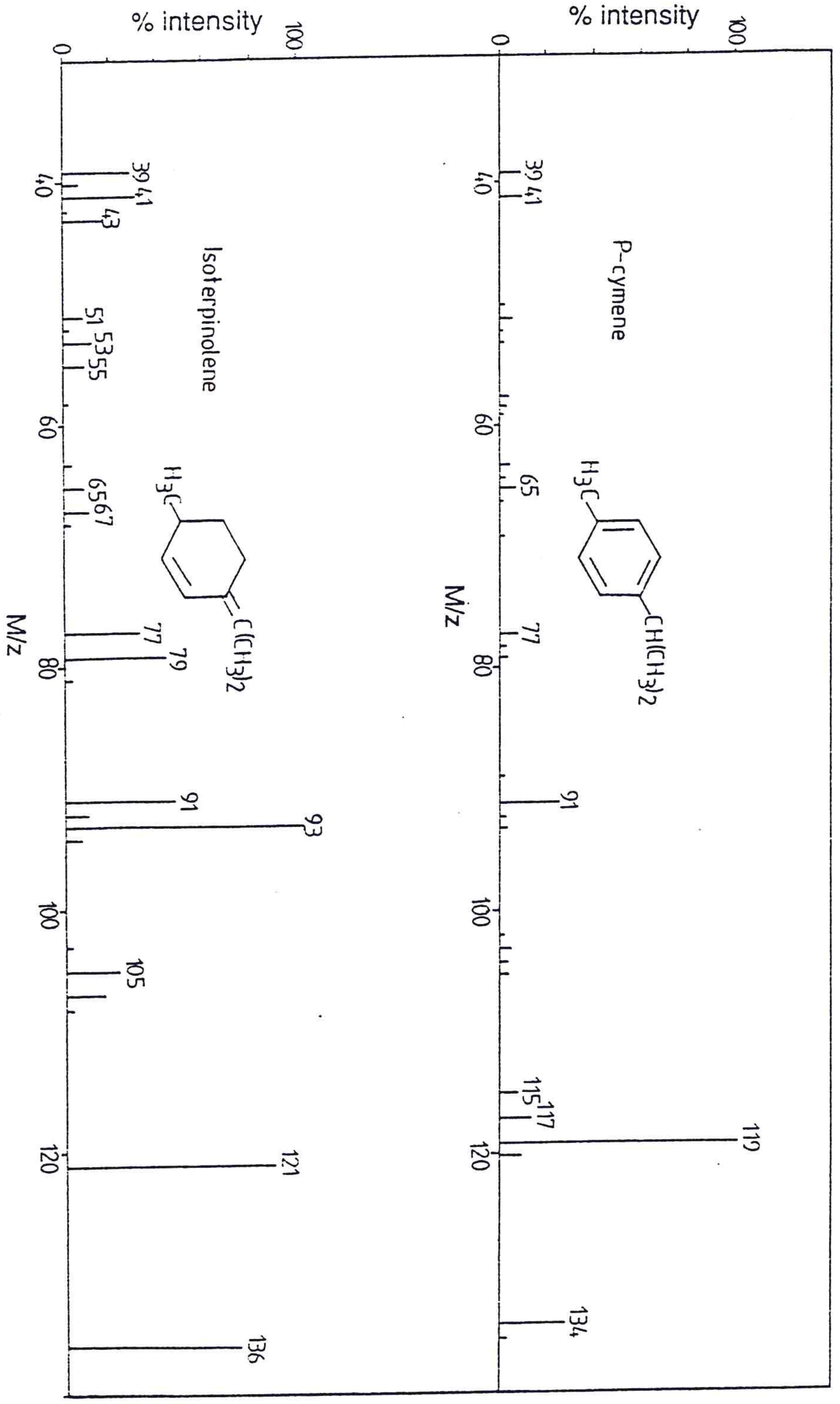


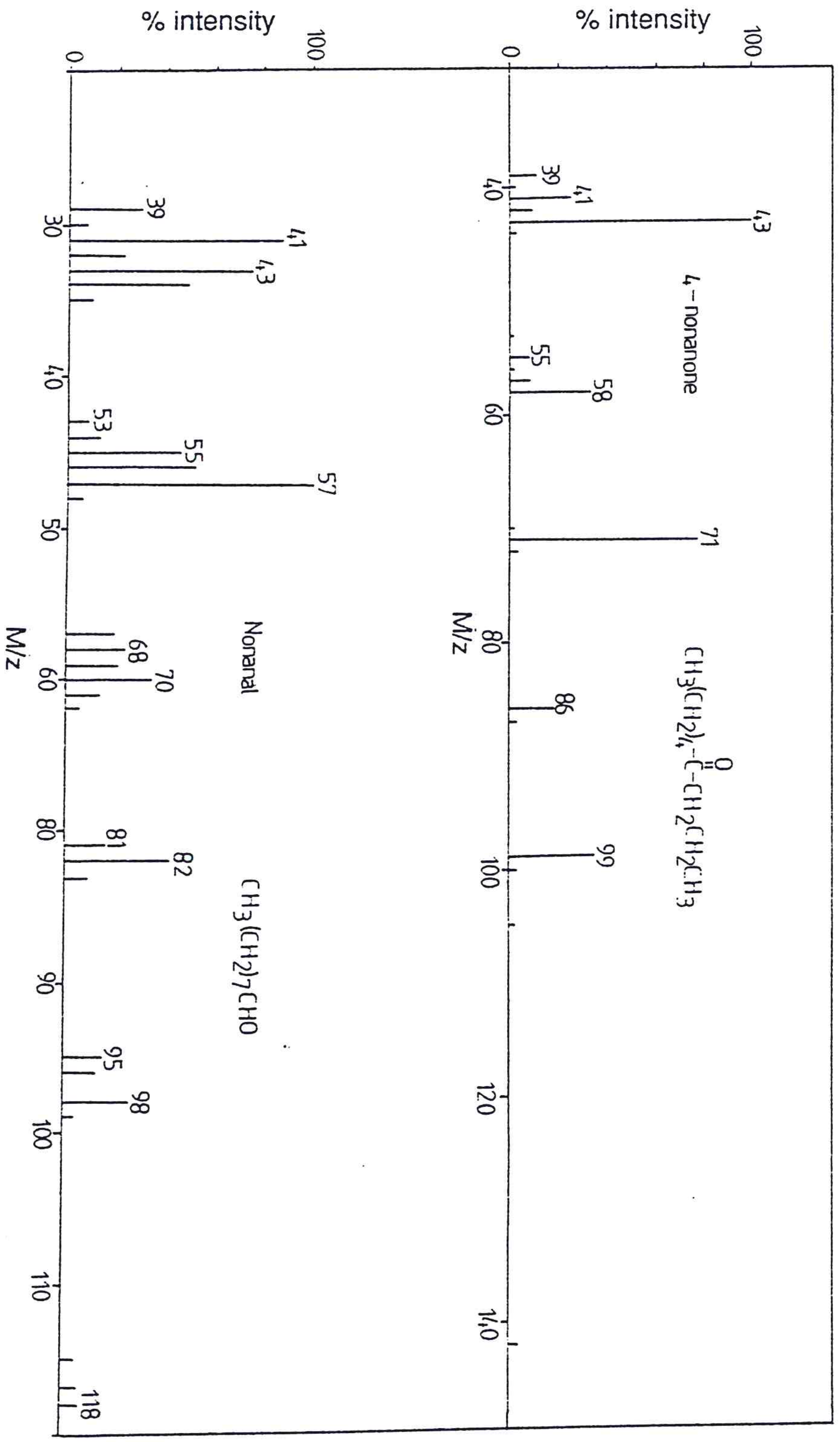
% intensity
Limonene
α – phellandrene
M/z

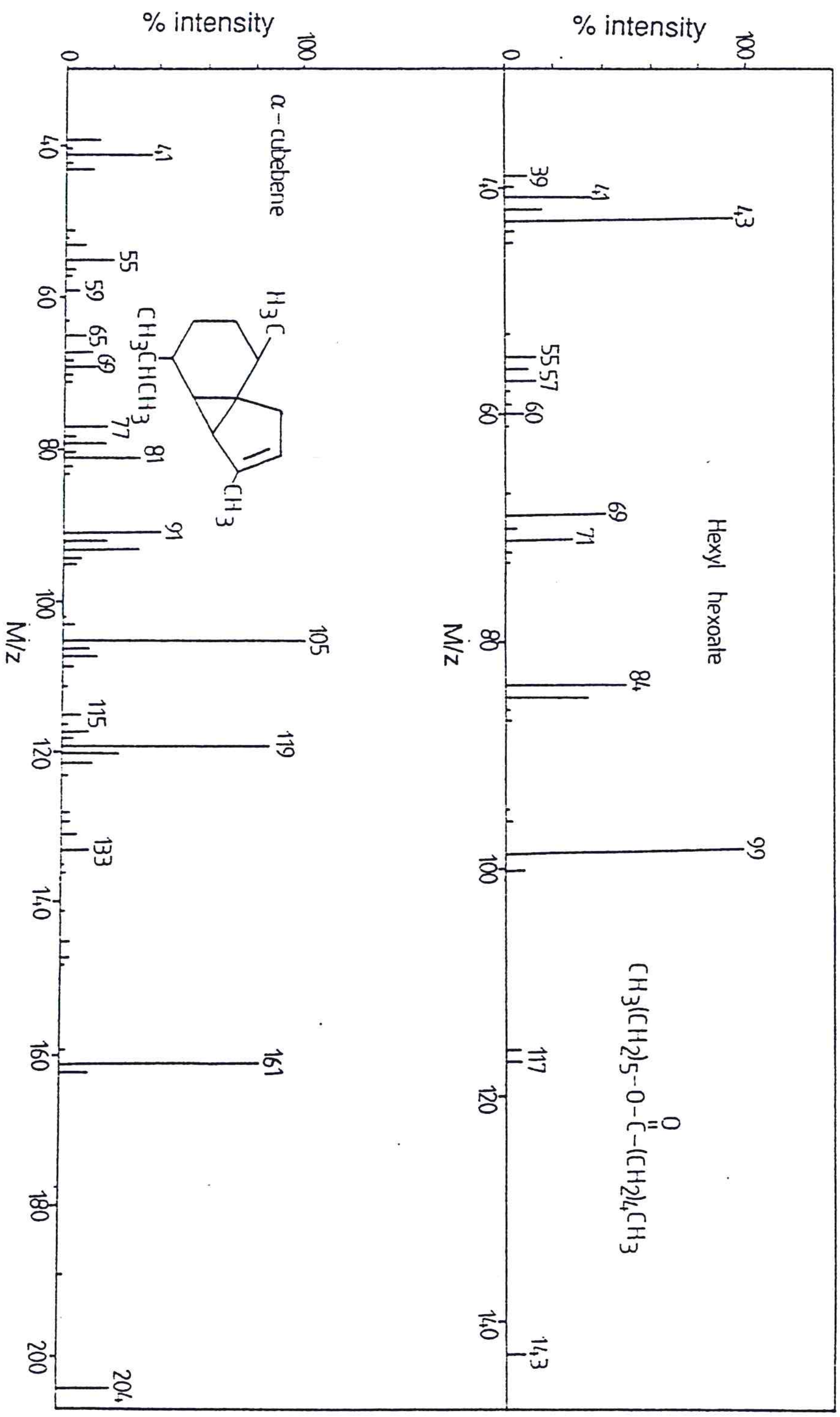


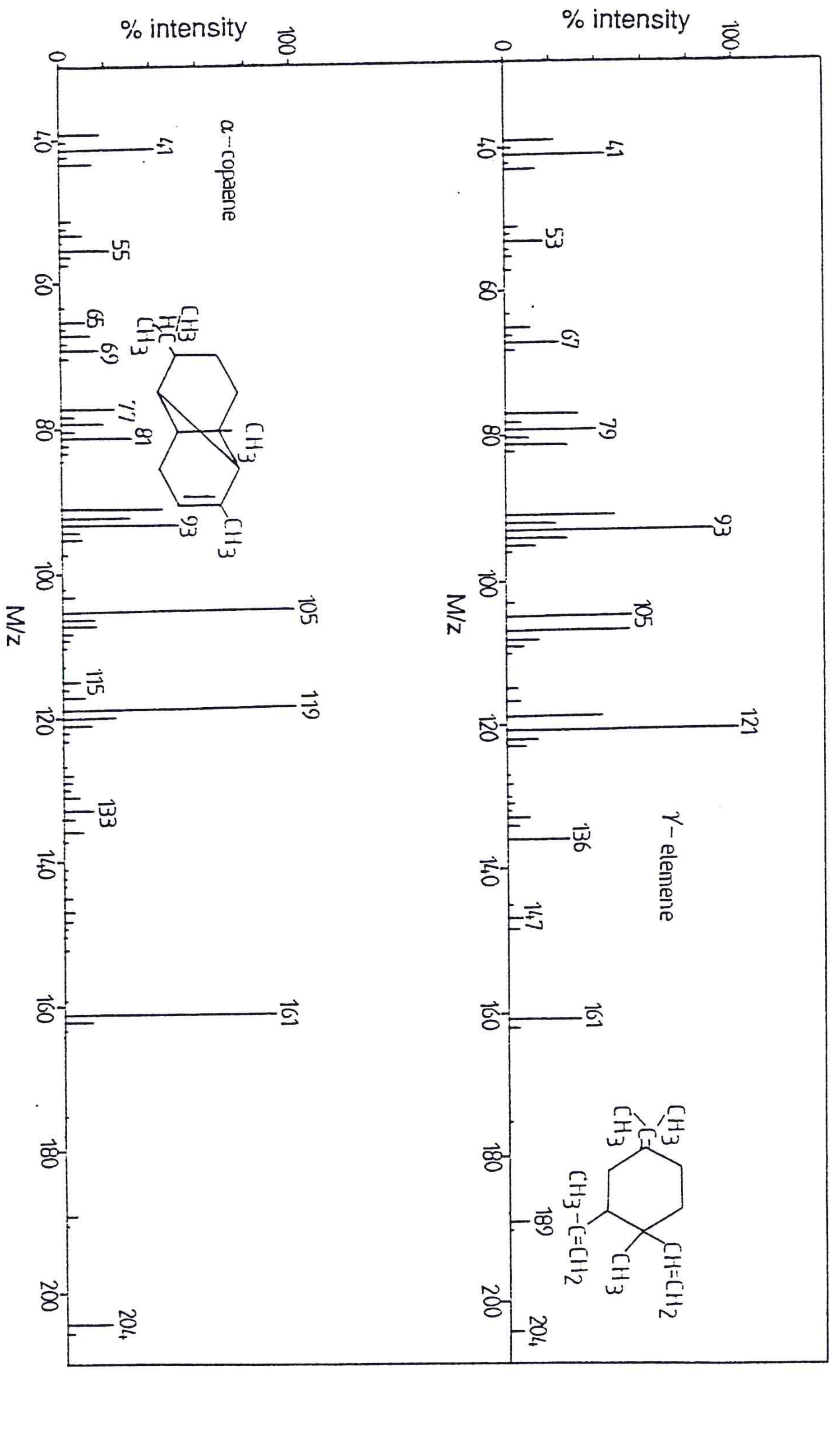
Trans,trans-nona-2,4-dienal
CH3(CH2)3CH=CH-CH=CHCHO
β-ocimene
% intensity
M/z

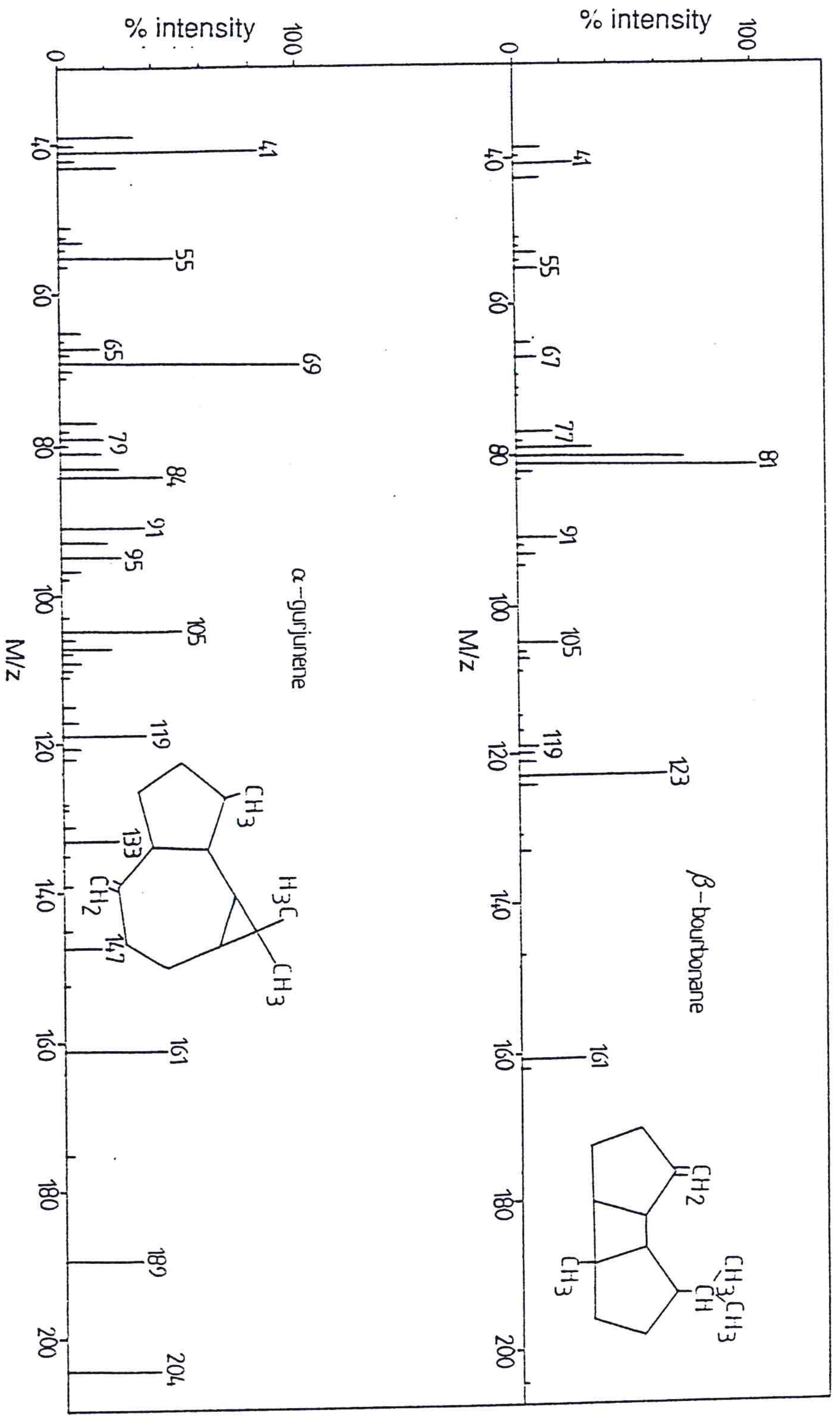

% intensity
% intensity
Δ3-carene
α-pinene
M/z
M/z
H_3C
CH_3

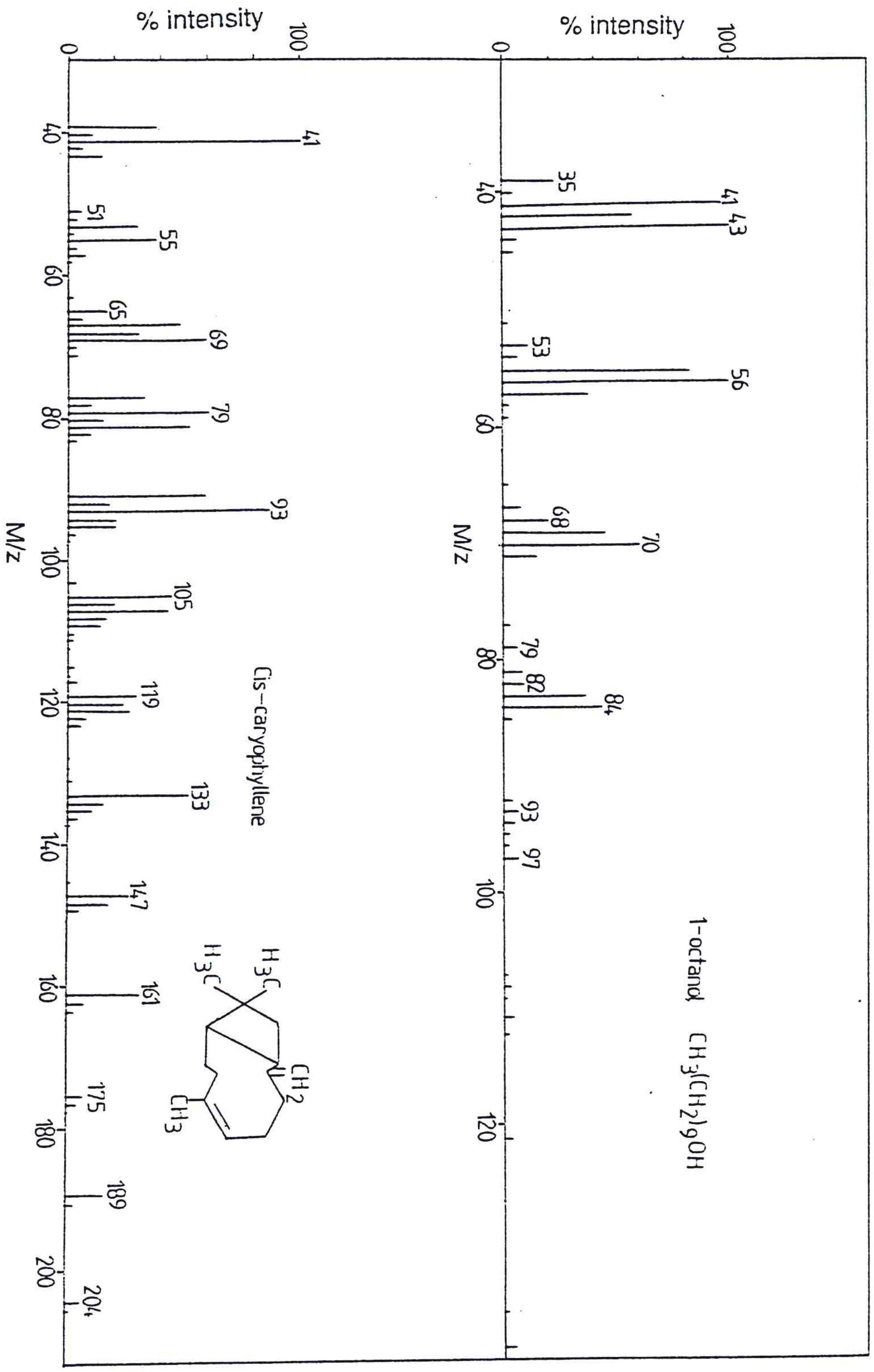

% intensity
P-cymene
H_3C
$CH(CH_3)_2$
M/z
% intensity
Isoterpinolene
H_3C
$C(CH_3)_2$
M/z

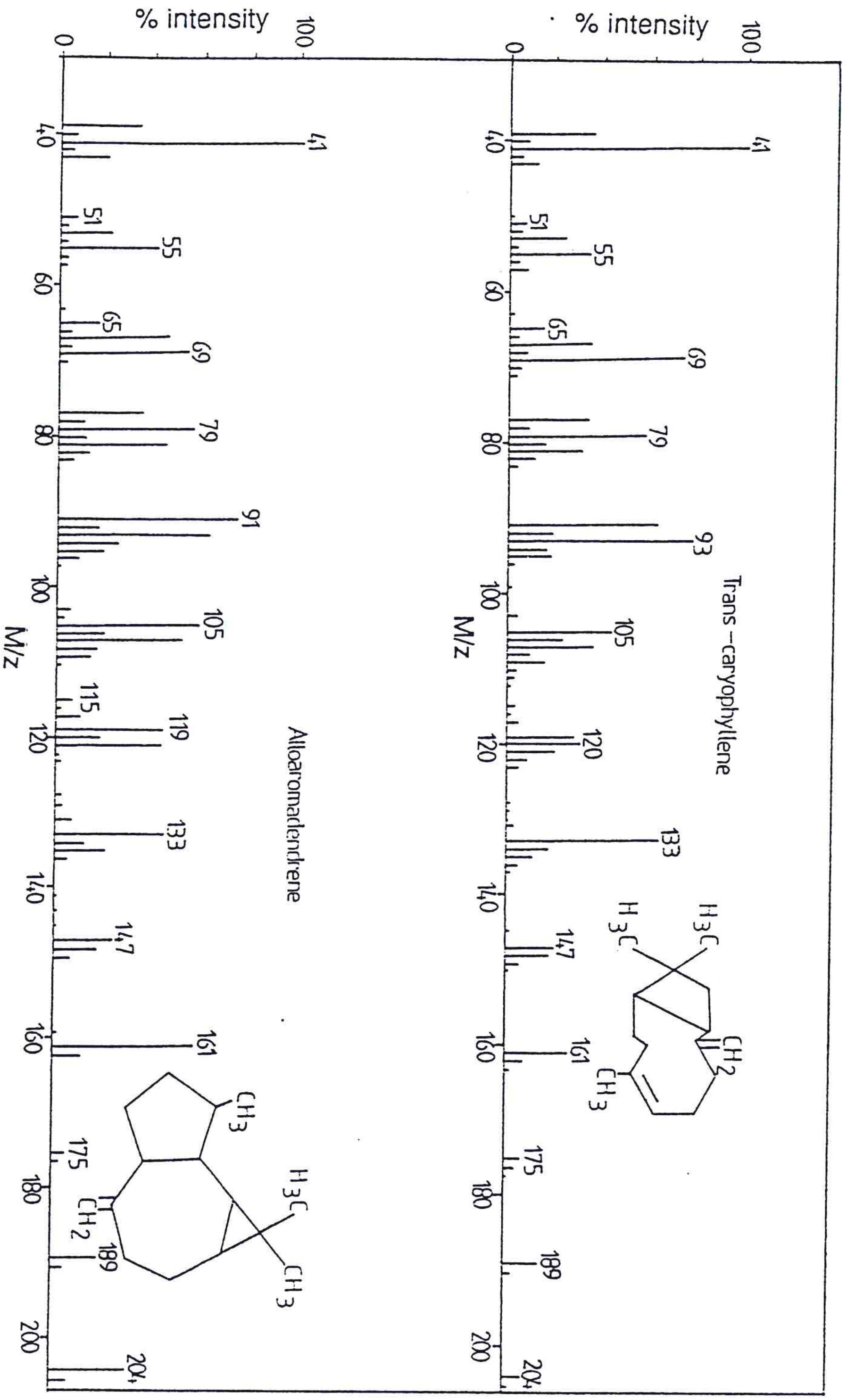

% intensity
% intensity
4-nonanone
CH3(CH2)4-C(O)-CH2CH2CH3
Nonanal
CH3(CH2)7CHO
M/z
M/z


% intensity
Hexyl hexoate
CH3(CH2)5-O-C(O)-(CH2)4CH3
39 41 43 55 57 60 69 71 84 99 117 143
M/z
% intensity
α-cubebene
H3C
CH3CHCH3
CH3
41 55 59 65 69 77 81 91 105 115 119 133 161 204
M/z

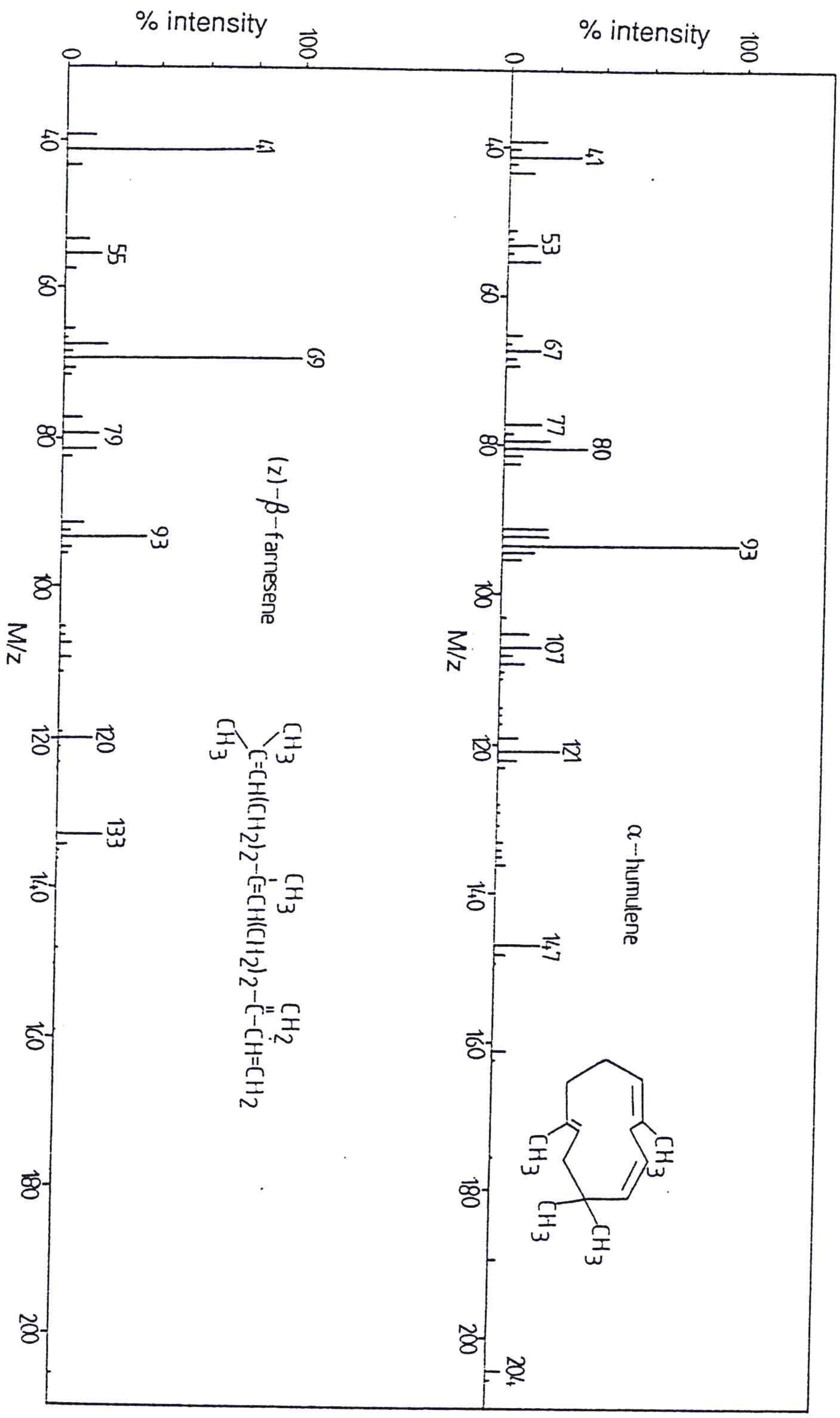

% intensity
% intensity
M/z
M/z
α-copaene
γ-elemene
41
55
65
69
77
81
93
105
115
119
133
161
204
41
53
67
79
93
105
121
136
147
161
189
204

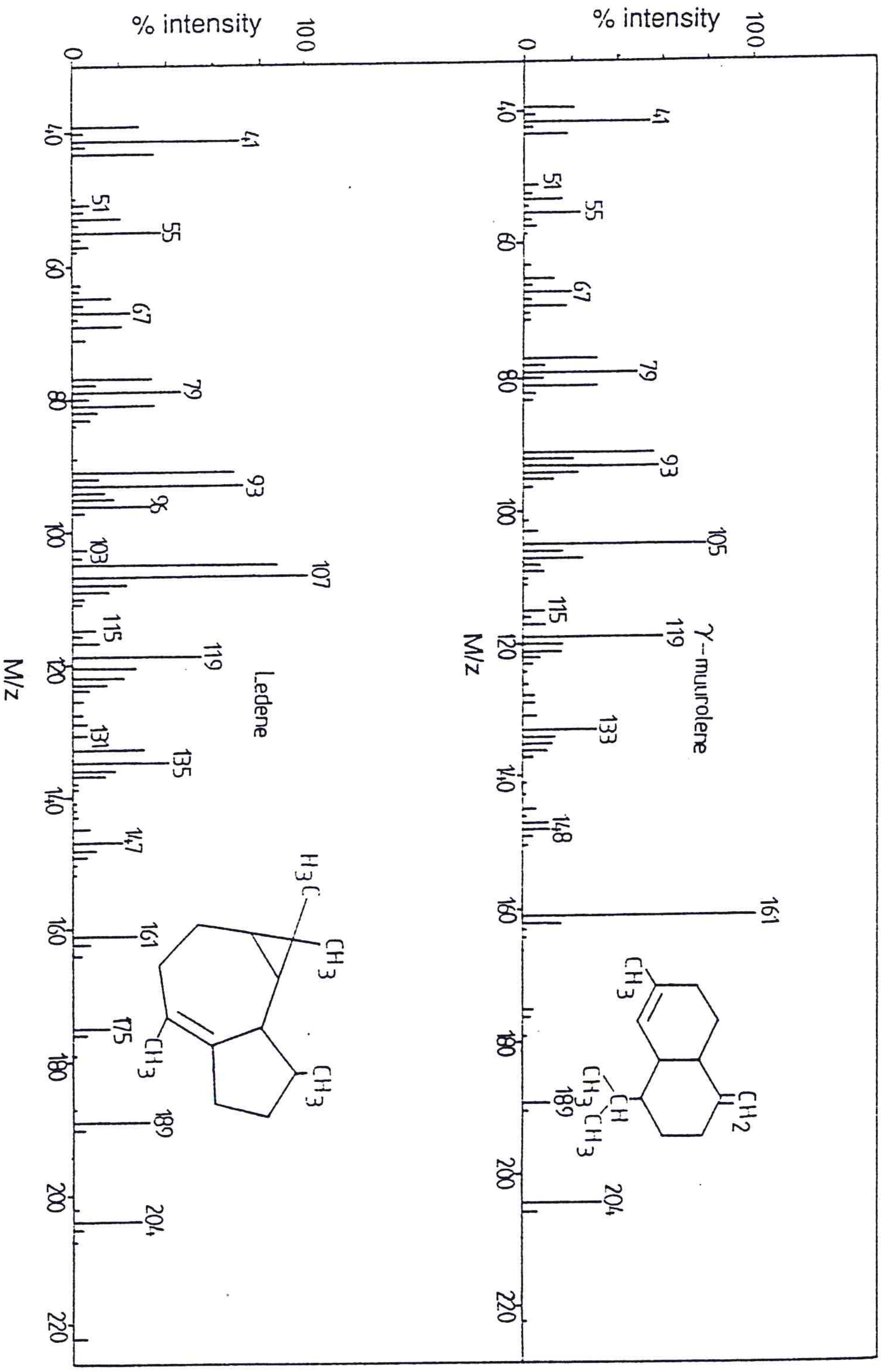

% intensity
M/z
β-bourbonane
α-gurjunene

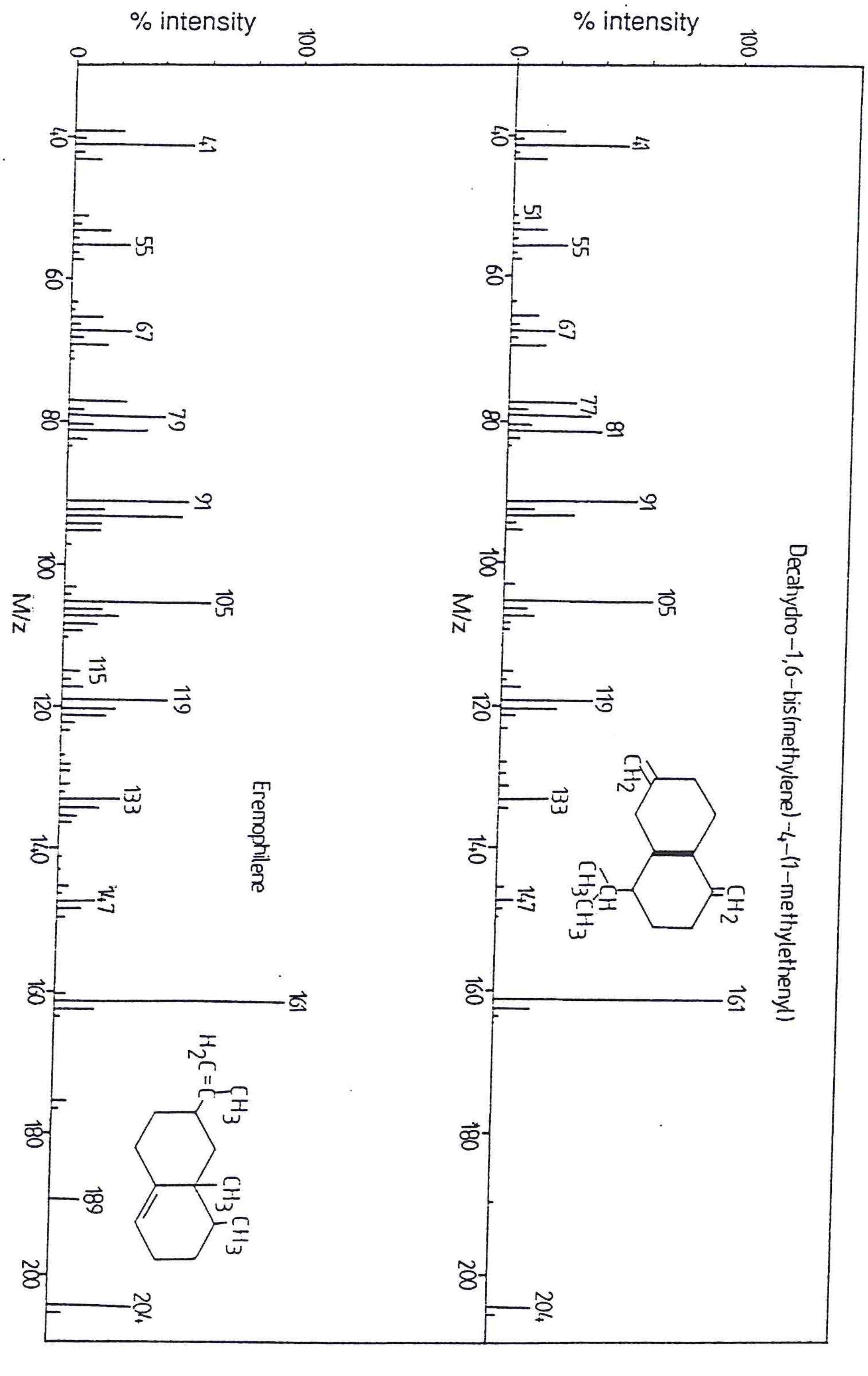

% intensity
% intensity
M/z
M/z
1-octanol
Cis-caryophyllene

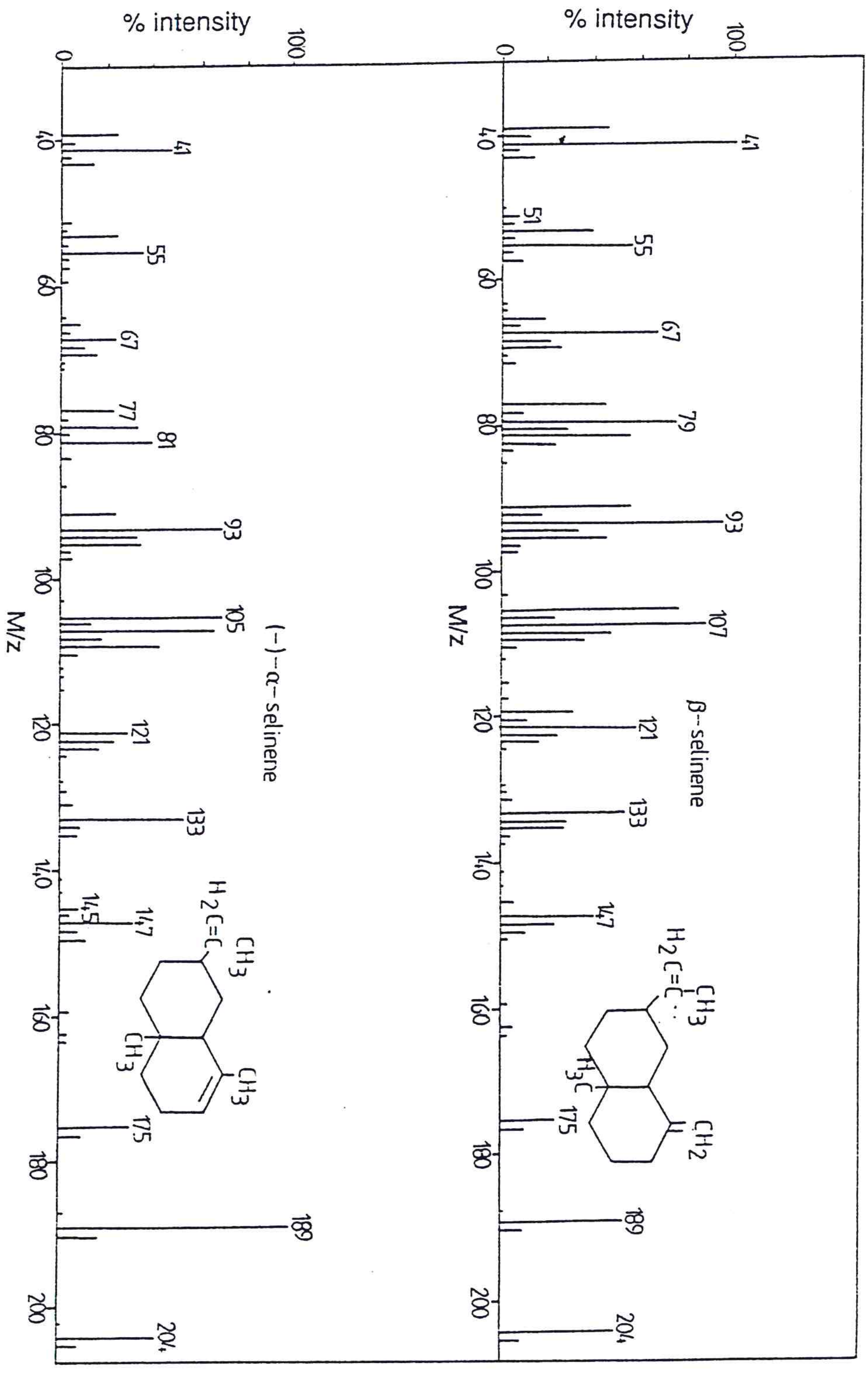


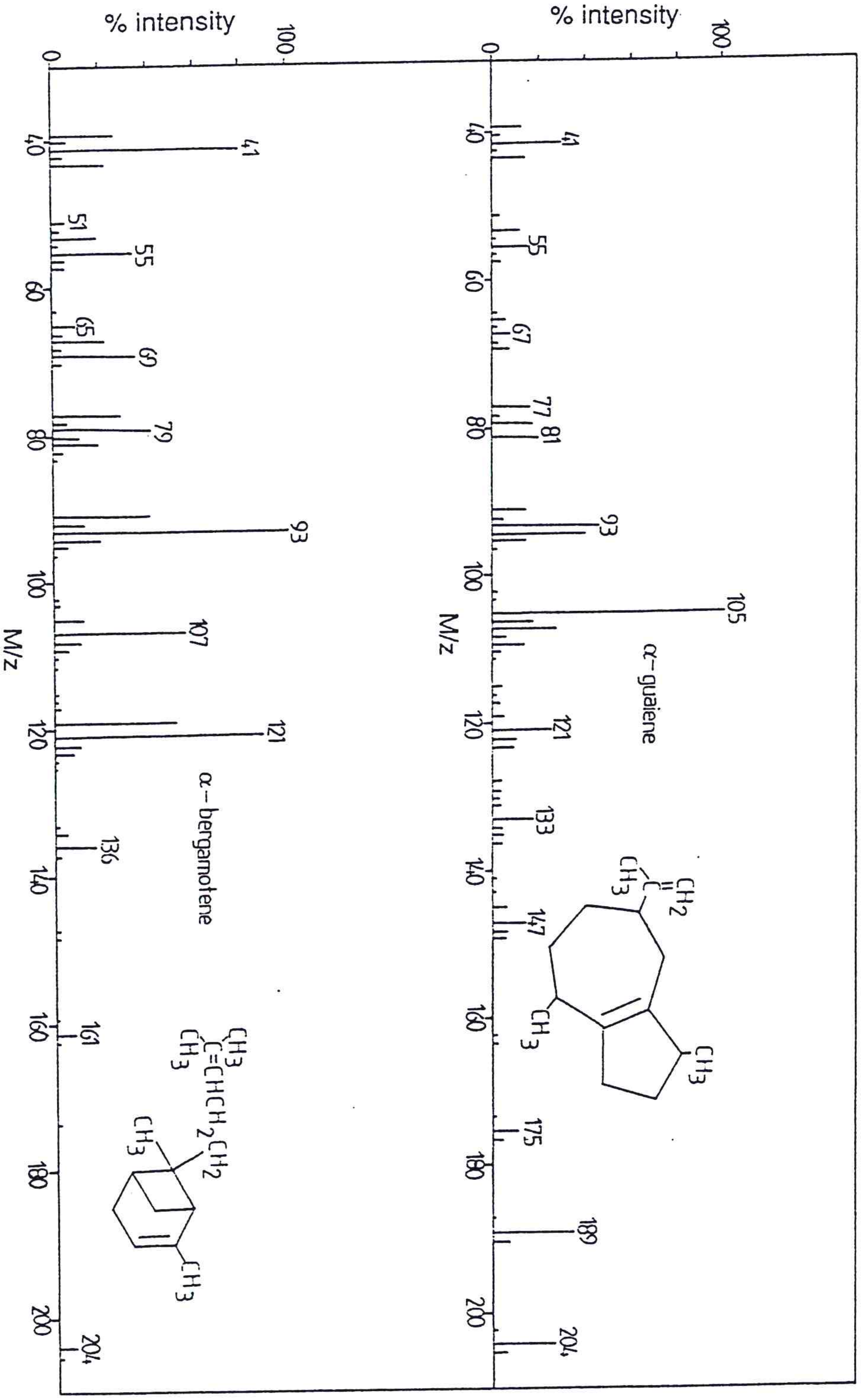
% intensity
Trans-caryophyllene
Alloaromadendrene
M/z

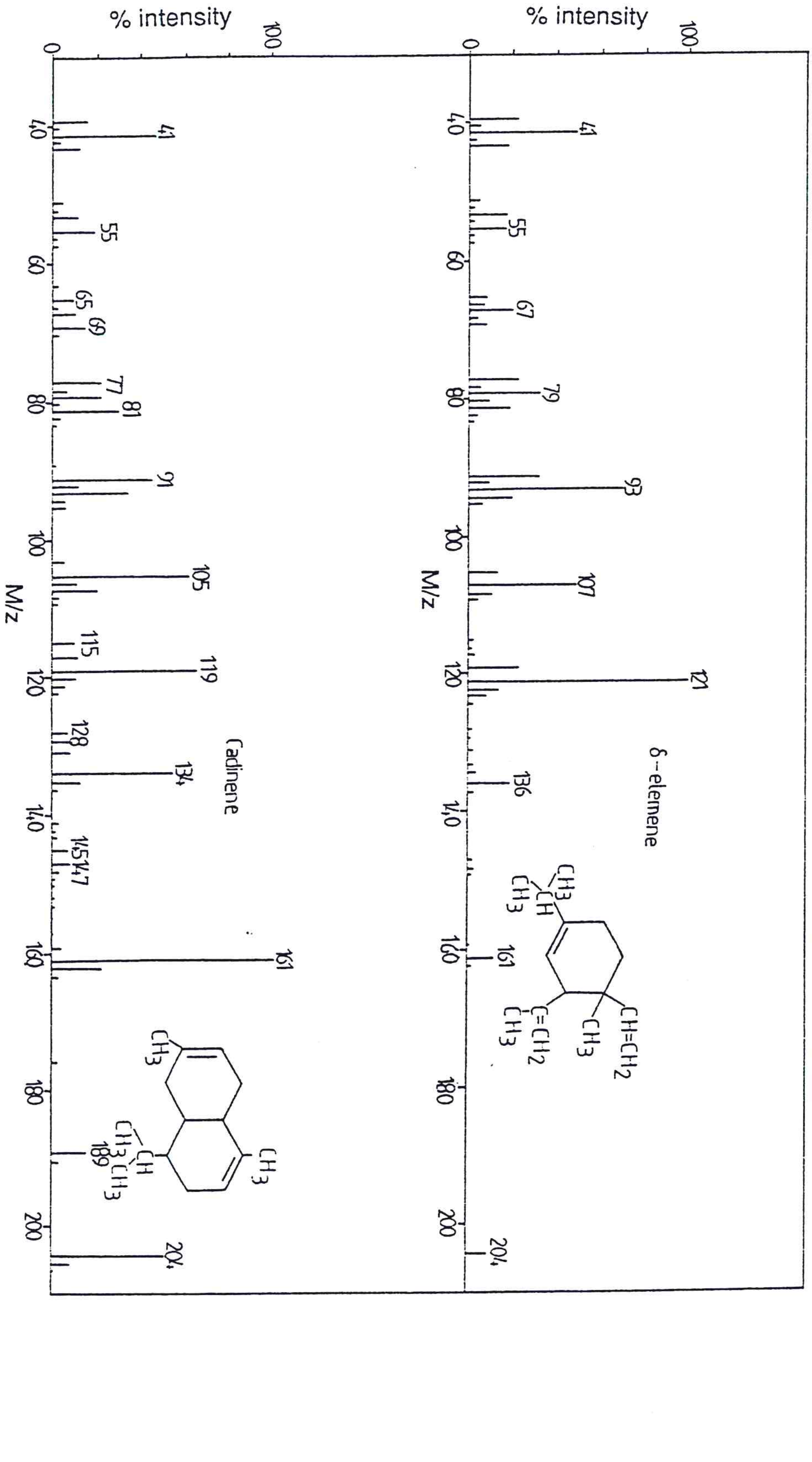

% intensity
100
0
α-humulene
M/z
% intensity
(z)-β-farnesene
M/z


% intensity
100
0
γ-muurolene
M/z
CH3
CH2
CH
41
51
55
67
79
93
105
115
119
133
148
161
189
204
% intensity
Ledene
H3C
107
131
135
147
175
M/z

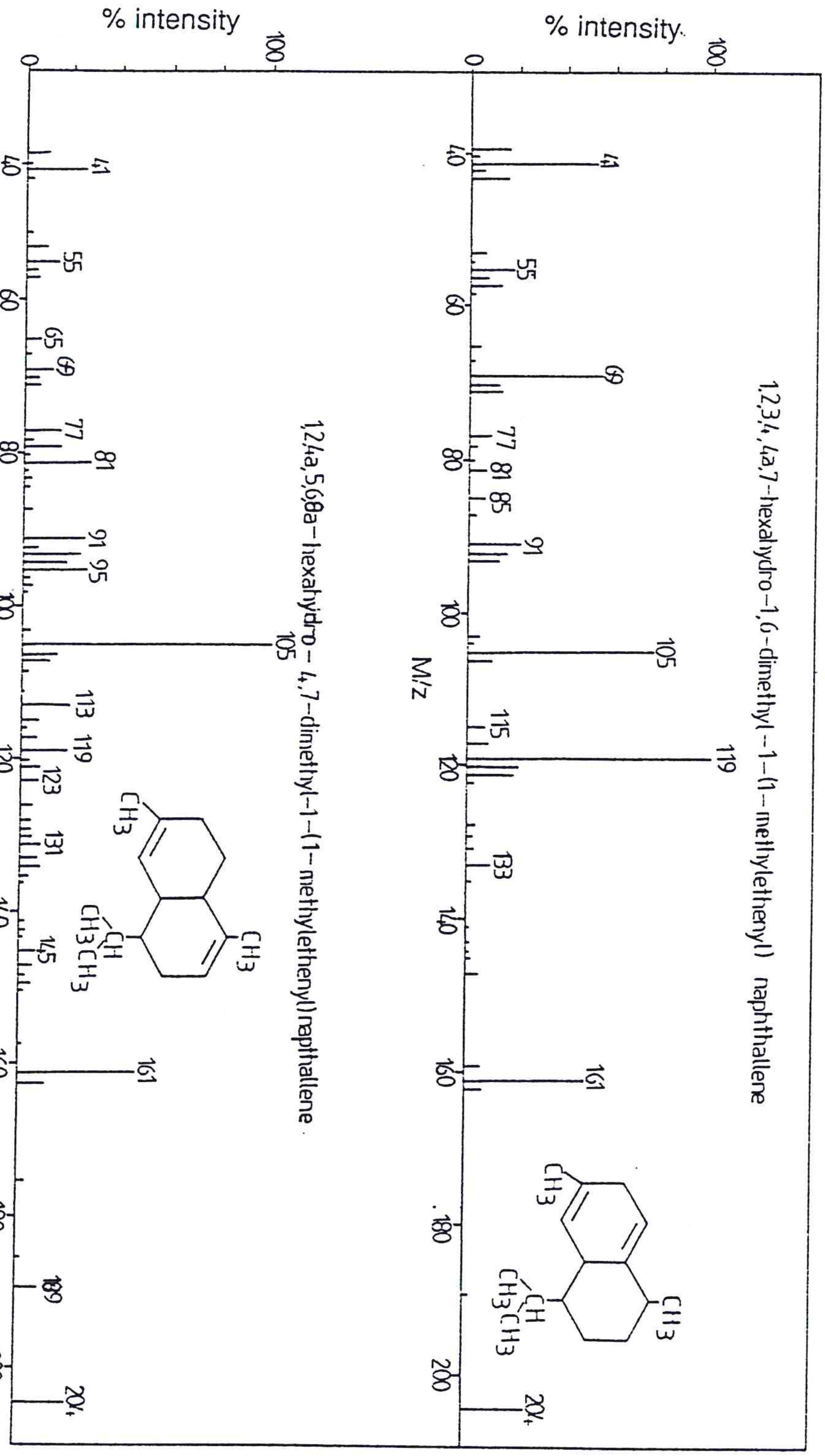

% intensity
% intensity
Decahydro-1,6-bis(methylene)-4-(1-methylethenyl)
Eremophilene
M/z
M/z

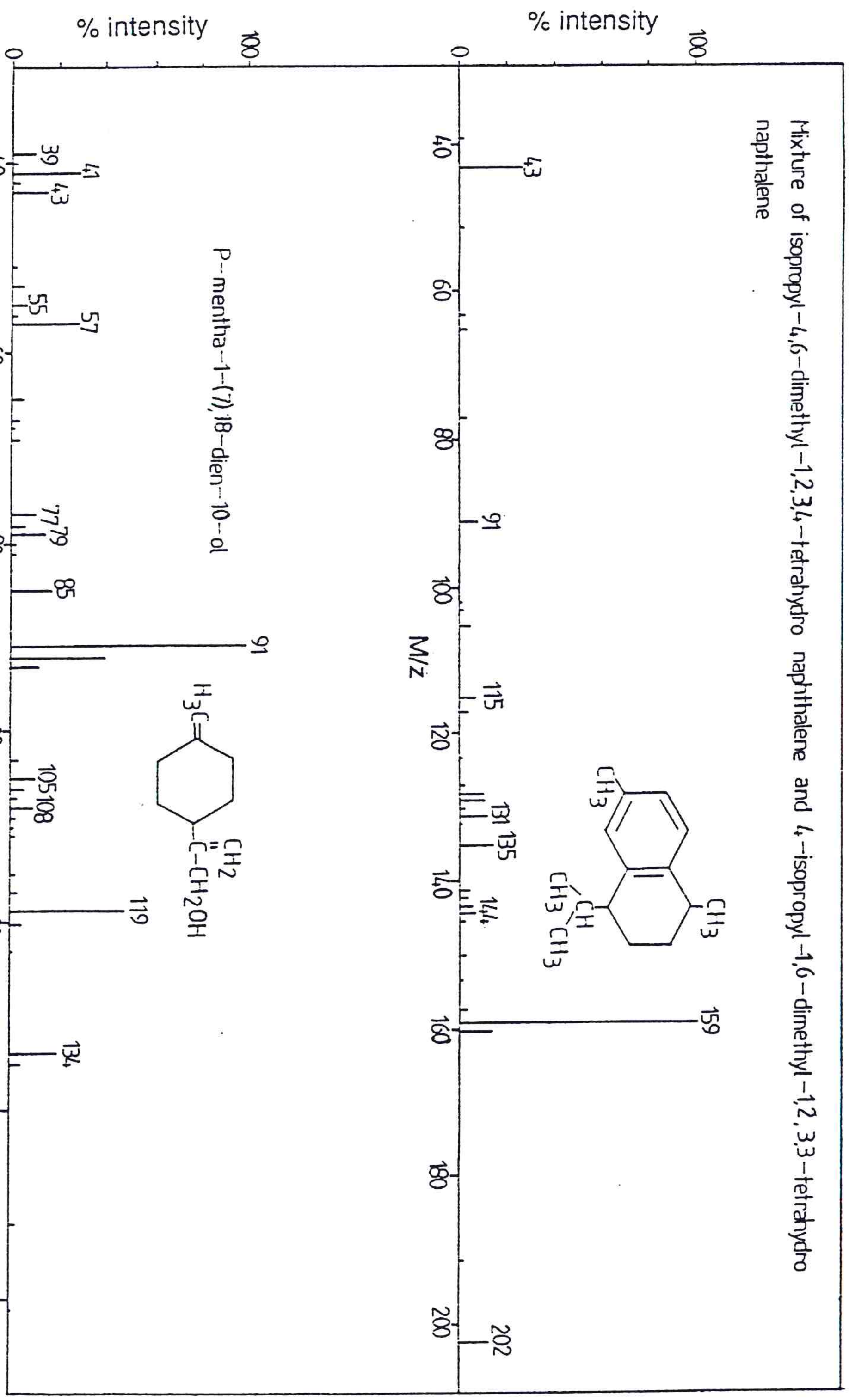

% intensity
% intensity
M/z
M/z
β-selinene
(−)-α-selinene
CH3
CH2
H2C=C
H3C
CH3
CH3
H2C=C
CH3


% intensity
% intensity
M/z
M/z
α-guaiene
α-bergamotene
41
55
67
77
81
93
105
121
133
147
175
189
204
41
51
55
65
69
79
93
107
121
136
161
204
CH2
CH3
CH3
CH3
CH3
C=CHCH2CH2
CH3
CH3
CH3

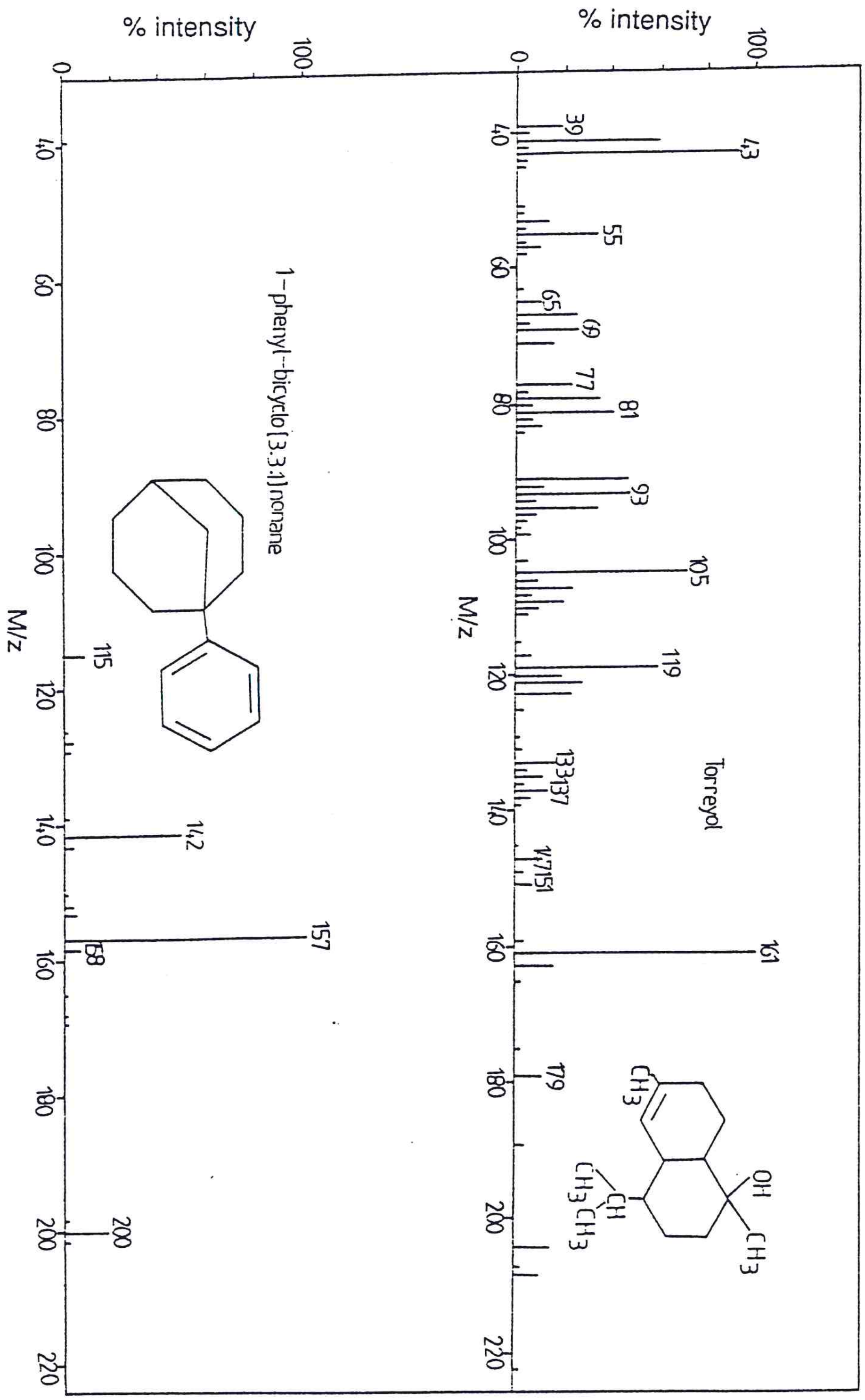


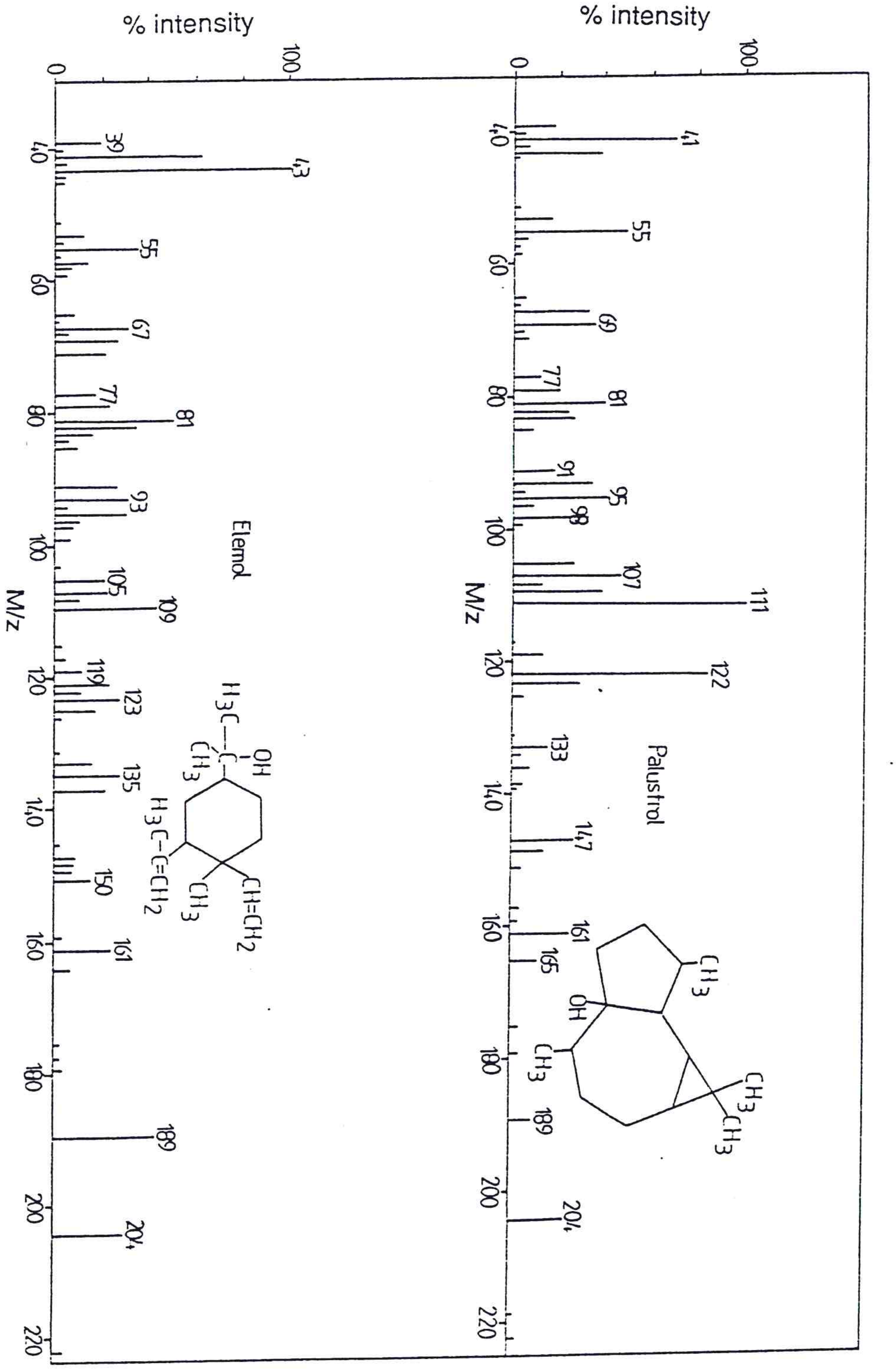
% intensity
% intensity
δ-elemene
Cadinene
M/z
M/z

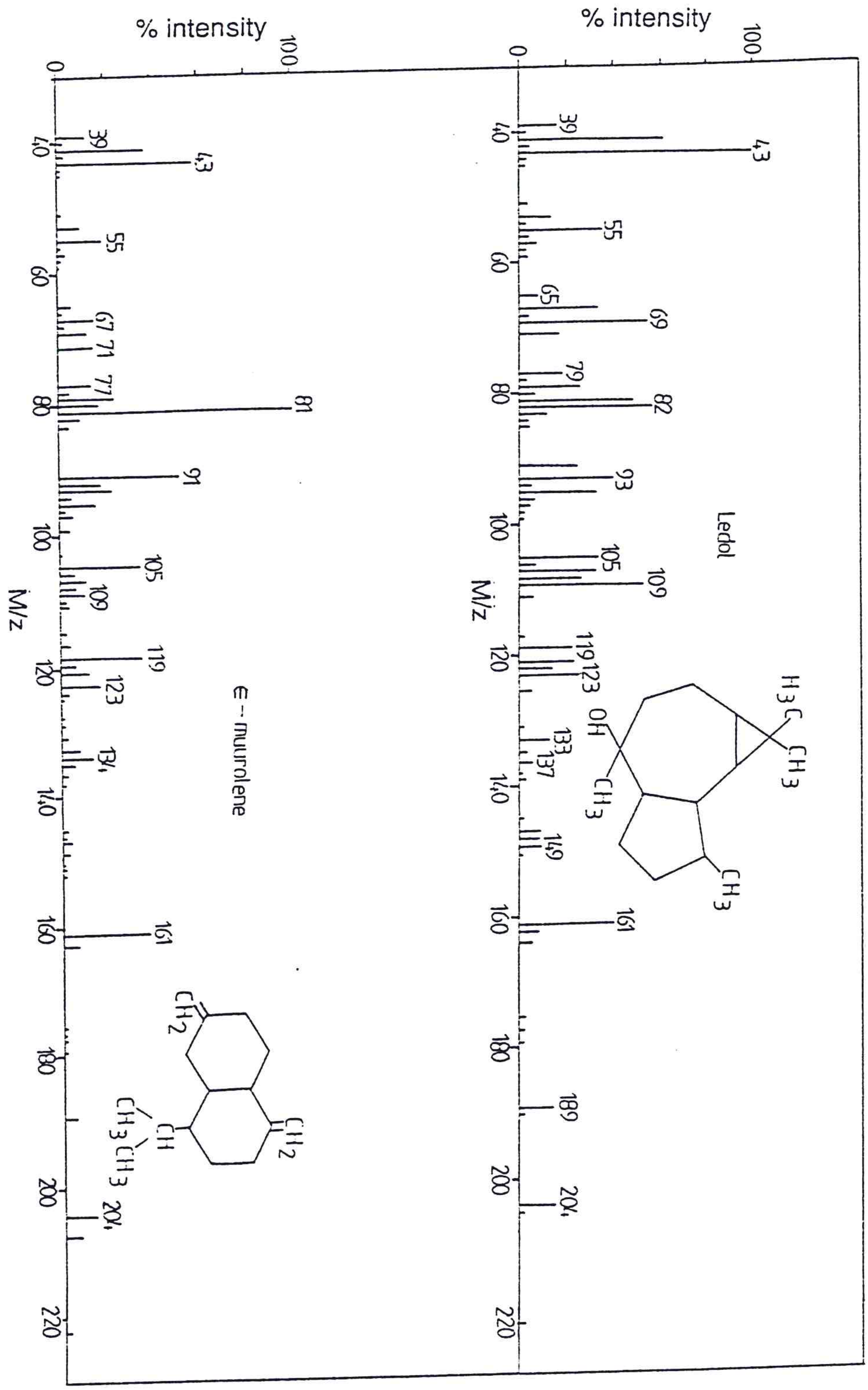

% intensity
% intensity
1,2,3,4,4a,7-hexahydro-1,6-dimethyl-1-(1-methylethenyl) naphthalene
12,4a,5,6,8a-hexahydro-4,7-dimethyl-1-(1-methylethenyl)napthallene
M/z
M/z
CH3
CH
CH3 CH3

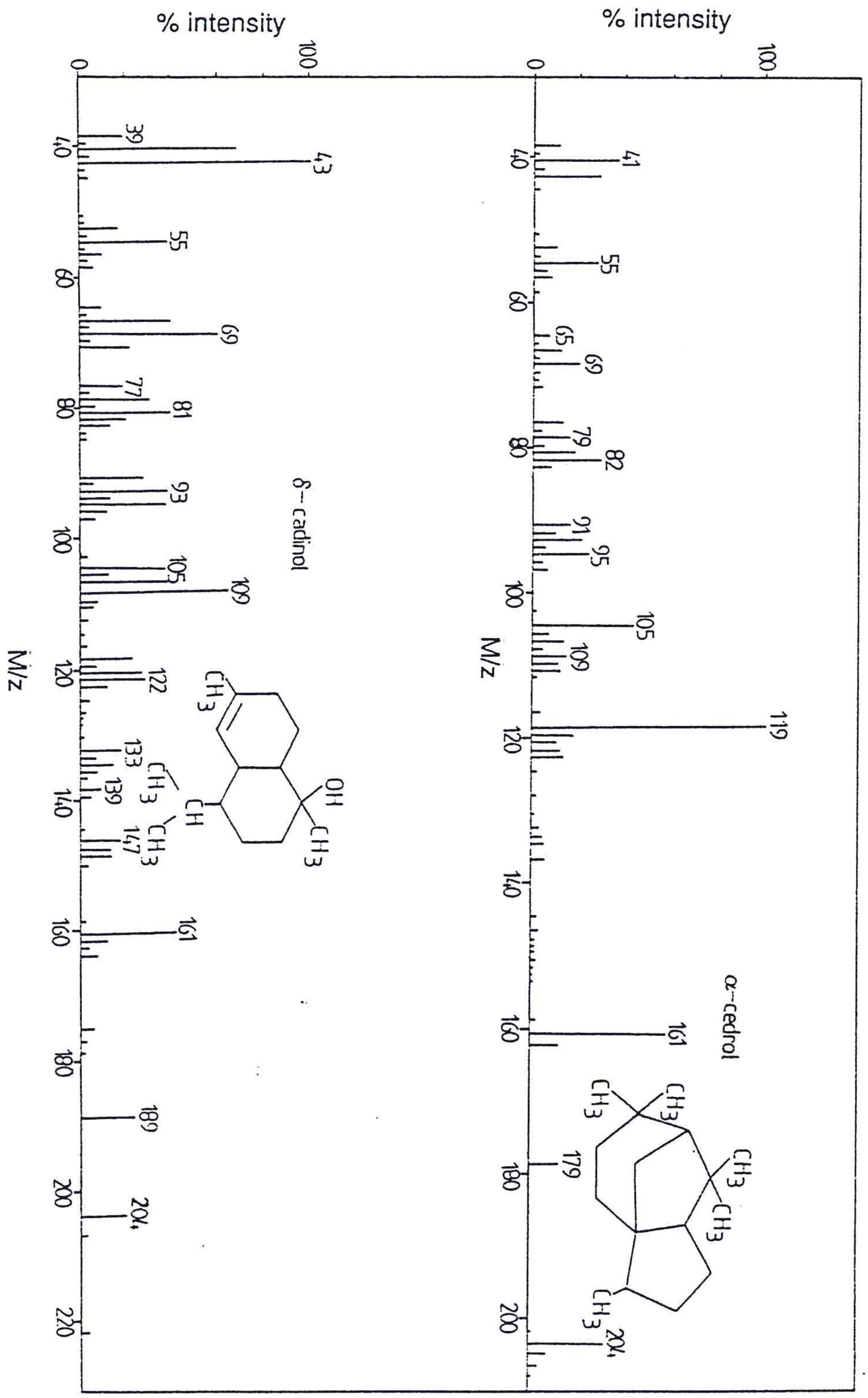


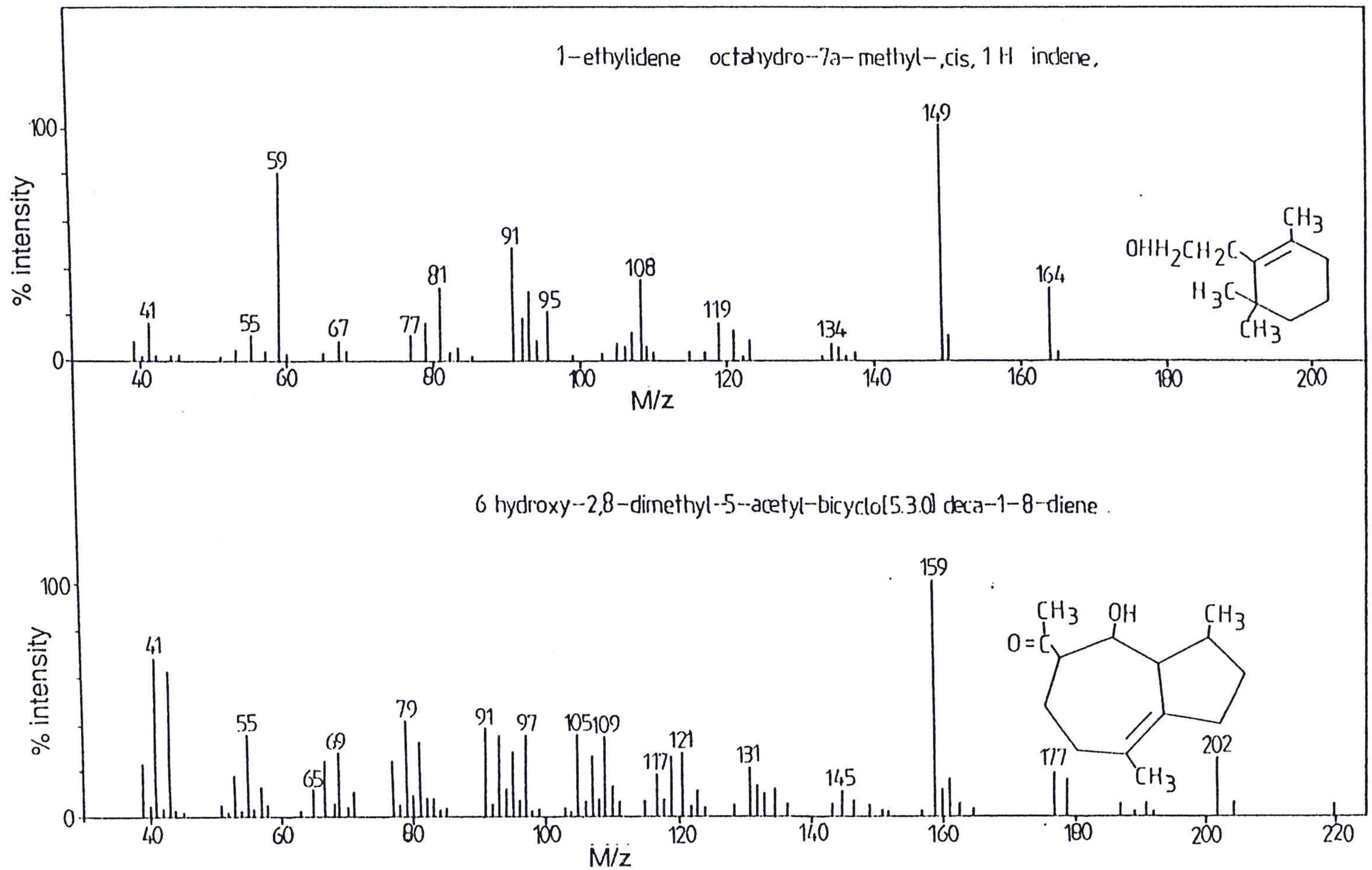
Mixture of isopropyl-4,6-dimethyl-1,2,3,4-tetrahydro naphthalene and 4-isopropyl-1,6-dimethyl-1,2,3,3-tetrahydro napthalene
% intensity
0
100
M/z
43
91
115
131
135
144
159
202
40
60
80
100
120
140
160
180
200
CH3
CH
P-mentha-1-(7),18-dien-10-ol
% intensity
0
100
M/z
39
41
43
55
57
77
79
85
91
105
108
119
134
CH2
C-CH2OH
H3C

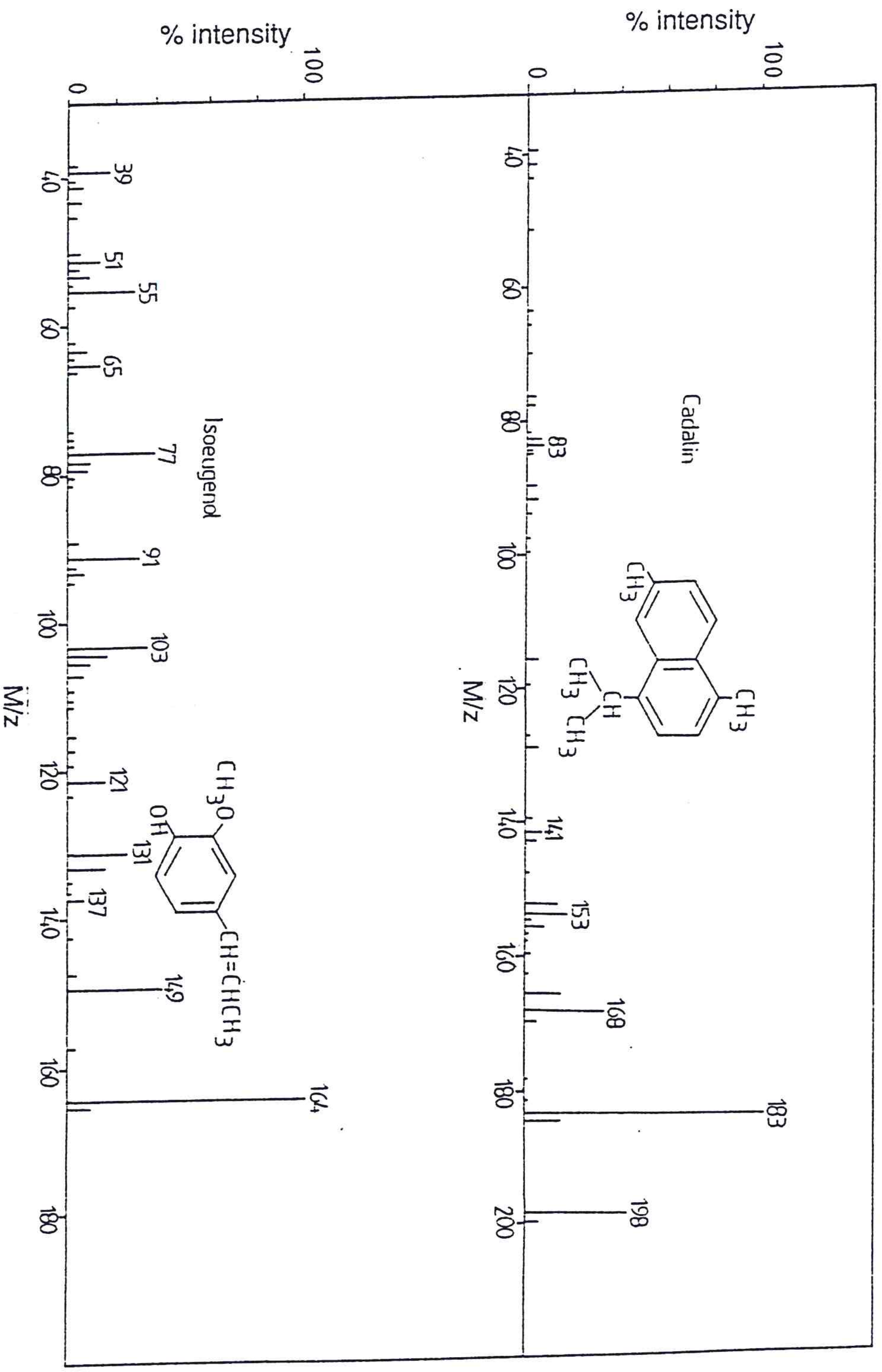

% intensity
Torreyol
1-phenyl--bicyclo[3.3.1]nonane
M/z
% intensity
M/z

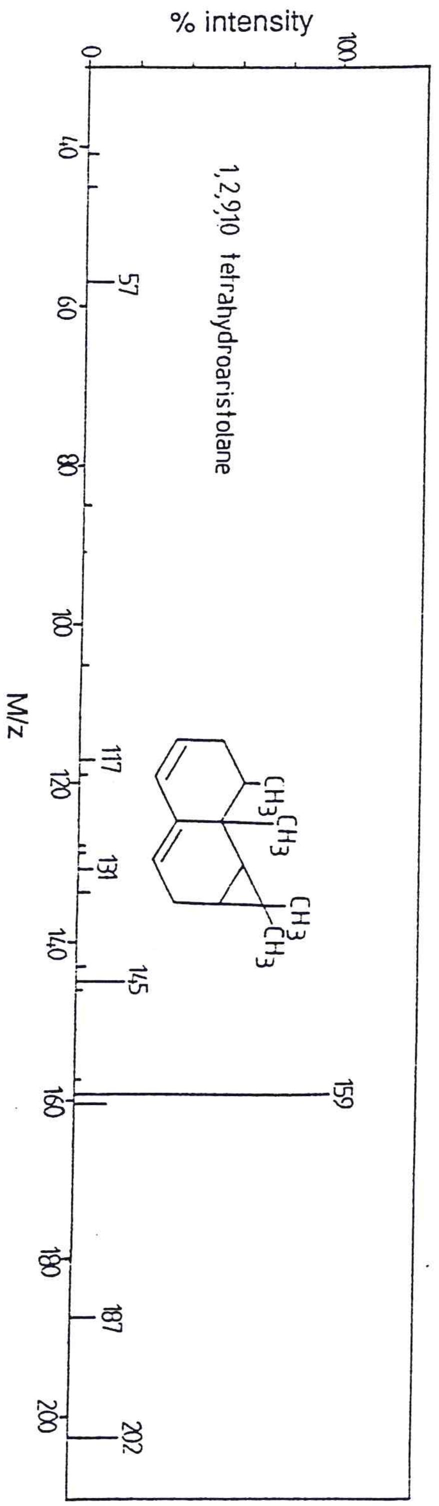

% intensity
% intensity
Palustrol
Elemol
M/z
M/z


% intensity
% intensity
Ledol
E--muurolene
M/z
M/z


% intensity
% intensity
α-cedrol
δ-cadinol
M/z
M/z


1-ethylidene octahydro--7a-methyl-,cis, 1 H indene,
% intensity
100
0
41
55
59
67
77
81
91
95
108
119
134
149
164
40
60
80
100
120
140
160
180
200
M/z
OHH_2CH_2C
CH_3
H_3C
CH_3
6 hydroxy--2,8-dimethyl-5--acetyl-bicyclo[5.3.0] deca-1-8-diene .
% intensity
100
0
41
55
65
69
79
91
97
105
109
117
121
131
145
159
177
202
220
M/z
CH_3
OH
CH_3
O=C
CH_3


% intensity
100
0
Cadalin
M/z
83
141
153
168
183
198
% intensity
Isoeugenol
M/z
39
51
55
65
77
91
103
121
131
137
149
164



% intensity
0
100
M/z
40
60
80
100
120
140
160
180
200
57
117
131
145
159
187
202
1,2,9,10 tetrahydroaristolane
CH3
CH3
CH3
CH3

Appendix (M). Anova tables.

Analysis of variance of immature males maturation time in the presence of 5th instar nymphs as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	4	1422.92	306.4	0.0001
Error	89	4.64		
Corrected Total	93			

C.V.=9.37

Analysis of variance of immature males maturation time in the presence of 5th instar nymphs as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	4	1424.36	213.01	0.0001
Error	89	6.69		
Corrected Total	93			

C.V.=10.69

Analysis of variance of immature males maturation time in the presence of one, two and four 5th instar nymphs as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	3	576.76	63.4	0.0001
Error	53	9.10		
Corrected Total	62			

C.V.=10.10

Analysis of variance of immature males maturation time in the presence of one, two and four 5th instar nymphs as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	3	572.87	58.99	0.0001
Error	59	9.71		
Corrected Total	62			

C.V.=10.24

Analysis of variance of immature females maturation time in the presence of 5th instar nymphs as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	4	190.94	172.96	0.0001
Error	91	1.10		
Corrected Total	95			

C.V.=5.44

Analysis of variance of immature females maturation time in the presence of 5th instar nymphs as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	4	835.26	274.71	0.0001
Error	91	3.04		
Corrected Total	95			

C.V.=8.13

Analysis of variance of immature females maturation time in the presence of 5th instar nymphs as assessed by oviposition

source	df	mean square	F value	Pr > F
Treatment	4	713.92	164.55	0.0001
Error	91	4.34		
Corrected Total	95			

C.V.=7.99

Analysis of variance of immature males maturation time exposed to (1, 3, 6 and 9g) of 5th instar faecal volatiles, immature males and 5th instar nymphs as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	5	729.97	121.62	0.0001
Error	130	6.00		
Corrected Total	135			

C.V.=11.62

Analysis of variance of immature males maturation time exposed to (1, 3, 6 and 9g) 5th instar faecal volatiles, immature males and 5th instar nymphs as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	5	720.18	125.97	0.0001
Error	130	5.72		
Corrected Total	135			

C.V.=11.18

Analysis of variance of immature females maturation time exposed to (1, 3 and 6 g) of 5th instar faecal volatiles, immature females and 5th instar nymphs as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	4	713.66	676.52	0.0001
Error	120	01.05		
Corrected Total	124			

C.V.=4.56

Analysis of variance of immature females maturation time exposed to (1, 3 and 6g) of 5th instar faecal volatiles, immature females and 5th instar nymphs as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	4	866.41	902.71	0.0001
Error	120	00.96		
Corrected Total	124			

C.V.=4.20

Analysis of variance of immature females maturation time exposed to (1, 3 and 6g) of 5th instar faecal volatiles, immature females and 5th instar nymphs as assessed by oviposition

source	df	mean square	F value	Pr > F
Treatment	4	820.03	565.06	0.0001
Error	120	1.45		
Corrected Total	124			

C.V.=4.68

Analysis of variance of immature males maturation time exposed to trapped volatiles of 5th instar nymphs, immature males and 5th instar nymphs as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	3	1027.64	103.92	0.0001
Error	73	9.89		
Corrected Total	76			

C.V.=11.34

Analysis of variance of immature males maturation time exposed to trapped volatiles of 5th instar nymphs, immature males and 5th instar nymphs as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	3	1002.16	108.94	0.0001
Error	73	9.20		
Corrected Total	76			

C.V.=10.83

Analysis of variance of immature females maturation time exposed to trapped volatiles of 5th instar nymphs, immature females and 5th instar nymphs as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	3	1865.79	227.08	0.0001
Error	86	8.22		
Corrected Total	89			

C.V.=11.21

Analysis of variance of immature females maturation time exposed to trapped volatiles of 5th instar nymphs, immature females and 5th instar nymphs as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	3	2047.78	387.29	0.0001
Error	86	5.29		
Corrected Total	89			

C.V.=8.43

Analysis of variance of immature females maturation time exposed to trapped volatiles of 5th instar nymphs, immature females and 5th instar nymphs as assessed by oviposition

source	df	mean square	F value	Pr > F
Treatment	3	1809.41	333.39	0.0001
Error	86	5.43		
Corrected Total	89			

C.V.=7.76

Analysis of variance of the number of eggs per pod of immature females in the presence of 5th instar nymphs and immature females of the same age.

source	df	mean square	F value	Pr > F
Treatment	1	220.500	1.68	0.2127
Error	16	130.903		
Corrected Total	17			

C.V.=20.05

Analysis of variance of the number of eggs per pod of immature females exposed to 5th instar faecal volatiles and immature females of the same age.

source	df	mean square	F value	Pr > F
Treatment	3	303.33	2.15	0.1037
Error	60	141.27		
Corrected Total	63			

C.V.=22.75

Analysis of variance of the number of eggs per pod of immature females exposed to 5th instar trapped volatiles 5th instar nymphs, immature females and control (CH_2Cl_2 + paraffin oil).

source	df	mean square	F value	Pr > F
Treatment	3	303.33	2.15	0.1037
Error	60	141.27		
Corrected Total	63			

C.V.=22.75

Analysis of variance of immature males maturation time exposed to *Commiphora quadricincta* crude steam distillate before and after the winter rains as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	7	175.80	31.23	0.0001
Error	149	5.63		
Corrected Total	154			

C.V.=15.05

Analysis of variance of immature males maturation time exposed to *Commiphora quadricincta* crude steam distillate before and after the winter rains as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	7	163.64	28.66	0.0001
Error	147	5.71		
Corrected Total	154			

C.V.=14.47

Analysis of variance of immature females maturation time exposed to *Commiphora quadricincta* crude steam distillate before and after the winter rains as assessed by colour

source	df	mean square	F value	Pr > F
Treatment	6	205.59	65.65	0.0001
Error	107	3.13		
Corrected Total	113			

C.V.=11.10

Analysis of variance of immature females maturation time exposed to *Commiphora quadricincta* crude steam distillate before and after the winters rain as assessed by copulation

source	df	mean square	F value	Pr > F
Treatment	6	195.26	61.99	0.0001
Error	107	3.15		
Corrected Total	113			

C.V.=10.88

Analysis of variance of immature females maturation time exposed to *Commiphora quadricincta* crude steam distillate before and after the winter rains as assessed by oviposition

source	df	mean square	F value	Pr > F
Treatment	6	231.11	71.59	0.0001
Error	107	3.23		
Corrected Total	113			

C.V.=9.57

Analysis of variance of the number of eggs per pod of immature females exposed to *Commiphora quadricincta* crude steam distillate before and after the winter rains, mature males and control (hexane + paraffin oil).

source	df	mean square	F value	Pr > F
Treatment	3	1121.40	13.55	0.0001
Error	60	82.78		
Corrected Total	63			

C.V.=19.61