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BIOLOGY AND ECOLOGY OF CYPRESS TWIG BORER, URACANTHUS CUPRESSIANA SP. N. (CERAMBYCIDAE)

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A Thesis
submitted for the degree of Doctor of Philosophy
in the Faculty of Agricultural Science to
the University of Adelaide

Department of Entomology,
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Plate 1 : Female beetle Uracanthus cupressiana on its host, Cupressus sempervirens.

To

My Mother

and

My Country

SUMMARY

The biology and ecology of the native Australian insect, the Cypress Twig Borer (CTB), Uracanthus cupressiana sp.n., on the exotic conifer, Cupressus sempervirens, were studied between 1983 and 1987.

Outbreaks of CTB have occurred periodically for some decades, yet the species is still undescribed and its biology not studied. In this present study, the species is described, the genus to which this insect belongs is reviewed, and 2 keys are presented, one to separate closely related genera, the other to separate species of the genus Uracanthus.

In the field this insect mostly has a biennial life cycle, with a few individuals developing in one year. Under laboratory conditions, some may even have a triennial life cycle. Beetle emergence and reproductive activity occur in spring and summer, reaching a peak in November. The number emerging increases on warm sunny days and decreases on cold cloudy days. The establishment of young larvae mostly occurs in summer. Most of the insect's life is spent in the larval stage. There are 6 to 7 larval instars, the larval stage taking 14 to 22 months, sometimes more than 2 years under laboratory conditions. The moisture content of the wood greatly affects the development and growth of larvae, particularly under laboratory conditions.

The insect enters diapause during the larval or prepupal stage. The diapause is sensitive to temperature and synchronises the life cycle with the seasons.

Laboratory study indicates that both male and female become very active when sexually mature, and they emit sex pheromone that can guide them to locate their mates. The ovipositing female retains her eggs when the host plant is not available. When both host and non-host plants are provided, the female tends to deposit fewer eggs, in other words the fecundity of beetles decreases under the influence of a non host-plant. The native host of this insect is probably Callitris spp.

Observations on caged-potted plants indicate that alteration of the water status of the host tree (by watering regimes) does not alter the reproductive behaviour of insects. However, it does alter the larval behaviour in feeding and constructing the pupal chamber and the insect does more damage to water-stressed trees than to regularly watered trees.

The response of host trees towards larval attack was investigated and discussed. There is a linear correlation between host tree size (surface area of tree) and population density.

The study showed that the role of natural enemies (parasites and predators) in the population dynamics of CTB was trivial. Study of the life table indicates that the key factors are more likely to be those that (1) operate on the first instar larvae, and (2) have a differential effect on the sex ratio.

Excessive resin flow, produced by trees in response to larval attack, may be a key factor in the population dynamics of the CTB. The results of the study support this hypothesis and account for both the distribution and the abundance of the insect in South Australia, particularly on the Adelaide plain. The operation of this key factor greatly depends on climatic factors, rainfall in particular.

Suggestions are made for the control of CTB in *Cupressus* trees without the use of insecticides. Based on the assumption that oleoresin flow is a key factor, it is suggested that regular maintenance (good watering) of the trees in spring and summer, the diversification of trees, and/or the change to native trees could all be worth trying. Tree removal or pruning (removal of all the attacked parts of the tree) is a useful method of controlling CTB. Adoption of a management program based on these suggestions should not only prevent future outbreaks of CTB but also provide better aesthetic values (healthier, better looking trees).

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and, to the best of my knowledge and belief, contains no material peviously published or written by another person, except when due reference is made in the text of this thesis.

November, 1987. (Saartje Jeanne Rondonuwu L.)

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CHAPTER I

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CHAPTER 1

GENERAL INTRODUCTION

1.1 INSECT PHENOLOGY

The cypress twig borer, Uracanthus cupressiana sp.n., an insect indigenous to Australia, is a newly recognised pest that is causing extensive branch or twig damage on such plants as Cupressus sempervirens, the pencil cypress, and other attractive ornamentals in home gardens and parks.

The early literature that concerns the taxonomy of the some other Uracanthus spp. (Lea, 1916, 1917; Mc Keown, 1938, 1940, 1942a) has been reported. However, the cypress twig borer (CTB) has hitherto not been described. So far, no study has been done on the members of this genus even though some species have caused extensive damage on both indigenous and introduced scrubs and trees. Some species have known damaging such as U. froggatti, larvae feed on the stem of Lasiopetalum ferrugineum (Froggatt, 1894), U. discicollis on Melaleuca sp., U. pertenuis on Loranthus sp. and Acacia armata, U. albatus (Lea, 1916), U. strigosus on Acacia sp. (Lea, 1916; French, 1911), U. acutus on peach, plum, and apricot (Froggatt, 1898 in McKeown, 1947); U. bivitta on Helichrysum ferrugineum and Acacia longifolia (French, 1911), U. cryptophagus on native finger-lemon (Citrus australasica) and cultivated citrus (Olliff, 1892; Froggatt, 1923; Brimblecombe, 1943), U. loranthi on Loranthus sp. (Lea,1916), U. maleficus on hazelnut hedges (Lea, 1917), U. simulans on Banksia australis, Helichrysum ferrugineum and Acacia (French, 1911), and U. triangularis on Eriostemon lanceolatus, Banksia integriflia, Acacia longifolia, Boronia pinnata, Acacia spp. (McKeown, 1947). The reason for why no study has been done still unclear, but may be due to the fact that these species have not been considered to be of any direct economic importance as agricultural pests.

This genus is widely distributed through Australia and New Guinea. In South Australia, species known to be established are U. bivitta, U. simulans, U. triangularis var. B, U. suturalis, U. albatus, U. pertenuis, U. fuscus, U. discicollis, U. dubius, and U. cryptophagus (Lea, 1916; McKeown, 1947).

1.2 HOST PHENOLOGY

The earliest record of the introduction of Cupressus spp. into Australia was in 1830 and into South Australia was in 1857 (J. A. E. Whitehill personal comm.).

Today Cupressus spp. are extensively planted as ornamental trees, hedges, and/or windbreaks in South Australia and other states in Australia. They are grown mostly in private yards, parks and in cemeteries. In private yards, some species of Cupressus are grown individually, in clump, or in row as hedges or as windbreaks. Some were pruned and shaped, and some naturally grew.

In South Australia, particularly on the Adelaide plain Cupressus spp. that are commonly found are C. sempervirens, C. macrocarpa, C. tolurosa, and C. glabra. However, in this recent study, all specimens used were taken from C. sempervirens as well as population field studies by ignoring the others species of Cupressus. The C. sempervirens (pencil cypress or pencil pine) was chosen in this study because it was more abundant than other species of Cupressus within study site.

The tree consists of a central axis or main trunk that supports the crown. The trunk bears dense short branches and this results in a columnar or conical shaped tree (wider at the lower part), or rather cylindrical tree (almost the same in diameter at all parts of tree), or ellipsoidal (wider about the mid-part) shaped tree. The pruned trees are almost cylindrical in shape.

1.3 DAMAGED CAUSED BY CTB

As previously mentioned, CTB is a newly recognized pest that is causing extensive branch or twig damage on Cupressus spp. (cypress). This is quite surprising because this species being recognised after probably some outbreaks or a prolonged outbreak have occurred. In Adelaide plain in particular, CTB is a serious pest on Cupressus trees. From survey data 1986, about 70% of C. sempervirens trees within the study site have been attacked by CTB. The remaining 30% trees are mostly young trees or newly planted trees.

The infestations vary in intensity, ranging from very light to very severe. The proportion of trees killed as a direct consequence of cutting by CTB larvae is small. In fact, the tree mortality is found only in very severely infested areas, particularly in coastal areas. Apparently climatic factors also contribute to the tree mortality.

Plate 2 : A severely attacked host tree, C. sempervirens. Brownish or yellowish spots on the tree crown are dried branches that had been girdled by larvae U. cupressiana (left). Dissected attacked twigs showing the larval mines along the centre (right).

The damage caused by CTB can be easily recognized on the tree crowns from some distance as whitish (if newly cut) or brownish spots or flags (after 2 or 3 years cut). These spots (flags) are actually dry branches or twigs resulting from larval girdling. Usually just one larva is to be found tunneling and feeding in a branch or twig. Only rarely are 2 larvae found, on severely attacked trees.

In South Australia, CTB are also found in the Murray Bridge plain, York Peninsula, and Barossa Valley plain. It is probably found in other areas in South Australia (the whole of South Australia was not surveyed in this study, because of constraining time and cost factors). In Victoria and New South Wales, this insect also exists, while it is not found in Tasmania.

1.4 THE STUDY AREA

The field study was undertaken on the Adelaide plain (see Fig. 1.1). All experimental materials were collected from this area. Studies on population and life tables were carried out in a particular part of this area (Chapter 6 and 4 respectively).

The basic features of the climate in the study area are much like that of the rest of South Australia, i.e. it has dry summer with relatively mild nights, and cool but not severe winter. Highest mean of daily air temperatures recorded during summer months, December to February, were 31.2, 27.9, 28.1, and 26.7°C, respectively in 1983, 1984, 1985 and 1986. The temperature starts to fall during autumn months of March to May. The winter months, June to August (July was the coldest), have the lowest mean of daily air temperatures recorded subsequently in 1983, 1984, 1985 and 1986 were 7.7, 7.3, 8.9, and 8.1°C. The temperature gradually rises in spring months (September to November) (see Appendix 3). Most of the rains are experienced between May and September. Rainfall during the rest of the year is generally light although heavy rains can occasionally occur in that period. Spatial and temporal distributions of rainfall strongly correlates to altitude. It is the lowest at the coastal area, increasing towards the slope of the Mt. Lofty Ranges (Schwerdtfeger, 1976).

Air temperature and rainfall recorded at Waite Institute during 1983, 1984, 1985 and 1986 are summarized in Appendices 2 & 3.

From "Generalized soil-landscapes and soil properties of the Adelaide Region" (see Fig. 1.2) can be summarised that the Adelaide soil,

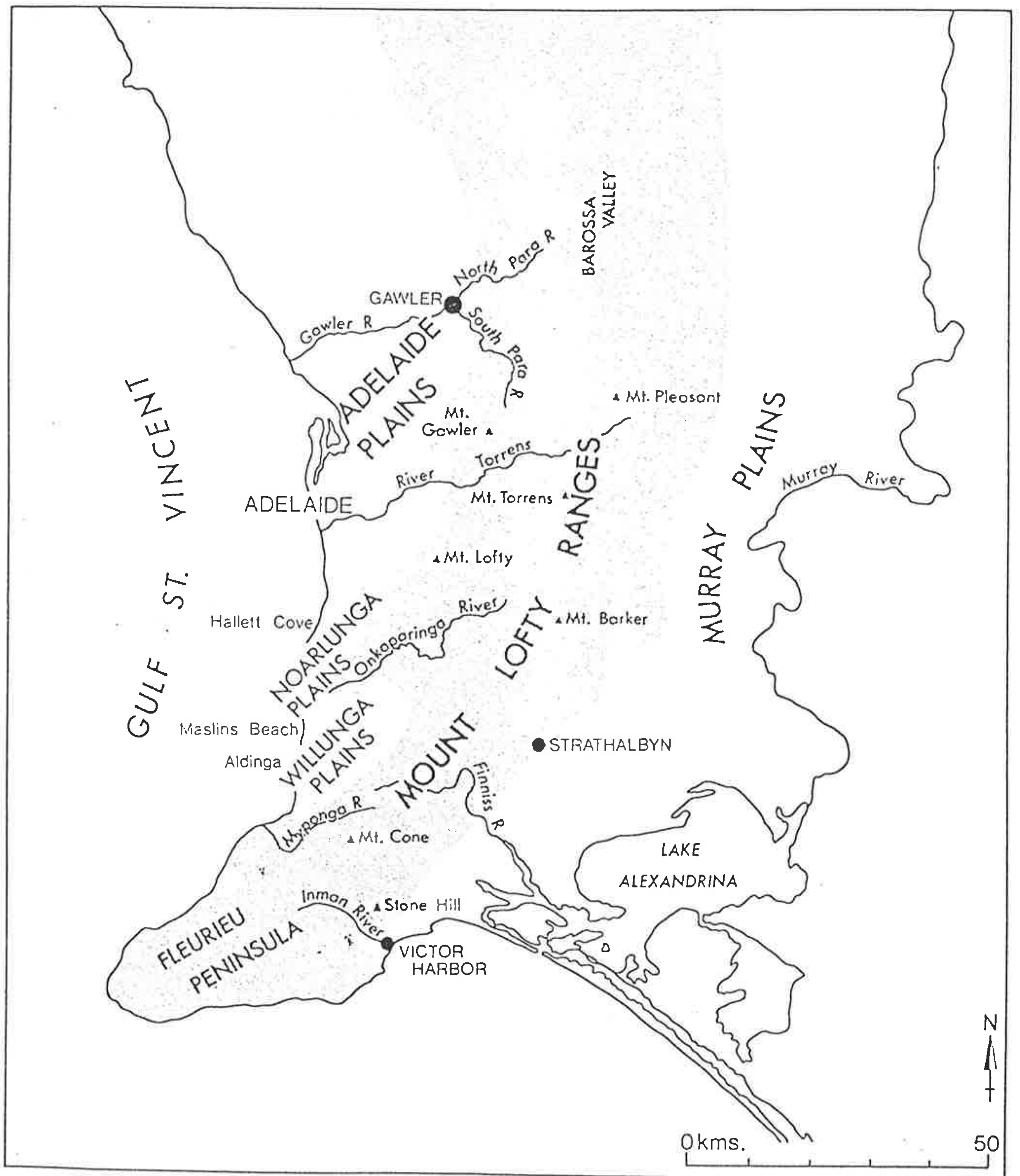


Fig.1.1 The Adelaide Region.

study site in particular, consists of 2 units, viz. A2 and 01. The characteristics of unit A2 : (1) Generalized parent materials are calcareous sands and siliceous sands; (2) highly permeable to water; and (3) chemical property with regard to deficiencies namely N, P, K, Cu, Zn, Ca, Mg, B, Fe, and Mn. The unit 01 characteristics are (1) finer grained and clay; (2) low permeability; and (3) deficiencies of N, P, Zn, MO, S, and Mn.

Sample areas (zones) 1 and 2 are located in the region that consists of soil type 01, zone 3 is partly located at region with soil types 01 and A2, and zone 4 is in a region with unit A2.

1.5 SCOPE OF THE STUDY

The present study investigates the biology and ecology of the cypress twig borer (U. cupressiana sp.n.). The study includes:

(1) Taxonomy of the genus Uracanthus, particularly description, and construction of Keys to genera and species to verify that the species is undescribed

(2) Life history and seasonal occurrence of the species

(3) Construction and analysis of life tables to try to determine which factor(s) may influence the population trend

(4) Aspects in reproductive behaviour that may be useful for an understanding of the population dynamics of the species

(5) Distribution and population growth of the species

(6) Evaluation of the role of host defence in the population dynamics of the insect.

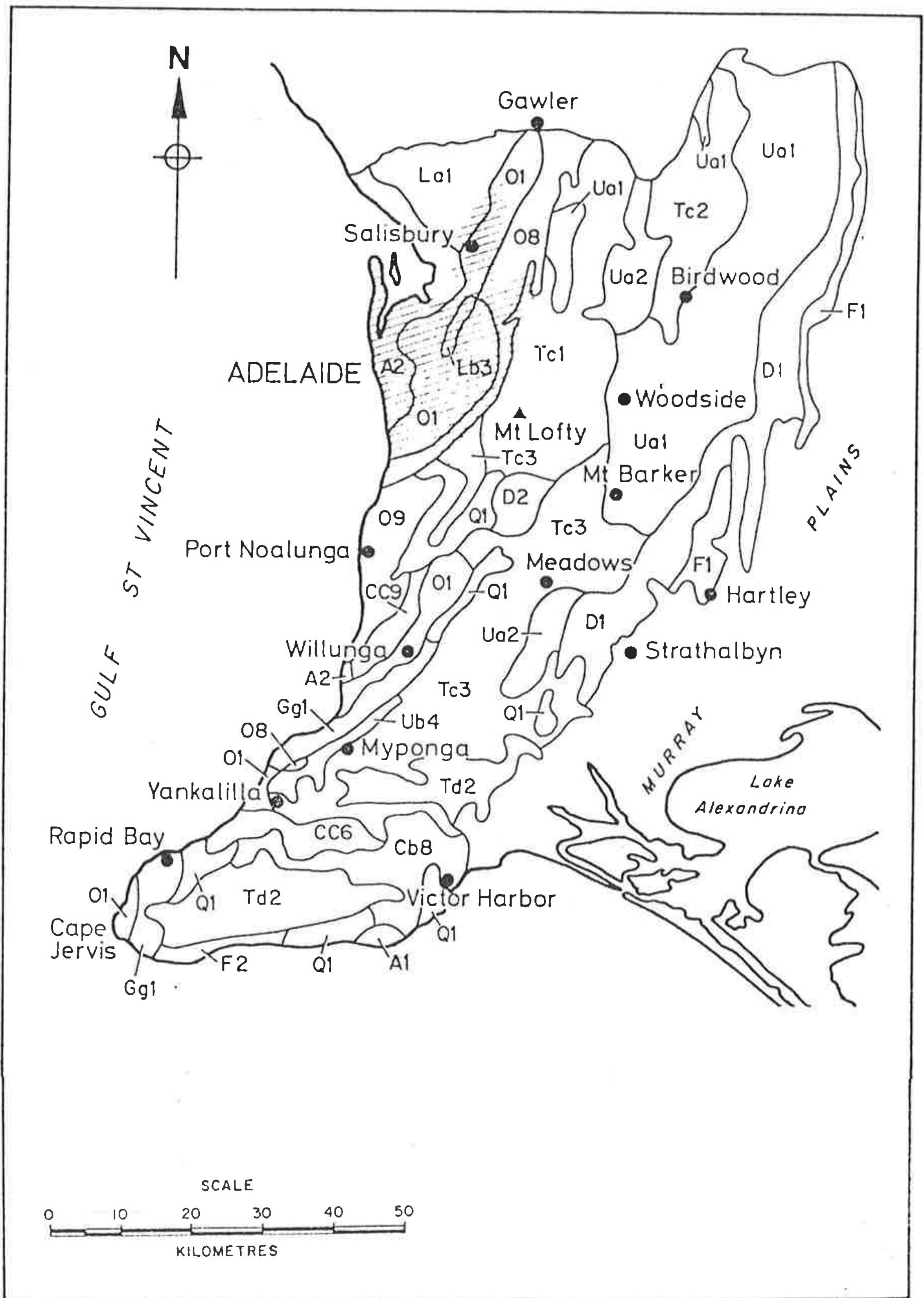


Fig. 1.2 Generalised soil-landscapes of the Adelaide region.

CHAPTER II

CHAPTER 2

GENERAL METHODS

2.1 MATERIAL COLLECTING TECHNIQUE

The preliminary survey was conducted on the Adelaide plain to map C. sempervirens trees being attacked by CTB. Insects were collected by climbing the trees and cutting their dry attacked twigs or branches. The cut twigs were transferred to laboratory and insectary after they were sorted and the unrequired parts were removed. They were placed vertically in plastic garbage bins (50cm high and 40cm in diameter) and sprayed with salt solution (5%) weekly until almost the beetles had emerged. The bins were kept under fluctuating temperatures.

Material collection was carried out from late winter to mid-spring every year from 1983 to 1986. To observe the factors affecting the biology of the species, the materials were collected monthly from the trees in sample areas chosen, exluding trees which have been specified for the study of population.

2.2 LABORATORY CULTURE

Beetles emerged from twigs were collected 4 times a day (0800-1000h, 1200-1500h, 1700-1900h, and 2100-2300h). They were sexed and kept separately in plastic containers with twigs of cypress. The beetles were paired and allowed to copulate in a mating chamber (9cm high and 4cm diameter). Each couple was transferred to an oviposition chamber (28cm high and 15cm diameter) with 6 fresh cut twigs of C. sempervirens (ca. 30cm long). The twigs were trimmed before placing them in the oviposition chamber. The twigs were replaced with freshly cut twigs daily until the death of the beetles. Twigs on which eggs had been deposited were examined under a light microscope. The number of eggs on each twig was reduced to a maximum of 6. The twigs were placed in a rectangular plastic container (65x40x40cm) with saturated salt solution (NaCl) at the bottom. The remaining procedure will be described in Section 4.2.2.4, experiment 1. The containers were kept in 20°CTR throughout the study. The twigs were sprayed with salt solution (5%) and were turned over monthly. So, the twigs being placed at the bottom layer were shifted to the upper layer and the reverse. Some beetles emerged from twigs after about 14 months. The remaining larvae were extracted from twigs, and individually placed

into a small vial (5x1cm diameter) with moist frass and cottonwool stopper, after they had stopped feeding and had made holes for adult emergence. The vials were kept in rectangular plastic containers (25x20x10cm) with saturated salt solution (NaCl) at the bottom, and the containers were covered with black cloths. The main culture was commenced in late spring (November 1984), and terminated in February 1987.

2.3 GROWING TREES

Plants required for the maintainance of the insect culture and for experiment were grown in the glasshouse, the rockpile insectary, and in cages placed in the Waite Institute orchard. Plants were repotted and allowed to grow about 2 months prior to the commencement of experiments. Plants used were about 2 to 3 years old.

2.4 THE MEASUREMENT OF WATER STATUS OF THE TREES

The relative moisture content (RMC) of plants was determined, using Weatherly's method, from twigs that were cut some time in the morning. The twigs were immediately cleaned of needles, then each twig was put into a small sealed plastic bag. The twigs were transferred to the laboratory, and weighed to define the original weight. After weighing, they were put back into the plastic bag that had been filled with distilled water, and left aside for 2 days. After been soaked for 2 days, the twigs were reweighed after putting them on a piece of tissue paper in order to absorb excess water. The twigs were then kept into the oven under 60 to 70°C for a week, and reweighed afterward to specify the dry weight. The RMC or relative turgidity was expressed with the formula:

$$\text{RMC} = \frac{\text{Original weight} - \text{Dry weight}}{\text{Fresh weight when fully turgid} - \text{Dry weight}} \times 100\%$$

The water potential of the trees were measured on twigs that were cut at dawn (0500-0700h). The cut twigs were immediately put into a sealed plastic bag and measured by using a pressure bomb. The twigs remain in the plastic bag and each of which was put into the pressure chamber after cutting one of the plastic bag angle to make a hole for pushing out the tip of the twig which will be required for observations the water pressure.

2.5 TOTAL NITROGEN ANALYSIS

The determination of total nitrogen was modified from the micro-Kjeldahl method that was employed by McKenzie and Wallace (1954) (C. Rivers pers. comm.). Sample twigs were taken, and oven dried at 85°C for 24 hours. The dry twigs were ground. Sample of 0.25g ground plant material were weighed into a 100ml Kjeldahl tube. One Keltab and 4ml of concentrate H2SO4 (autodispenser) were added to the tube with ground material. Samples were digested on a digestion block. The digested samples were heated gently at first, then boiled for 30 minutes after clearing. The clearing time was about 25 min. The digested samples were allowed to cool, and diluted with distilled H20 to 75ml. Before distillation, the tip of the condenser was immersed into 5ml of boric acid + indicator solution. An aliquot of 5ml was taken, put into a distillation apparatus, 10ml of NaOH solution was added (400g NaOH were dissolved in one liter distilled H20), and distilled. When 10ml of solution had been distilled over, the flask containing the indicator solution was lowered, and then the remaining solution was allowed to distil over. The flask was removed, and the sample was ready for titration. The distilled samples were titrated with 0.01 N KH(IO3) (dissolved 3.899g KH(IO3)2 in distilled H20 and diluted to one litre) to a lilac end point by using 10ml auto-burette.

2.6 COUNTING OF ATTACKED TWIGS (FLAGS) IN THE FIELD

The attacked dry twigs were directly counted on the tree with aid of 2 to 4 hand counters. The dry twigs were easily recognized some distance away from the tree. On thin tree, the counting was done on both sides of the tree, after the tree was aproximately divided into 2 parts, run from top to the bottom of the tree. On wide trees, the counting was done after the tree was divided into 4 parts, run from top to the bottom part of the tree. The tree crown was divided into 3 strata (upper, mid- and lower parts). All dried twigs or branches indicating the presence of an individual were counted. They were categorized into: (1) current growth attacked twigs (NO), (2) currently attacked twigs (N1), (3) previous generation attacked twigs (N2), (4) old attacked twigs (N3), and (5) very old attacked twigs (>N3 or N4) (the generations were counted backwards) (these 5 categories of twigs will be defined clearly in Chapter 6). The counting of dry attacked twigs for the population study was carried out in late summer and early autumn (February and March, 1986).

Plate 3 : An attacked host tree of C. sempervirens and a two-metre wooden stick that was used for measuring trees: for measuring the height (left) and for width (right).

At that time the young instar larvae just established. So, for the first category (NO) can be easily counted, by counting the small dry twigs in which the young instar larvae just penetrated and established. The second category (N1) can be recognised from the colour of the needles which look light greenish (just dried after the older stage larva girdled the branch of big twigs) to whitish or creamish in colour. The third (N2) can be recognized from brownish to dark brownish needles colour of the twigs, and or the needles have partly drooped or hang down. The 4th (N3) can be recognized from those with needles have partly to totally fallen down, but the bark is still in complete, and the colour has not changed. The fifth (N4) can be recognized from those with bark have peeled off, and the wood colour has been totally changed from brownish to grey. Sometimes branch or twig appearance was found in between 2 categories mentioned above. They were placed into closer category by comparing the colour, and composition or amount of the needles.

2.7 TREE MEASUREMENT

The height and width of the trees were measured for the description of the tree. The method measuring these variables will be described in Section 6.2. The trees were categorized into 3 main shapes, viz. conical, cylindirical, and oval (ellipsoidal). The description of these 3 shapes of tree has been mentioned in Section 1.2.

The determination of the surface area of the trees using the geometric formula (Smith, 1954) is as follows:

(1) cone surface area:

$$CS = S/2 \times pi \times W.$$

where CS = cone surface area,
S = side
W = width or diameter.

The total surface area of conical trees is :

$$CS + HS \quad \text{or} \quad S/2 \times pi \times W + \frac{pi\ W^2}{2}$$

where HS = hemispheroidal area.

(2) cylinder surface area:

$$pi \times W \times H + 2pi \times R^2$$

where R = radius

The total surface areas of cylindrical trees is :

$$pi \times W \times H + 2pi \times R^2$$

(3) Prolate spheroid (ellipsoidal) surface area:

$$2pi\ ab\ \left(\frac{b}{a} + \frac{\arcsin e}{e}\right)$$

where $2a = H$ (height), $2b = W$ (width)
e = eccentricity.

The total surface area of oval tree is :

$$2pi\ ab\ \left(\frac{b}{a} + \frac{\arcsin e}{e}\right).$$

e = ~~square root $\left(1 - \frac{b^2}{a^2}\right)$~~ $\sqrt{1 - \frac{b^2}{a^2}}$

The total surface area of each tree used in this study was calculated by using a computer program.

CHAPTER III

CHAPTER 3

TAXONOMY OF THE GENUS URACANTHUS HOPE AND DESCRIPTION OF THE NEW SPECIES

3.1 INTRODUCTION

Most members of the Family Cerambycidae (Coleoptera: Chrysomeloidea) are easily recognized by their very long antennae which reach to at least the base of the elytra. Sometimes the antennae are 4 or 5 times the length of the insect itself. It is from their antennae that these insects receive their popular name, longicorn beetles. The Cerambycidae is a very large group that has a world wide distribution. The Neotropical Region has the largest diversity of species which are divided into 8 subfamilies, i.e. Parandrinae, Prioninae, Lepturinae, Oxypeltinae, Disteniinae, Aseminae, Cerambycinae, and Lamiinae (Duffy, 1960). In Africa 7 of the above subfamilies have been recorded (Duffy, 1957) with the Oxypeltinae being absent from this region. The longicorns recorded from North America comprise 6 subfamilies with the Oxypeltinae and Disteniinae being absent (Craighead, 1923), while from the British Isles (Linsen, 1959), Pacific region (Curran, 1946) and Australia (McKeown, 1942b) only 3 subfamilies are known, viz. Prioninae, Cerambycinae, and Lamiinae.

The Cerambycinae is the second largest subfamily after the Lamiinae and contains the tribe Uracanthini. The taxonomy of this tribe has been studied by Lacordaire (1869), Lea (1916, 1917), and McKeown (1938, 1940, 1942a,—). Following these workers, no further investigations have been carried out on the tribe to date. In Australia, there are 6 genera in the tribe (McKeown, 1947), viz. <u>Scolecobrotus</u> Hope, <u>Uracanthus</u> Hope, <u>Neurocanthus</u> McKeown, <u>Emenica</u> Pascoe, <u>Rhinopthalmus</u> Thomson and <u>Aethiora</u> Pascoe. The distributions of these genera are as follows: <u>Scolecobrotus</u> widely distributed in mainland Australia but not in Queensland and Tasmania; <u>Uracanthus</u> found in all states of Australia including Tasmania and New Guinea (Gressitt, 1959); <u>Neurocanthus</u> recorded only from Queensland; <u>Emenica</u> recorded only from Western Australia; <u>Aethiora</u> recorded only from South Australia; and <u>Rhinopthalmus</u> found in all states of Australia except Western Australia (Aurivillius, 1912; McKeown, 1947). Of these genera <u>Uracanthus</u> contains the largest number of species,

37 in total, with the majority being described by Lea (1916, 1917) and McKeown (1938, 1940, 1942a,—).

In 1960 Dr F.D. Morgan (Waite Agricultural Research Institute - WARI) sent specimens of the Uracanthus species, which is the subject of this study, to the British Museum (Natural History), London. Staff there were unable to identify it and they assumed it to be an undescribed species (F.D.Morgan, personal comm.). The aim of this chapter therefore is to review the taxonomy of the genus Uracanthus, verify that the species is undescribed and present a formal description of it. This work was necessary so that a solid taxonomic foundation could be provided for the investigation of the species' biology, ecology, behaviour and host-plant relationships.

3.2 MATERIALS AND METHODS

3.2.1 General

Live specimens were obtained from infested twigs that were collected from the field and reared out in the laboratory. Male genitalia was examined after abdomens were cut and soaked (4-6 hrs) in 10% KOH. Dissections were performed under distilled water in a cavity block using 2 pairs of fine forceps. After removing unwanted tissue, the genitalia were dehydrated in 10% acetic acid for 15 mins and either permanently mounted in Berlese's fluid or temporarily mounted in glycerol for examination. Samples were always mounted in ventral aspect and viewed under a stereomicroscope. Measurements of slide-mounted material were taken using a calibrated eyepiece micrometer. Larger measurements, such as the body length of whole specimens were taken with a pair of vernier calipers. Taxonomic descriptions were compiled using freshly killed beetles so that their true colour and the actual size of some morphological characteristics could be accurately recorded.

All specimens of Uracanthus which were available at the South Australian Museum (SAM), the Australian National Insect Collection (ANIC), and WARI were examined. Dried specimens that were borrowed from these institutions were examined using the same procedures as mentioned above, except that male genitalia from ANIC specimens were mounted on slides in Berlese's fluid, while those from SAM were mounted in small tubes in glycerol.

Descriptions of the larval stages were compiled from specimens examined under 80% alcohol in a cavity block, except for

sculpturing and pilosity characters which were examined by placing specimens on filter paper to remove excess fluid. Very small features such as spiracles, antennae and legs were detached, put on a slide with a few drop of water and examined under a compound microscope.

3.2.2 Terminology

Most morphological terms used in the following keys and descriptions are defined in Sharp and Muir (1912), Duffy (1953), Torre-Bueno (1962), Eady (1968), Harris (1979) and Pershing and Linit (1985). The main terms and abbreviations used in this chapter are presented below for ease of reference.

Aedeagus: the combined median lobe and tegmen of male genitalia (Fig. 3.3).

ANIC: Australian National Insect Collection, CSIRO, Canberra.

AM: Australian Museum, Sydney.

Ampullae: large fleshy oval protuberance of the abdominal segment of larvae.

Azygos: the azygotic portion of the male genital tube which comprises all the unpaired portion of the tube, from body wall to the junction of the seminal duct.

Basal piece: the basal part of tegmen of male genitalia (Fig. 3.3).

Basal struts: a pair of elongated lateral lobes on the basal parts of the median lobes of the male genitalia that project anteriorly into the abdomen (Fig. 3.3).

Bilabiate: having 2 lip-like sutures.

Binodose: with 2 knots; specifically of the disk of the prothorax, one on each postlateral side.

Bisinuate: with 2 sinuations or incisions.

BMNH : British Museum (Natural History), London.

Cervix: upper part of the neck behind the vertex of the head.

Coxite: the basal segment of stylus of the female ovipositor (Figs. 3.5 & 3.6).

Dorsal lobe: the dorsal part of the median lobe of the male genitalia (median lobe composed of 2 lobes, i.e dorsal and ventral) (Fig. 3.3).

Emarginate: notched; with an obtuse, rounded or quadrate section cut from a margin.

Epileurum: the abdominal area which separates the abdominal segments into a dorsal and ventral region.

Epistoma: an infolding between mandibular articulations.

Exuviae: the cast skin of larvae at metamorphosis.

(f): female.

Flagelliform: whip-shaped.

Glabrous: smooth, devoid of pubescence; devoid of any sculpturing.

Granulate: covered with or made up of very small grains or granules.

Inermis: unarmed; without spines or any other sharp processes.

Internal sac: the enlarged portion of the azygos of the male genitalia which is more or less everted during copulation (Fig. 3.4).

L: larval instar, e.g. L1, L2 are the first and second larval instars.

Lateral lobes: the distal portion of the tegmen of the male genitalia (parameres) (Fig. 3.3).

Lineate: longitudinally striped.

(m): male.

Median lobe: the central portion of the male aedeagus upon which the median orifice is situated (Fig. 3.3).

Median orifice: the opening or area on the median lobe of the male genitalia through which the internal sac is everted (Fig. 3.3).

Muzzle: lower part of head from lower eyes to mouthparts.

MV : Museum of Victoria, Melbourne.

NRS : Natural History Museum, Stockholm.

Peritreme: the sclerotic plate around a spiracle.

Pilose: with piles or setae (cf. setose).

Prominant: raised or produced above the surface or beyond the margin; standing out in relief (cf. protuberance).

Pseudopod: foot-like appendage of larvae.

Pubescence: short, fine, soft, erect hairs.

Punctate: set with fine, impressed points or punctures; appearing as pin-pricks.

Reticulate: superficially net-like or made up of a network of lines.

Rugose: wrinkled.

Rugulose: minutely rugose; minutely wrinkled.

Salient: projecting .

SAM : South Australian Museum, Adelaide.

Shoulder: humerus.

Sinuate: cut into sinuses; waves, specifically of edges or margins.

S : sternite.

Spinose: armed with thorny spines.

Spicule: a minute pointed spine or process.

Strigate: having narrow, transverse lines or streaks, either raised or impressed; composed of fine, short lines.

Strigose: furnished with longitudinal raised ribs or ridges (cf. costate).

Stylus: a small rod-shaped projection at the tips of lateral sides of ovipositor (Fig. 3.6).

Supplementary process: a minute supplementary joint occurring on the second joint or segment of the antennae.

T : tergite.

Tegmen: the layer of sclerites external to the median lobe of the male genitalia, or the term applied to the lateral lobes and basal piece together (Fig. 3.3).

Umbricate: with a brick-like shape.

Undulate: with broad and nearly parallel depressions running more or less into each other (cf. undose).

UMO : University Museum, Oxford.

Undose: with undulating, broad, nearly parallel depressions running more or less into each other (cf. vermiculate).

Vermiculate: with tortuous markings resembling the tracks of a worm.

WAM : Western Australian Museum, Perth.

WARI : Waite Agricultural Research Institute, Adelaide.

3.3 THE GENUS URACANTHUS

3.3.1 Key to separate *Uracanthus* from related genera (Modified from Lea, 1916)

1. Antennae composed of eleven segments (Figs. 3.1A & D)....2
- Antennae composed of twelve segments (Figs. 3.1B, C, E & F)..6
2. First segment of antennae long but apically broad (Figs. 3.1A, & D).......................................3
- First segment of antennae extremely long and thin (Fig. 3.1G)..5
3. Elytra with apices armed, or if rounded then more acute and asymmetrical (Figs. 3.60 & 3.85)....................4
- Elytra with apices broadly and evenly rounded.....*Emenica*
4. Elytra strongly strigose or costate.. ....*Neurocanthus*
- Elytra with feeble elevated lines (e.g. Fig. 3.1A)........ ....*Uracanthus*
5. Sides of prothorax straight.....................*Aethiora*
- Sides of prothorax elongate and tapering anteriorly...... ....*Rhinopthalmus*
6. Antennal segments dentate or serrate; segment 12 almost as long as 11 or longer, separated by a clearly delineated and articulated suture (Figs. 3.1E & F)....... ....*Scolecobrotus*
- Antennal segments cylindrical or flat, never dentate or serrate; segment 12 much shorter than 11, separated only by a feeble suture which does not articulate (Figs. 3.1B & C)..*Uracanthus*

The genus *Uracanthus* may be separated from all other genera of the Uracanthini as indicated in the above key. Of these genera it most closely resembles the genus *Scolecobrotus*. Comparison of these 2 genera, using the material in the WARI collection, shows that they are morphologically very similar. The only consistent difference between them appears to be the form of the antennae. In *Uracanthus* the antennae are usually 11-segmented, with segments 4-11 being cylindrical or almost so (e.g. most *Uracanthus cupressiana* sp.n., Fig. 3.1A), slightly flattened (e.g. *U. fuscus*, Fig. 3.1D), or produced on one side at apex (e.g. *U. triangularis*, Fig. 3.1C). In a few species a feeble suture is present

approximately one-third the distance from the distal end of segment 11 but it is never divided into 2 articulated parts (e.g. U. fuscocinereus, U. triangularis, Figs. 3.1B & C).

In Scolecobrotus the antennae are always 12-segmented with the 11th and 12th segments being subequal in size and always clearly divided and articulating. Furthermore, segments 4-12 are dentate, serrate or finely granulate along the outer margin (Figs. 3.1E & F), a feature absent in all known Uracanthus.

3.3.2 Diagnosis of the Genus Uracanthus

Male :

Antennae usually composed of eleven segments, segments 4-10 produced on one side at apex or cylindrical, segment 11 longer than 10, sometimes with feeble suture so antennae appears 12 segmented; clypeus triangular or semicircular; mandibles with rounded sides; maxillary palps cylindrical; pronotum with sides triangular or rounded about middle; hind basitarsus longer than tarsal segments 2 and 3; elytra widest at base, the width decreasing posteriorly or parallel sided, apices mostly armed (spinose or toothed) rarely rounded, but if rounded then more acute and asymmetrical (Fig. 3.60 & 3.85); scutellum small, rounded posteriorly, hairless or almost hairless; abdomen elongate, terminal segments with S7, T7, and T8 rounded, notched or truncated posteriorly; male genitalia curved, yellowish-brown in colour, some parts hyaline, with strongly sclerotised lateral lobes (parameres) and median lobe.

Female :

Antennae slightly shorter or same size as male; legs short, ventral surface of femur sparsely pilose; abdomen robust, terminal segment with S7 and T7 rounded or truncate, often with long, brownish-yellow or golden hairs; otherwise same as male.

3.3.3 Species of Uracanthus and their identification

Lea's and McKeown's original descriptions of Uracanthus species are adequate (Lea, 1916, 1917; McKeown, 1938, 1940, 1942a) but some additional useful characteristics are provided in this chapter for accurate separation of species. Male genitalia in particular has been found to be an important characteristic for diagnosing species. It varies between species but shows little or no variation within species. On the other hand, some characteristics, such as the apices of elytra, sculpturing, and

pilosity, vary within a few species but remain useful in diagnosing the majority of species. The original descriptions of Uracanthus species were based on very little material, e.g. 16 species were described from single specimens, 10 being male, 6 being female. In this study multiple specimens of each species were examined where possible to assess the degree of intra- and interspecific variability.

For one species, U. triangularis, Lea described 3 varieties (A, B, and C) that were separated on differences in elytral pilosity. Examination of the male genitalia of these varieties shows that they differ to the point where they could be considered as a sibling complex. However, this problem will not be resolved until more material from a wider geographic area is collected and examined. Other species, such as U. gigas, show differences in some external characteristics (i.e. body colour, body size, shape of elytral apices, elytral pilosity, pronotal sculpturing, and shape of terminal segment of abdomen), but all the material examined of this species had identical male genitalia. Thus U. gigas appears to be a valid species even though it is morphologically variable for some characters.

To determine the taxonomic status of Uracanthus species all holotypes of Australian species (except U. gigas which is lost) were borrowed, along with all non-type material held in SAM, ANIC, and WARI collections. Sixteen characteristics were scored for each species: 1) muzzle shape, 2) clypeus shape, 3) antennal shape, position and segmental number, 4) antennal fringe, 5) pronotal shape, 6) pronotal pilosity, 7) pronotal sculpturing, 8) femoral pilosity, 9) shape of elytral apices, 10) elytral pilosity, 11) elytral sculpturing, 12) male genitalia, 13) shape of terminal segments of abdomen, 14) abdominal pilosity, 15) body colour, 16) size of body (width and length). These species were compared with that under study here. The latter could not be assigned to any described species and obviously represented a new species which is descibed below. A key to Uracanthus species is given in Appendix 1 along with additional imformation that will assist with their identification.

3.4 TAXONOMIC DESCRIPTION OF URACANTHUS CUPRESSIANA SP.N.

3.4.1 Adult male

Size: length 11.0-17.1mm (mean 14.4±0.33 (SE)mm), width 2.0-3.0mm (mean 2.45±0.06 (SE)mm), (n=22).

Colour: reddish brown, dark brown or partly dark brown on head, shoulder, and scutellum; pilosity pale yellow to yellow.

Head: muzzle short, length 1/3-1/2 of width; clypeus triangular, flat or slightly convex, coarsely punctate and sparsely pilose; clypeal suture deep, wide, and triangular; median line narrow, shallow, and terminated near base; pilosity dense from vertex to occiput; eyes coarsely facetted; antennae shorter than body, composed of 11 segments, segments 3-11 thin and cylindrical, 4-10 slightly produced on one side at apex, some specimens having segment 11 divided by feeble suture (i.e. appearing 2-segmented), pilosity fine and sparse.

Thorax: pronotum longer than basal width, base wider than apex, sides angular about middle and slightly depressed posteriorly, pilosity dense along postlateral sides, uneven about the middle, sparse on both lateral sides, sculpturing strigate from base to apex across the midline but becoming curved near the midline about the middle (Fig. 3.1A) (in some specimens the sculpturing toward the apex is very irregular and there is a hairless patch from about the middle to the base); elytra wider than prothorax, width decreasing posteriorly, toothed in the middle of apices, pilosity slightly denser toward the base, sculpturing with 4 feeble elevated lines and moderately punctate towards the base (Fig. 3.1A); scutellum rounded posteriorly and almost hairless; femur stout, pilosity fine and sparse; hind tibia curved distally with 2 apical spurs; tarsal segment 1 longer than 2 and 3 for hind legs; tarsal segment 1 shorter for mid and fore legs; ventral surface of tarsi with dense pilosity, claw long and strong.

Abdomen: pilosity uniform, moderately dense; terminal segments shorter than basal width, tapering posteriorly, S7 rounded, slightly notched, and depressed in the middle with pilosity dense but short; T7 rounded (in some specimens rounded slightly but also notched to strongly notched medially); T8 rounded or rounded and slightly notched, with pilosity moderately dense (Fig. 3.2).

Male genitalia: tegmen with lateral lobes (parameres) cylindrical, apex rounded with 4 thick long setae mixed with a few short fine setae, finely punctate with basal piece thin and folded but becoming

Fig. 3.1A: Uracanthus cupressiana sp.n. whole body dorsal view.

3.1B Right antenna of U. fuscocinereus (female).

3.1C Right antenna of U. triangularis (female).

3.1D Right antenna of U. fuscus (female).

3.1E Right antenna of Scolecobrotus westwoodi (male).

3.1F Right antenna of S. westwoodi (female).

3.1G Right antenna of Rhinopthalmus sp.

Figs. 3.2 - 3.7 Uracanthus cupressiana.

3.2 Terminal segments of abdomen (S7, T7 and T8).

3.3 Male genitalia showing the aedeagus.

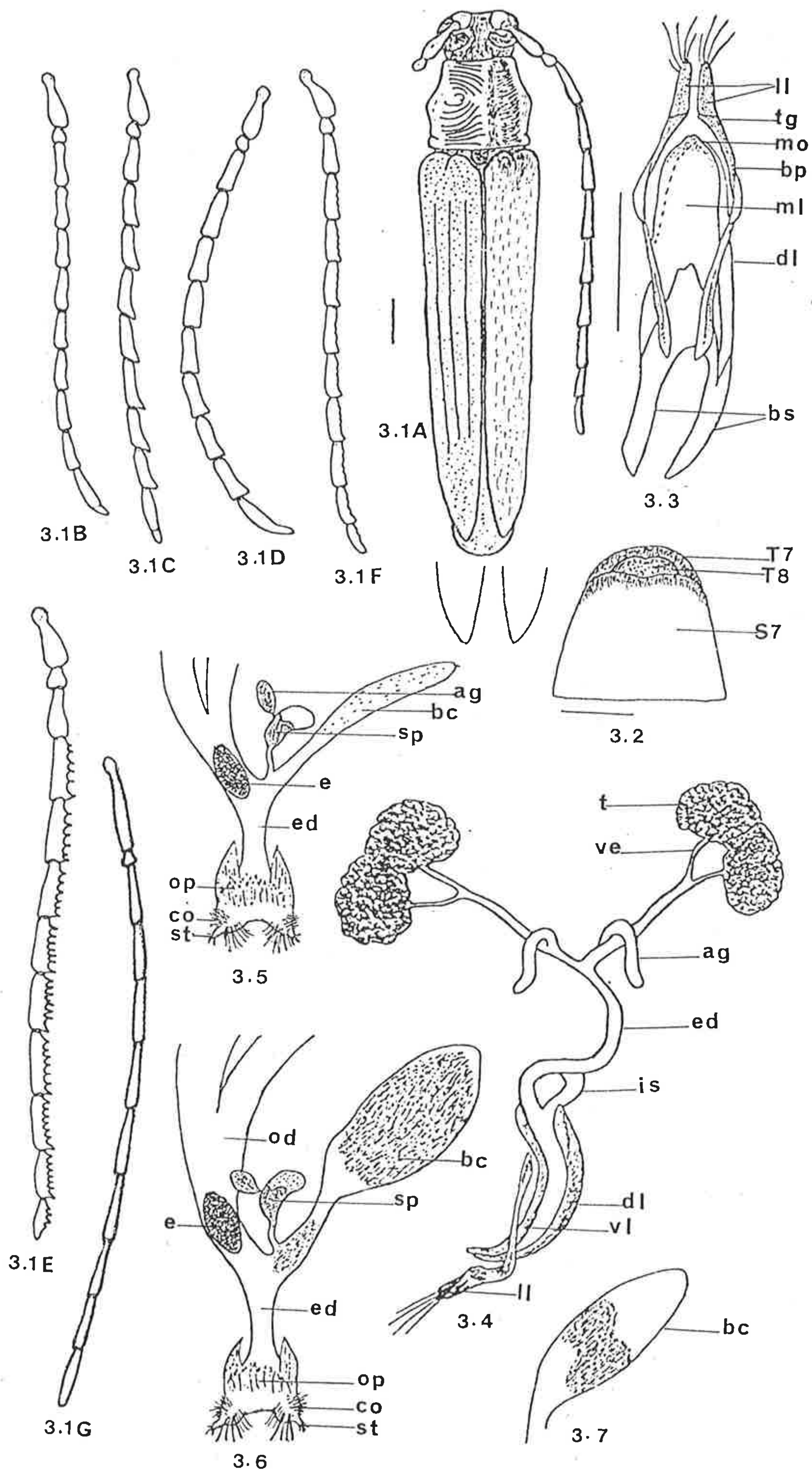
3.4 Male genitalia showing the aedeagus, ducts, glands and testes.

3.5 Female genitalia.

3.6 Mated female genitalia showing the cloudy mass in bursa copulatrix which was transfered from male.

3.7 Parous female bursa copulatrix showing the remaining cloudy mass transfered from the male.

[ag, accesory glands; bc, bursa copulatrix; bp, basal piece; bs, basal struts; co, coxites; e, egg; ed, ejaculatory duct; dl, dorsal lobe; is, internal sac; ll, lateral lobes; ml, median lobe; mo, median orifice; op, ovipositor; ov, oviduct; sp, spermatheca; st, styli; t, testes; tg, tegmen; vd, vasa deferens; ve, vas eferens; vl, ventral lobe; scale bars: 3.1A - 1.5 mm, 3.2 - 0.2 mm]



3.1A
3.1B
3.1C
3.1D
3.1F
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T7
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flat and wider at tip; median lobe parallel-sided becoming narrow at apex; lateral margin of median orifice narrowed apically, rounded, slightly notched and punctate; dorsal lobe as wide as ventral lobe, apex rounded posteriorly, basal struts short; internal sac with a knot behind aedeagus (Figs. 3.3 & 3.4).

3.4.2 Adult female

As for male except as follows:

Size: length 13.9-20.3mm (mean 16.73±0.04 (SE)mm), width 2.1-3.9mm (mean 3.29±0.10 (SE)mm), (n=20).

Thorax : pronotum wide; elytra parallel sided; legs short.

Abdomen: robust, terminal segment with long golden hairs, T8 retracted into the genital chamber; genitalia formed by 9th abdominal segment, with ovipositor very short (fully extended about 5mm from proximal edge of the 8th segment), bearing pair of styli at distal edge; styli subdivided into basal coxites and apical styli, coxites bearing 6-8 long hairs interspersed with short tactile hairs medially and dorsolaterally; styli bear 2-4 long, fine hairs interspersed with short tactile hairs (Fig. 3.5 & 3.6).

3.4.3 Immature stages

3.4.3.1 Larval instars (L1 to L3)

There are considerable differences between the young instars (L1 to L3) and succeeding mature instars. The characteristics of the first instar larvae (L1) are: antennal segment 3 tube-like in shape and hyaline; supplementary process small and hyaline (Fig. 3.10); mandibles not strongly sclerotised; pronotum not sclerotised, spiracles very small; abdominal segment 10 without caudal armature (process) and bearing a few fine, hyaline setae (Fig. 3.8). The second instar (L2) is similar to the first (L1) but differs in having 3 small caudal tubercles on segment 10 (Fig. 3.9). The caudal process becomes well defined on third instar (L3), but is still not strongly sclerotised. The entire structure becomes well defined and distinct on fourth instar (L4) larvae.

3.4.3.2 Larval instars (L4 to L7)

Size: length of mature larvae (L6 & L7) 20mm (range 14-32mm), width 2.0mm (range 1.3-2.9mm), n=32 (see Appendix 4).

Shape and colour: body elongate and subcylindrical, yellow to white in colour; pronotum with brownish and pink patches; mouth frame bright red-brown; mandibles dark red-brown.

Head: deeply retracted into prothorax, almost parallel sided but slightly converging posteriorly; epistoma indistinct, with 4 epistomal setae; frons coarsely punctate, vermiculate, weakly sclerotised, bearing about 12 setae; median suture well defined but frontal suture indistinct; hypostoma strigate, bearing 5 long setae anteriorly near gular sutures; gular sutures raised and curved; gular region raised, hairless and weakly sclerotised; gena gradually receding, with 3 contiguous or almost contiguous black ocelli and a few genal setae; ocelli almost contiguous with antennae; antennae salient, with 3 strongly sclerotised segments, segments 2 and 3 bearing stout setae and a small supplementary process beside segment 3 (Fig. 3.13); clypeus membraneous, trapezoidal, narrow, and hairless; labrum circular and fringed anteriorly with long thick setae; mandibles short and stout, with rounded cutting edges, basal part with 2 long setae on outer face, surface rugose (Fig. 3.18); maxillae large, fleshy, and protected; submentum semicircular anteriorly, with 4 long setae; mentum square with some setae on basal half; maxillary lobes thick, rather rounded apically, and sparsely setose, the inner margin hairless and hyaline; palpifer and first palpal segment with a process; cardo, stipes, and palpifer with sparse setae.

Prothorax: pronotum large, rectangular and sclerotised, basal third longitudinally rugose or striate, with 18-20 brown spots, sparsely setose but denser anteriorly (Fig. 3.14); presternum sparsely setose, coarsely punctate, slightly sclerotised; eusternum semicircular, sparsely setose, finely punctate; sternellum surrounding first pair of legs very sparsely setose (6-10 fine setae).

Meso- and metathorax: mesotergum bearing x-shaped suture; metatergum with irregular suture; both these tergites with long reddish brown setae laterally; mesosternum and metasternum bearing irregular transverse furrow.

Figs. 3.8 - 3.18: _Uracanthus cupressiana_ larvae.

3.8 L1, terminal segments of abdomen, ventrocaudal view, showing trilobate anus.

3.9 L2, terminal segments of abdomen, ventrocaudal view.

3.10 L1, 3-segmented antenna.

3.11 L7, terminal segments of abdomen, vetrocaudal view, showing the intermediate bifurcating process.

3.12 L7, terminal segments of abdomen, lateral view, showing the dorsal extension and intermediate bifurcating process.

3.13 L7, 3-segmented antenna.

3.14 L7, pronotum showing the sculpturing and pilosity.

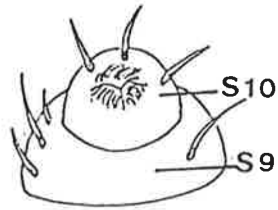
3.15 L7, dorsal ampulla showing the impression.

3.16 L7, leg showing the segments and shape of tarsal claw.

3.17 L7, spiracle showing number of marginal chambers (8) and cells (22).

3.18 L7, outer face of right mandible showing the rounded cutting edges and sculpturing.

[A1-3, antennal segments; S9 & 10, sternites 9 &10; bs, base; sp, suplementary process; scale: 3.12, 3.14, & 3.15 - 1 mm]



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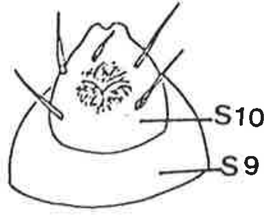

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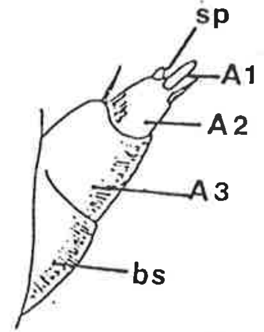

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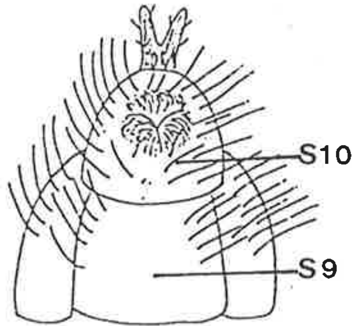

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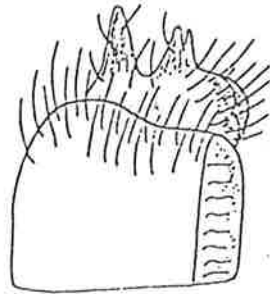
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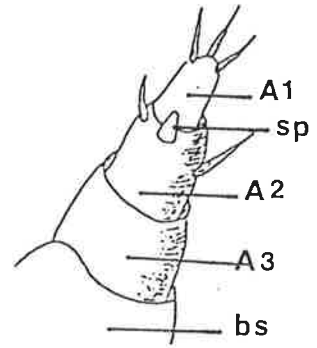

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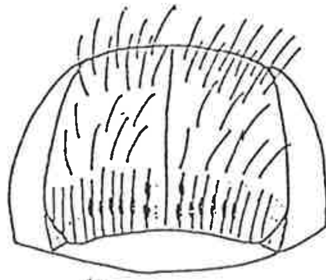
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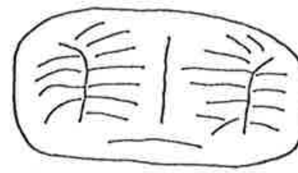
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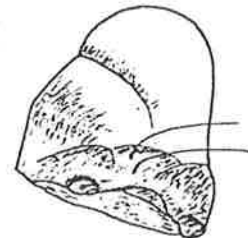
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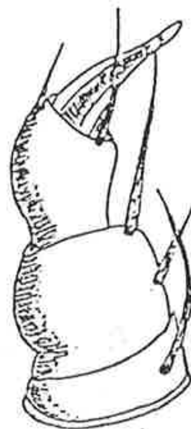
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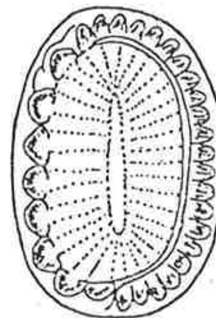

3.17

Legs: small, 4 segmented; basal segment strongly transverse, trochanter narrow with one seta; femur thick with 2 setae; tibiotarsus thinner and longer than femur with 3 to 4 setae; tarsal claw flagelliform and umbricately spinose (Fig. 3.16)

Abdomen: first 2 dorsal ampullae bearing 4-5 transverse impressions that are delimited by one pair of lateral furrows and one median longitudinal furrow (Fig. 3.15), the remaining ampullae with indistinct tranverse impression; first 4 ampullae densely setose laterally, remaining 3 very sparsely setose; first 5 ventral ampullae with just one tranverse impression, last 2 ampullae with 2-3 impressions; first 4 epipleura not protuberant, bearing roundish pleural disc, 5-7 epipleura slightly protuberant, each with a single thick, long seta and a few fine ones; segment 8 not protuberant, with small round pleural disc; segment 9 rounded posteriorly with numerous long thick reddish-brown-setae; terminal segment (10) bearing trilobate anus ventrally which is used as a pseudopod, anus surounded by long thick setae; tip of segment 10 bearing one long, strongly sclerotised, dorsal extension and an intermediate, strongly sclerotised, bifurcating process between anus and dorsal extension, each with short but thick setae (Figs. 3.11 & 3.12) (sometimes the dorsal extension has one or 2 small short additional processes).

Spiracles: bilabiate type, each lip being a complicated process; peritreme broadly oval, red-brown in colour, thickly sclerotised, with 8 almost contiguous strongly developed marginal chambers which are fan-shaped, also with 22 contiguous marginal cells which occupy entire inner margin of peritreme, chamber 8 small and closed (Fig. 3.17).

Sexual dimorphism: the sex of mature larvae could be determined by dissecting individuals longitudinally along ventral abdominal segment 5. Male larvae differ from females by having 2 prominant testicular follicles that are reddish-yellow in colour, located ventrolaterally in abdominal segment 5. They can also be distinguished by having stouter and larger mouth parts. The ovaries in the females are hard to distinguish, but can sometimes be seen as thread-like diffuse structures embedded in fat bodies.

3.4.3.4 Prepupae and pupae

Prepupae:

There is a progressive contraction of the body during the prepupal period, which is initiated soon after the fully-grown larva has stopped feeding.

The segmentation is very distinctive due to deep inter-segmental infolds, which develop as a result of the contractions. The body colour changes to dull white or yellow, the body becomes shorter (12-25mm), the thorax becomes thicker and the head turns under. Numerous fat bodies are visible through the semi-transparent body wall.

Pupal female:

Size: length 12.5-19.5mm (mean 15.83±0.69 (SE)mm), width 2.5-3.83mm (mean 3.08±0.15 (SE)mm) (N=16).

Head: strongly bent beneath the prothorax; vertex totally concealed from above, elongate, convex and rugulose; frons hairless; clypeus impressed and hairless; mandibles without setae; maxillary palps rather enlarged apically; labrum hairless and with a longitudinal median depression; eyes moderately convex; antennae extending to abdominal segment 2, then recurving ventrally and terminating almost at the base of elytra.

Thorax: pronotum with posterior margin wider than anterior margin, enlarged laterally about middle; basal and apical disk with long sclerotised setae, rugulose across middle; scutellum with apex narrowly rounded and hairless, scutellar groove shallow; mesonotum with a few short and fine setae; metanotum surface strigate; elytra extending to abdominal segment 4; legs with hind femora stout and extending to abdominal segment 4.

Abdomen: T 2-7 with paired transverse groups of short stout spicules which are inclined backwards, some shorter and slightly erect; T 1 with a few spicules only; T 8 rounded posteriorly with a few setae; T 9 retracted behind T 8, with numerous long thick setae and a small caudal protuberance; S 1-7 hairless but finely setose laterally; S 8 finely setose; posterior to S 8 there are 2 almost contiguous rounded lobes, each with a minute, brownish, circular pattern in middle.

Pupal male:

Size: length 12.0-14.5mm (mean 13.40±0.20 (SE)mm); width 2.36-2.82mm (mean 2.56±0.04 (SE)mm) (N=12).

As for female but differing in having no contiguous rounded lobes posterior to S 8, and S 9 is narrower and strongly contracted.

3.4.3.5 Egg

Eggs are ovoid with one end slightly tapering and bearing a group of spicules; the other end is strongly tapering, truncate, and has spicules that are roundly inclined. The chorion is light to dark grey and coarsely reticulate. They are 1.5mm in length and 0.6mm in width.

3.4.4 Type material

Holotype: (m), Adelaide (North Glenelg), South Autralia, host-plant Cupressus sempervirens, 5.X.86 (S. Rondonuwu), WARI.

Paratypes: 26 (m), 26 (f), Adelaide (North Glenelg and South Brighton), South Ausralia, host-plant C. sempervirens, 5.X.86 and 10.XI.86 (S. Rondonuwu), WARI; 60 eggs, 140 larvae (L1 - L7), and 12 (m & f) pupae, 10.XII.86 (WARI).

3.4.5 Discussion

Uracanthus cupressiana is distinct from all other species described so far. In general it is most similar to U. acutus but differs from this species in the following: pronotum strongly strigate from base to apex across the midline, becoming curved near midline about middle; apices of elytra toothed or slightly produced medially; elytral sculpturing moderate with 4 feeble elevated lines, elytral pilosity slightly denser towards the base. U. acutus has the pronotum almost hairless, weakly strigate at the base and apex, smooth along midline; apices of the elytra acutely unispinose or strongly drawn out to a point in middle; the surface of elytra coarsely punctate towards base and sparsely pilose. U. cupressiana also bears a superficial resemblance to U. longicornis and U. loranthi, but the apices of elytra and elytral and pronotal sculpturing and pilosity are very different for these species. U. longicornis has the pronotum strongly strigate from base to apex and uneven pilosity; elytra coarsely punctate, sutural apices acutely unispinose and outer side armed. U. loranthi has the pronotum irregularly strigate and nodulate, with 2 post lateral bands on each side; elytra coarsely punctate and sparsely pilose, and the apices bispinose.

3.5 KEY TO AUSTRALIAN SPECIES OF URACANTHUS

(see Appendix 1)

N.B. The figure numbers in Appendix 1 follow on from this chapter, i.e. 3.19 - 3.161.

Table 3.1: Species of Uracanthus and number of specimens (including holotypes) examined in this study (* holotype examined; x holotype missing; + species known from South Australia).

	Species	Holotype depository	Other material examined
1.	acutus Blackb. (*)	m, BMNH	3m, 4f - SAM, ANIC, WARI
2.	albatus Lea (*)	m, SAM	3m, 2f - WARI, SAM
3.	ater (*)	m, SAM	1m, 0f - SAM, ANIC
4.	bivitta Newm. (*,+)	f, BMNH	5m, 6f - SAM, ANIC, WARI
5.	corrugicollis Lea (*,+)	m, SAM	1m, 1f - SAM, ANIC
6.	cryptophagus Oliff (*)	f, AM	2m, 3f - SAM, ANIC
7.	discicollis Lea (*,+)	m, SAM	4m, 6f - SAM, ANIC, WARI
8.	dubius Lea (*,+)	m, SAM	1m, 2f - SAM, ANIC
9.	froggatti Blackb. (*)	m, BMNH	2m, 1f - SAM, ANIC
10.	fuscus Lea (*,+)	m, SAM	2m, 1f - SAm, ANIC
11.	lateroalbus (*)	m, SAM	1m, 1f - SAM, ANIC
12.	leai Lea (*)	m, SAM	1m, 1f - SAM
13.	insignis Lea (*)	f, SAM	0m, 2f - SAM, ANIC
14.	glabrilineatus (*)	m, SAM	1m, 0f - SAM
15.	gigas Lea (x)	x, BMNH	6m, 2f - SAM, ANIC
	gigas var A Lea (*)	x, SAM	5m, 5f - SAM, ANIC
16.	longicornis Lea (*)	m, SAM	2m, 1f - SAM
17.	loranthi Lea (*)	m, MV	1m, 5f - SAM, ANIC
18.	maleficus Lea (*)	m, SAM	2m, 2f - SAM, ANIC
19.	parvus Lea (*)	m, SAM	1m, 0f - ANIC
20.	pallens Hope (*)	m, UMO	0m, 2f - SAM, ANIC
21.	pertenuis Lea (*,+)	m, SAM	4m, 3f - SAM, ANIC
22.	marginellus Hope (*,+)	m, UMO	6m, 5f - SAM, ANIC
23.	simulans Pascoe (*,+)	m, BMNH	5m, 3f - SAM, ANIC
24.	strigosus Pascoe (*.+)	m, BMNH	2m, 3f - SAM, ANIC
25.	triangularis Hope (*,+)	f, UMO	13m, 5f - SAM, ANIC, WARI
	variety A Lea (*)	m, SAM	1m, 3f - SAM, ANIC
	variety B Lea (*,+)	m, SAM	1m, 3f - SAM, ANIC
	variety C Lea (*,+)	m, SAM	1m, 0f - SAM, ANIC
26.	suturalis Lea (*,+)	m, SAM	2m, 0f - SAM, ANIC
27.	ventralis Lea (*)	m, SAM	2m, 0f - SAM, ANIC
28.	tropicus Lea (*)	f, SAM	2m, 0f - SAM, ANIC
29.	fuscocinereus White (*)	f, BMNH	0m, 3f - WARI, ANIC
30.	regalis McKeown (*)	m, AM	2m, 1f - ANIC
31.	multilineatus McKeown (*)	m, WAM	2m, 1f - ANIC
32.	fuscostriatus McKeown (*)	m, WAM	1m, 0f - ANIC
33.	dentiapicalis McKeown (*)	m, WAM	-
34.	paralellus Lea (*)	m, MV	1m, 0f - ANIC
35.	minatus Pascoe (*)	f, BMNH	-
36.	inermis Aurivillius (*)	f, NRS	-
37.	cupressiana sp.n. (*.+)	m, WARI	numerous - WARI

Plate 4: Four stages in the life cycle of *U. cupressiana*: egg, larvae (7 larval instar & prepupae), pupae (male & female), and adults (male & female). Note: larval colour has already changed after death by keeping them at the low temperature before taking picture. For the actual colour see text.

CHAPTER IV

CHAPTER 4

BIOLOGY

4.1 INTRODUCTION

The long-horned beetles comprise numerous species that are highly injurious to both growing trees (Bilsing, 1916; Frogatt, 1923; Anderson, 1960; Graham, 1963; Hay, 1972; Solomon, 1972, 1974, and 1977; Linsley, 1959; Kalshoven, 1981; Rondonuwu et al., 1979) and to timber (Hayes and Tickell,—; Duffy, 1953, 1957, 1960; and Powell, 1982). Some excellent papers have been published dealing either with some important species, distribution and their host range (Rice, 1981, 1985; Rice et al., 1985; Gosling, 1984a & b; Water & Hyche, 1984; Donley & Rast, 1984; Rogers, 1977) or their damage and control (Kennedy et al., 1981; Anderson, 1960; Graham, 1963; Wollerman et al, 1955). Nevertheless, there are some rather important features of the biological aspects of these beetles that seem to have attracted only scant attention, and which have hitherto not been subjected to a systematic analysis. The reason for this might be due to the difficulty of working on an insect with a long life cycle.

In this section, imformation on uncertain or neglected aspects of the biology of U. cupressiana in particular will be described and discussed .

4.2 LIFE HISTORY

4.2.1 Introduction

Experiments have been carried out under laboratory conditions either in fluctuating or in constant temperature to determine the life history of the species. Culture was done mainly at 20°C constant temperature with relative humidity 70-76% (in containers with saturated salt solution). Data from the field were used for comparison with that from the laboratory results.

4.2.2 The egg

4.2.2.1 Egg development

The newlaid egg is uniformly light to dark grey. About a week before the emergence of the larva, the egg swells slightly and its colour becomes dull. These changes in the external appearance indicate

the development of the embryo. On completion of embryogenesis, the larva seems to make characteristic attempts to liberate itself.

4.2.2.2 Egg eclosion

Two or 3 days before eclosion, the young larva begins to eat or gnaw the inner side of chorion. The latter becomes transparent, and the larva can be easily seen under low magnification. Its reddish brown head and prothoracic shield are in the anterior part of the egg, and the yellowish body with the tip of the abdomen is in the posterior part. The young larva then begins to gnaw a hole through the chorion and its minute reddish brown mandibles can be seen at work under low magnification. It takes about 3 to 24 hours to cut a hole large enough for it to crawl through. It then forces its head through the opening and slowly wriggles out by making characteristic peristaltic movements of the body. From 5 to 10 minutes are required for the larva to release itself from the egg but it depends on the fitness of the larva. Sometimes it takes longer or fails to release itself at all. The young larva cuts a hole in the chorion where it is attached to the bark and tunnels directly into the twig. It also makes another hole on the opposite side of the egg for discarding the frass. After 24 hours the chorion has filled with frass, and we can observe that after a short while the young larva pushes out the frass through the hole with its mouth parts.

4.2.2.3 Infertile eggs

Normally, the proportion of infertile eggs is small (1-3%). In some cases, however, the proportion rises to 15%, or even more, depending on the size or the age of male or on the success of mating (see Chapter 5). All such eggs shrink after one day.

4.2.2.4 Development and survival of eggs

The length of the egg stage varies considerably depending on the environment, particularly physical factors such as temperature and relative humidity. Hence the emphasis in the study of egg development is on the effect of both these factors. For the experimental work described in this section, all eggs used were less than 24 hours old. In each experiment, all eggs were kept until no further hatching occurred.

Experiment 1. Development and survival of eggs in different constant temperatures

At each of the selected temperatures (15, 20, 25, and 30°C), 100 eggs were detached from twigs, placed on filter paper and kept in a petri dish. The hatching time and the number of eggs hatched were recorded. Counts of eggs hatched were done at a twelve-hour interval. The eggs used were laid by beetles that had emerged from the twigs which had been collected from the field. The threshold temperature for egg development was estimated using the x-intercept method, and the degree-day or heat unit (HU=K) summation was calculated using the formula K=Y (t -a), for the development of each life stage above the threshold temperature; where Y=time for development, t=temperature, and a=threshold temperature (Walgenbach and Wyman, 1984). The index of development (ID) was calculated from the mean incubation period (Y) as ID=100°Y (Lamb et al., 1984; Rawat, 1957).

The effect of temperature on the length of the egg stage is shown in Table 4.1 and Fig. 4.1. It is as short as 17 days at 30±1°C, extends to over a month at 20±1°C, and to over 2 months at 15°C. Between 20°C and 30°C the hatching of the group of 100 eggs was completed within a week. At 15°C it was very irregular, and occupied a much longer period (see Fig. 4.2). However, there were no significant differences in the percentages of eggs hatched over a temperature range of 15 to 30°C ($P>0.2$). The effect of temperature on the rate of development was highly significant ($P<0.01$). Between 20 and 30°C the rate of development was directly proportional to the increase in temperature. Low temperatures are therefore unfavourable to development of eggs. A linear response was obtained when the rate of development (percentage development per day) was regressed against temperature (Fig. 4.1), therefore the dotted extensions of the regression lines represent linear extrapolations to obtain estimates of the threshold temperature, which was 9.47°C for egg development, and HU=341 day-degrees above 9.47°C (see Table 4.1).

Experiment 2. Development and survival of eggs in different relative humidities

At each of the selected relative humidities, 100 eggs were used. The eggs were detached from twigs and placed on filter paper in an open petridish and then they were placed in airtight plastic containers (25x19x9cm) containing the required saturated salt solution. The 2 sets

Table 4.1: Effect of temperature on the rate of development and survival of eggs

T (°C)	MIP	ID	TEH (%)	HU
15±1	63.3	1.68	81	350.0
20±1	33	3.03	100	347.5
25±1	20.5	4.88	97	318.4
30±1	17	5.88	90	349.0
Average				341.0

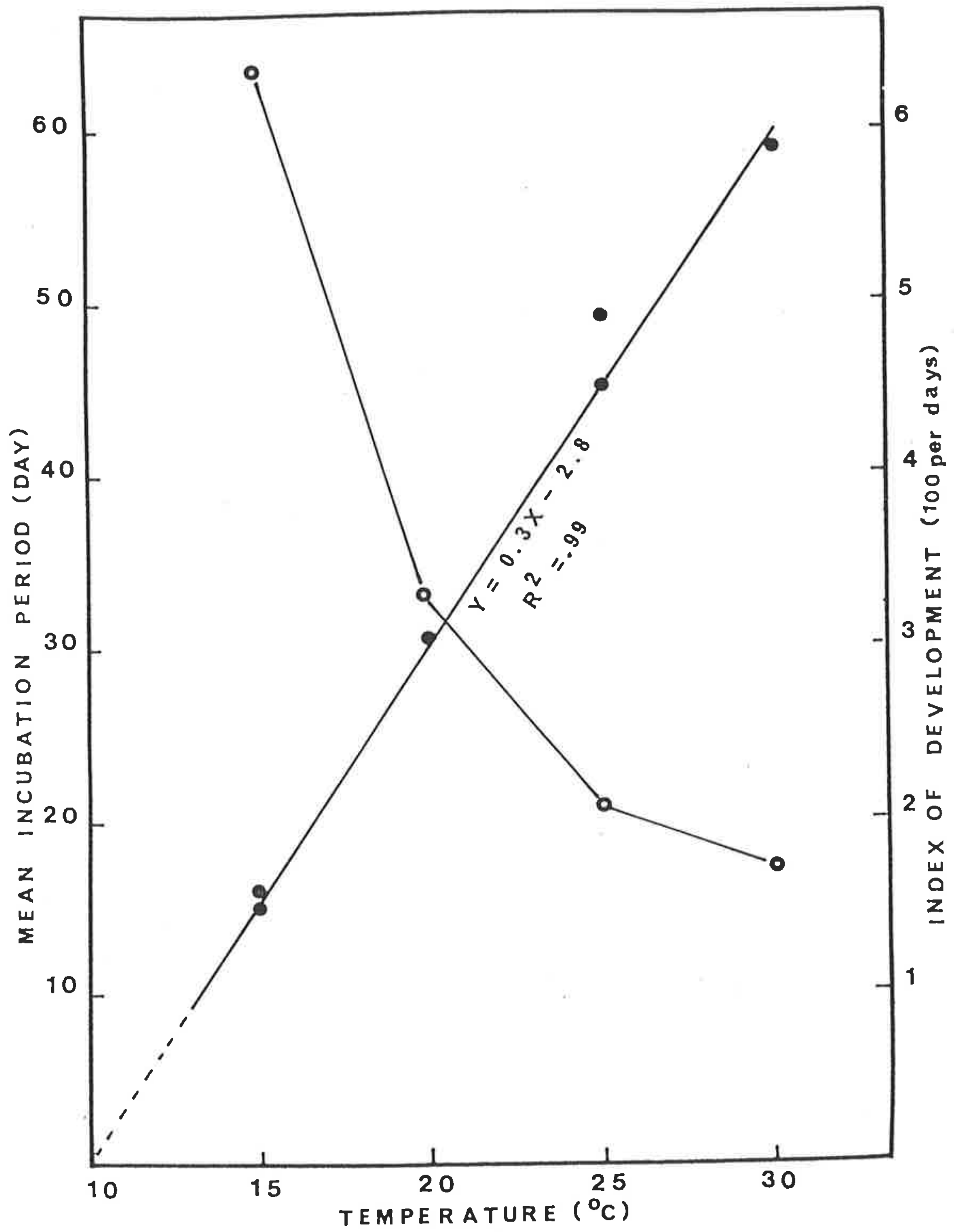
T : temperature
MIP : mean incubation period (days)
ID : index of development
TEH : total eggs hatched (%)
HU : heat unit = K.

Table 4.2: Effect of relative humidity on the rate of development and survival of eggs

T(±C)	RH	MIP	ID	TEH
25+1	31	20.5	4.88	74
	43.5	18	5.55	94
	60.5	19	5.26	94
	74	19	5.26	100
	80	19.5	5.13	100
	>90	-	-	-
15+1	32	61.8	1.61	39
	46	59.6	1.68	76
	62	55.8	1.79	68
	76	58.4	1.71	90
	82	56.5	1.77	90
	>90	-	-	-

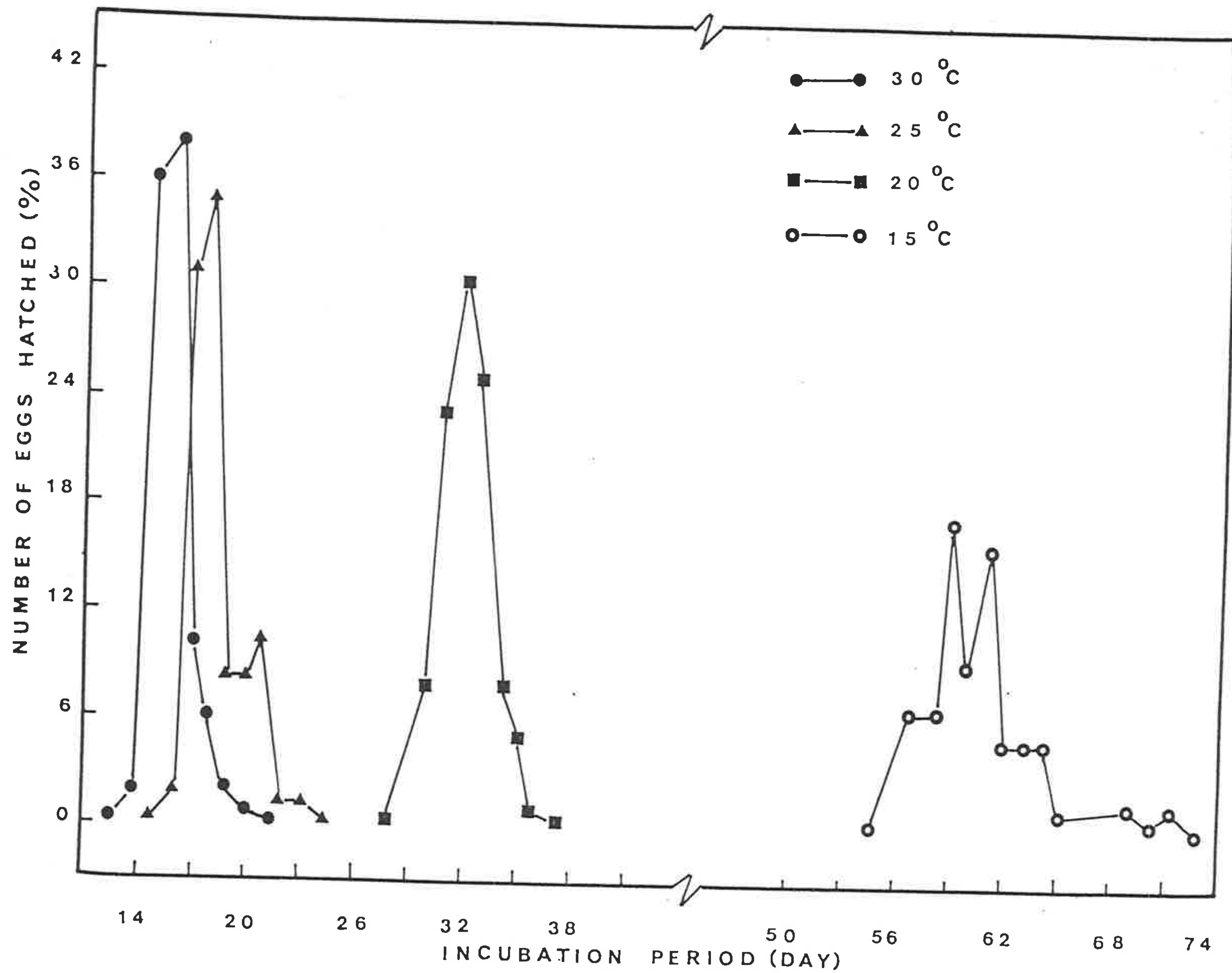
RH : relative humidity
MIP: mean incubation period
ID: index of development
TEH: total number of eggs hatched.

Fig. 4.1: Mean incubation period and indices of development of eggs at different temperatures.



MEAN INCUBATION PERIOD (DAY)
60
50
40
30
20
10
INDEX OF DEVELOPMENT (100 per days)
6
5
4
3
2
1
Y = 0.3X − 2.8
R2 =.99
10
15
20
25
30
TEMPERATURE (°C)

Fig. 4.2: Distribution of egg hatching at different constant temperatures.



NUMBER OF EGGS HATCHED (%)
42
36
30
24
18
12
6
0
30 °C
25 °C
20 °C
15 °C
14
20
26
32
38
50
56
62
68
74
INCUBATION PERIOD (DAY)

of containers were kept at 25°C and 15°C respectively with 14°10 L°D. Hatchings were recorded at 12-hourly intervals. The eggs were treated as in experiment 1. The following saturated salt solutions were used: Li (31%), Mgcl (43.5%), Nacl (76%), Kcl (80%), and H20 (>90%). The latter group was not included in the analysis because all eggs died, having been covered by fungus before hatching.

The effect of relative humidities on the length of egg stage and the rate of development was not significant ($P>0.5$) but it was significant on the viability of eggs over 15 and 25°C ($P<0.05$) as shown on Table 4.2 and Fig. 4.3. Moisture is required for the proper development of the eggs of many insects. A high percentage eclosion occured within the range 74-82% relative humidity at 15°C, and 43-80% RH at 25°C (see Table 4.2). Thus eggs could develop over a wider range in the high temperature than in the low temperature. Perhaps in the low temperature the length of the egg stage is prolonged and a low air moisture may result in a fatal loss of water from the embryo (Khoo, 1979). Low relative humidities are, therefore, unfavourable to the survival of eggs (see Fig. 4.3).

Examination of the eggs on the potted plants that were placed in the field cages after larval eclosion showed that fertile eggs always hatched. Obviously the moisture requirement for eclosion is met in nature. In late spring and summer when the eggs are usually found, the temperature is high (ca. 20°C) and the humidity is moderate (50-60%). Thus these conditions are favorable for egg development.

Experiment 3. Development and survival of eggs in different photoperiods

Two photoperiods were selected, namely 14°10 and 0°24 L°D. For the latter a thick black cloth was used to cover the eggs that were placed on the petridish. The eggs were then kept at 20°C CT. Hatchings were recorded at 12-hourly intervals. The eggs were treated the same as in the previous experiment.

The effect of photoperiod on the rate of development and on the survival of the eggs was not significant, as shown in Table 4.3.

Table 4.3: Effect of photoperiod on the rate of development and survival of eggs

L/D	MIP	ID	TEH	Distribution	
				Days	EH(%)
0/24	28.3	3.53	100	26	9
				27	34
				28	44
				29	7
				30	5
				31	1
14/10	27.8	3.59	100	25	3
				26	17
				27	33
				28	30
				29	10
				30	6
				31	1

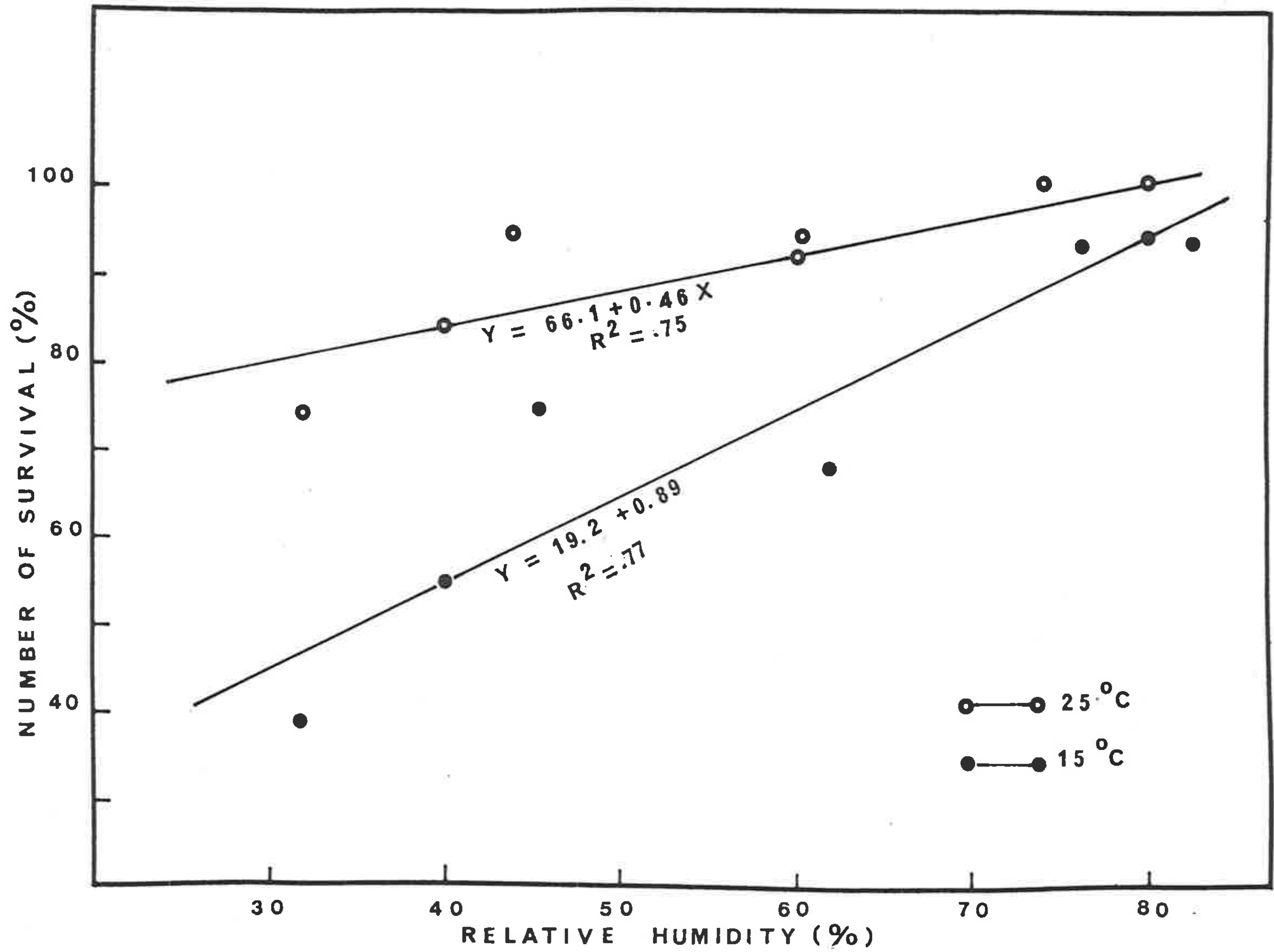
L/D : light/ dark

Table 4.4: Effect of alternating temperatures on the rate of development and survival of eggs

Treatment	MIP	ID	MR	TEH (%)	N
15 to 25±C	42 ± 0.82	2.4	2.37	92	200
25 to 15±C	42.5 ± 1.04	2.4		94	300
15±C	61 ± 1.15	1.68	3.62	86	200
25±C	18 ± 0.71	5.55		94	200

MIP : Mean Incubation Period ± SE(days)
ID : Index of Development
TEH : Total Eggs Hatched (%)
N : Number of eggs
MR : Mean Rate of Development

Fig. 4.3: Viability of eggs in different relative humidities at 15 and 25°C CTR.


100
80
60
40
NUMBER OF SURVIVAL (%)
30
40
50
60
70
80
RELATIVE HUMIDITY (%)
Y = 66.1 + 0.46 X
R2 = .75
Y = 19.2 + 0.89
R2 = .77
25 °C
15 °C

Experiment 4. Development and survival of eggs in alternating temperatures

The experiment was carried out at both 15 and 25°C CT. 200 eggs were detached from twigs and placed on filter paper within a petridish. They were kept at 15°C for 30 days by which time the eggs had already undergone about half their development. Then they were transferred and retained at 25°C until they hatched. Another group of 300 eggs were kept at 25°C for 9 days (half development) then transferred and retained at 15°C hatching. Two other groups of 100 eggs each were kept throughout at 15°C and 25°C as control. Hatchings were recorded at 12-hourly intervals. The eggs were treated the same as in the previous experiment.

As shown in Table 4.4, there was no difference in hatching time and survival of eggs, though hatching time was distributed over a larger time at the low temperature at which the eggs completed their development. Eggs which had already undergone about half their development were more resistant than those whose development was only beginning. However, the rate of development of eggs for a given group at alternating temperatures did not always correspond to the rate for the mean of the 2 temperatures (15 and 25°C) (see Table 4.4).

It has been suggested by a number of authors, i.e. Huffaker (1944), Matheson & Decker (1965), that the variation of the temperature may stimulate or inhibit the rate of development. On the other hand, Cloudsley-Thompson (Guppy, 1969) and Howe (1967) conclude that there is little real evidence to show that such influences occur. It may suggest that perhaps differences between the alternating regimes and their respective means are not due to fluctuating temperatures but to differences in number of day-degrees above minimum temperature for development. This supports Guppy's (1969) statement on the immature stage of armyworm.

Experiment 5. Development and survival of eggs under fluctuating temperatures

The experiment was carried out in the laboratory with fluctuated temperatures (temperature range 16-27°C, RH range 35-68% mean 49.5%). 200 eggs were detached from twigs, placed on filter paper, and kept in a large petridish (14cm diameter). Hatchings were recorded at 12-hourly intervals. The eggs were treated the same as in the previous experiment. Temperatures and relative humidities were recorded.

Under fluctuating temperatures the incubation period recorded for eggs ranged from 27-34 days, and the mean was 30.5±0.87 days (Table 4.5). The eggs' viability was 96%. From the data the estimated heat unit (day-degrees) was calculated using the threshold temperature from the CT (t=9.47°C) and the mean temperature in the fluctuating conditions during the time at which the eggs were developing. Similarly, the threshold temperature was estimated from the fluctuating condition data assuming that the HU was 341D° as determined in the CT. The results show that the mean of the estimated HU values was 367D° and the mean of the estimated t-values was 10.3°C, which may be considered to be reasonably closed to the values of HU and t obtained in the CT, i.e. 341D° and 9.47°C respectively. These values can be useful to estimate the HU and t values in the field.

General Conclusion

Under suitable moisture conditions, the viability of eggs is unaffected by temperatures between 20 and 30°C. Above or below this range, however, it is progressively reduced. The eggs are susceptible to desiccation if the length of egg stage becomes prolonged. Under favourable conditions, 94 to 100 percent of fertile eggs complete their development and hatch. The proportion of infertile eggs is small.

4.2.3 The larva

4.2.3.1 Larval behaviour

At hatching, the larva makes a small hole in the chorion where it is attached to the twigs. It also makes another hole at the other side of the egg for discarding the frass. It then tunnels into the bark through the hole on the twig side, and bores through the cambium to the sapwood . In the sapwood the young larva tunnels spirally twice or 3 times round the twig. Then it tunnels straight up the distal end of the twig parallel to the axis of the twig until the size or diameter of that twig still fits the size of the larval head. It is commonly found in the field that the larva tunnels about 10 to 20cm from the oviposition site, sometimes even more if the twig is long enough, before it backs down. The tunneled twig starts to wilt and dry one to 2 weeks after egg hatching. Before reaching that point, the larva has moulted to the second instar. From the end of the twig it returns in the opposite direction (downwards) while enlarging the mine to the heartwood but not penetrating the bark.

It tunnels through the entrance hole to the proximal (bottom) part of the twig, and then proceeds to tunnel this part as far as the branch or even the trunk of a young tree. Before reaching the branch the larva has already moulted to the third or forth instar (L3 or L4) (for young potted trees), or to L5 or L6 (in mature trees). In the field there are usually L4 found in the small fresh cut twigs.

The older larva tunnels down the branch about 2-5cm and then eats around the branch just beneath the bark, a natural process of ring barking, which causes the branch to wilt and dry. The branch is easily broken off at this point. Sometimes the larva leaves behind at the one spot a small part of the sap wood and cambium if the branch is quite large. In a large branch it produces a flat cutting area when it tunnels to about the centre of the branch (heart wood) then eats and tunnels around the centre towards the bark 2 or 3 times. Before reaching the bark it tunnels back to the centre, then follows the previous tunnel to the distal part of the branch. In a small twig the larva tunnels spirally from the centre of the twig towards the bark while widening distally the distance from the bark. It produces a rather V-shaped cutting area. The larva then continuously tunnels and develops in the upper dry branch until it becomes a pupa and then an adult. The action of the larvae sometimes causes a considerable resin flow from the cutting area.

Based on the field observations, most of the dry girdled twigs or branches remain attached to the trees for more than 10 years although some dry twigs or branches fall off in strong wind or break off under their own weight.

Girdling behaviour of larvae U. cupressiana mainly to stop the oleoresin flow that may flood their mines and may kill the larvae (see Chapter 7).

According to Stride & Warwick (1960), biologically the cerambycids may be divided into 2 groups with regard to their methods of attacking living trees, i.e. (1) the adults deposit in living timber and the larvae feed thereon; and (2) the larvae feed on dead or dying timber, which is provided for them by the adults. U. cupressiana forms a third group in which the adult provides living wood and the larva then kills the twig. So the larva eats living, dying, and dead wood at different times.

After a few months or sometimes a year the branch or twig which has been girdled becomes dry. It can be seen easily on the tree as a whitish to brownish spot, depending on how long the branch has been cut

Table 4.4A: Number of adult emergence holes and twig size (diameter)

Twig diameter (mean ± SE)	Number of hole	Number of twigs examined	P*
9.30 ± 0.41	1	47	0.001
5.98 ± 0.21	2	40	

*T test.

Table 4.5: Effect of fluctuating temperatures on development and survival of eggs

Temp. (°C)	Incubation period (days)	Egg viability (%)	t (°C)	HU
Mean: 21.5	30.5 $\pm$ o.87	96	10.3	367
Range:16–27	27–34			
N: 200				

t : Threshold temperature
HU : Heat unit (day degree)

by the larva. The longer the branch has been cut the browner the colour until all the needles drop off and the colour changes to grey with just dry bark or wood. From the colour and the composition of the branches, the number of generations attacking the tree can be determined. Generally in a dry branch or twig just one larva or pupa can be found. By counting the number of the dry branches and twigs the number of the population can be roughly determined. These matters will be comprehensively discussed in Chapter 6.

Periodically, the larva constructs an oval cavity from the longitudinal tunnel, and this ends in a small opening on the surface of the twig or branch. This opening is used for frass ejection and possibly also for aeration. Sometimes blind tunnels filled with excreta are found.

When the time approaches for prepupation (2 to 6 months before pupation) the larva cuts an oval hole on one or both sides of the tunnel where the adult emerges. The number of holes through which the beetle emerges is one or 2, depending on the size or diameter of the twig or branch. In large twigs or branches (ranges 5.38–17.5mm) the larva makes just one hole, while in small twigs (3.0–9.38mm) it makes 2 holes (see App. 5). For constructing the pupal chamber, it plugs the tunnel just before the emergence hole and about 6cm from that to another end with shreds of wood torn from the wall of the tunnel and mixed with excrement. Sometimes the larva moves down or upwards in the tunnel and makes another chamber and another emergence hole. This can happen both in the field and in the laboratory. Generally, in the field, the larva pupates within the tunnel at the proximal end of the dry branch or twig just 2 to 3cm from the ring bark where the dead twig is attached to the fresh, moist part of the branch.

Under certain circumstances, after feeding stops, the larva tunnels from the dry part down into the fresh part of the branch, then proceeds to enclose itself in a chamber where it pupates. This behaviour can seriously damage young trees, because the chamber may be constructed down in the stem and may kill the tree. In such a case the larva rarely makes an emergence hole. The adult emerges through the distal end of the twig where the dry part of the twig has fallen off. The dry part of the twig easily falls off because when the larva passes through the ring bark it enlarges the tunnel. In section 7.3 the vigour of the tree as a factor influencing the selection of pupation site is examined.

The active feeding larva placed in a small plastic vial can gnaw a hole in the vial and escape. The mature larva sometimes secretes a yellowish viscous fluid from between its mandibles and often does so when it is being extracted from its tunnel. This larval behaviour possibly as a defence to discourage intruders.

4.2.3.2 Process of larval moulting

The details of moulting in all larval instars are essentially the same. Two to 3 days before ecdysis the larva stops feeding and becomes inactive. The body colour changes slightly, becoming dull. Just before ecdysis, the prothorax of the larvae is conspicuously swollen posteriorly and the cervical region is considerately distended. These changes are brought about by the retraction of the relatively wider head of the next instar into the cervix of the moulting larva. The pale yellowish or creamish head of the next larval instar, with its reddish brown mandibles and ocelli, is clearly visible through the cervical membrane. Pressure applied by the new instar to the weaker membranous cervix causes it to rupture. The head capsule is thus shed separately and earlier than the remaining exuviae. More or less simultaneously with the shedding of the head capsule, the old cuticle splits along the mid-dorsal region as far as the second abdominal segment. The larva then begins to wriggle out, gradually forcing the old cuticle back by a series of convulsive contractions and expansions of the body. Within a half to 2 hours, moulting is complete, and the exuviae are completely shed. Sometimes moulting is not completed for several days and the larva dies. This often happens under laboratory conditions, where the food-wood becomes very dry, resulting in the inability of the larva to free itself from the old cuticle. The body surface of the newly moulted larva is pale and wet with moulting fluid, drying after about half an hour. The body colour begins to deepen after a few hours and is completely sclerotised after 2 to 3 days or longer, depending on temperature and other factors.

The newly-moulted larva does not recommence feeding until some time after ecdycis, perhaps when the internal changes connected with moulting have been completed.

4.2.3.3 Larval instar and growth ratio

The larval instar of insects is commonly determined by counting the number of their moults but wood borers' moults are difficult

to determine. Many workers have successfully used the head-capsule to determine larval instars, such as Taylor (1931) on larvae of the grapevine sawfly, Bedard (1933) on Douglas fir beetle, Gaines & Campbell (1935) on corn ear worm, Maltais (1980) on larch sawfly, Loerch and Cameron (1983) on bronze birch borer, and Nemjo and Slaff (1984) on mosquitoes.

The number of instars can be estimated by direct observation or by developing a frequency distribution of measurements of the widths of the larval head capsules (Mizell III & Nebeker, 1979; Prebble, 1933 in Walters & McMullen 1956; Bedard, 1933; Raske, 1976; Walters & Mc Mullen, 1956, and Stevenson, 1967).

In this study the number of larval instars of U. cupressiana was determined by measuring the width of the dorsal aspect of the head capsule while pushing back the prothorax with fine forcep since the head capsule is partly retracted into the prothorax. It was measured to the nearest division with an ocular micrometer.

1392 larvae were examined. They were from laboratory culture (20°C) and from field collection. Among those from laboratory culture, 10 larvae were extracted every 2 weeks and the head-capsules were measured. Of those collected from the field, some were taken from potted plants that were placed at field cages and others from the field once a month. Before the examination was carried out, the larvae were killed by putting them in 70% alcohol. For the first instar, larvae were provided from eggs laid by beetles in laboratory conditions which were detached from twigs and kept in the petridish until they hatched.

The measurements (Table 4.6 and Fig. 4.4) ranged from 8 to 64 micrometer divisions or, expressed in milimeters, from 0.36mm to 0.45mm (0.045mm per division). The frequency of larval measurements for each division was recorded.

It will be noted that, for some instars, there is seemingly some overlaps between sizes of the head-capsules of those taken from the laboratory culture and those collected from the field. The measurements of head-capsule for the laboratory culture larvae was slightly lower. However, when a doubtful case occurs in determining to which instar a head capsule belongs for a given measurement, it can be indicated with the aid of observing the other morphological characteristics, i.e. the presence of caudal processes, the colour of the head, which is pale immediately following ecdysis which occurs coincidentally with the time after hatching or with the age of the larvae, the sclerotisation of setae and the caudal

Table 4.6: The distribution of width of larval head capsule

Div.	I	II	III	IV	V	VI	VII
	Instar						
8	17						
9	83						
10	26						
11		18					
12		47					
13		4	3				
14			15				
15			17				
16			36				
17			26				
18				5			
19				22			
20				26			
21				30			
22				35			
23				14	2		
24					25		
25					33		
26					49		
27					44		
28					33		
29					17		
30					3	15	
31						30	
32						60	
33						50	
34						66	
35						40	
36						52	
37						46	
38						37	
39						25	
40						4	25
41							28
42							51
43							44
44							37
45							25
46							27
47							18
48							14
49							10
50							10

continued.

continued.

Div.	I	II	III	IV	V	VI	VII
51							7
52							10
53							8
54							8
56							8
60							2
64							2

Div: divisions (measurement in micrometer units which equals 0.0454 mm).
Instar VII just for larvae collected from field.

process. Hence, based on those characteristics and the width of head-capsule, the range of each instar measurement can be defined.

The width of the head capsule was analysed to calculate the mean, the standard error of the mean, and the coeficient of variation. All calculations were made in the micrometer units for convenience, but conversions in millimeters were made in these final figures. The data in Table 4.7 are given in millimeters only.

Brooks'(Dyar's) rule (Loerch & Cameron, 1983) states that growth of the sclerotized structures proceeds in a regular geometric progression between successive instars. Brooks' rule was applied by plotting the mean head capsule width, for each instar against the instar number. Linear regression was used to determine closeness of fit. Brooks' ratio was calculated as the mean measurement for an instar divided by the mean measurement for the preceeding instar. Note that Loerch & Cameron (1983) defined the Brooks' ratio as........"the logarithm of mean measurement for an instar divided by the logarithm of the mean measurement for the preceeding instar. However, in their Table 1 (Measurements of 7 variables on larvae of *Agrilus anxius*, and statistics for determining the larval instars) the Brooks' ratios are dealing calculation from mean/mean rather than log/log.

The calculated mean was obtained by multiplying the mean of each instar by the average growth ratio (Brooks' ratio). Crossby's growth rule (Loerch and Cameron, 1983), which states that a 10% or greater difference between Brooks' ratios indicates incorrect grouping, was applied as an additional check for overlooked instar.

The mean of the head capsule widths was compared for laboratory culture larvae among those at 15, 20, and 25°C CT, to determine the effects of temperature upon the head capsule size.

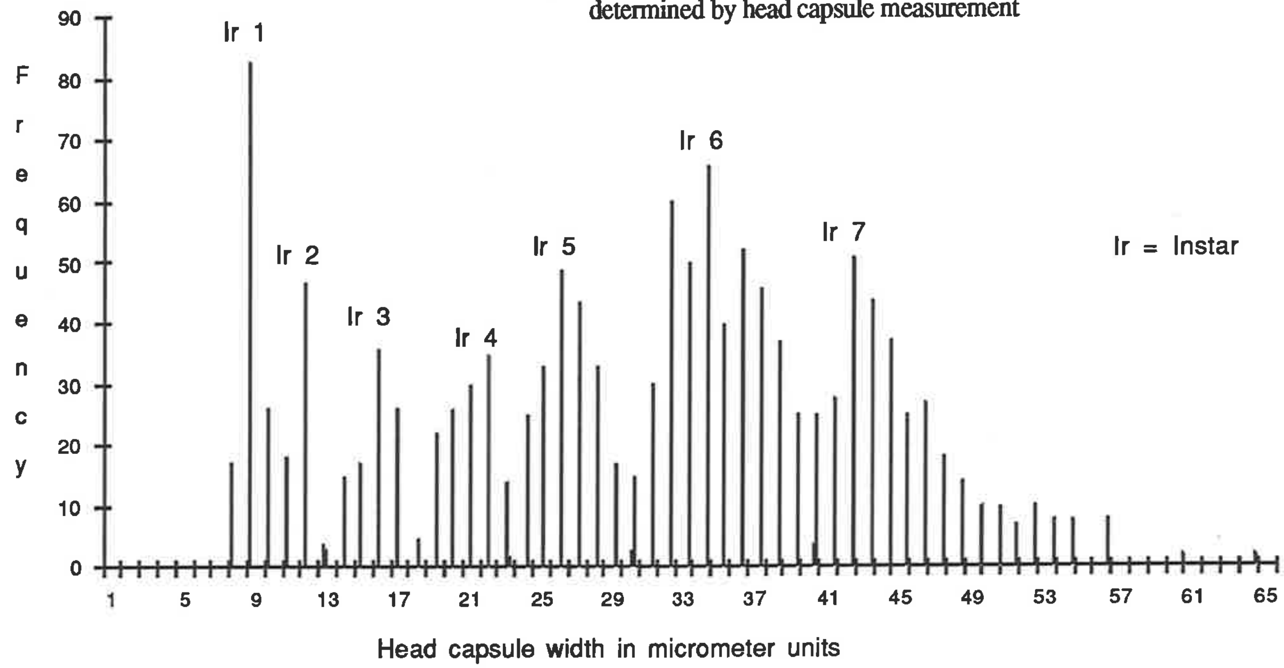
Frequency diagrams of head-capsule width of larvae from laboratory culture and from field are presented in Fig. 4.4 and Table 4.6. From the distribution patterns and from the analysis of head-capsule widths, it might be suggested that *U. cupressiana* may take 7 instars to complete their development. However, the data show that all larvae in laboratory culture take 6 instars, while those from field may take 6 or 7. This might be due to the twigs being excessively dried under laboratory conditions, resulting in the slow or even retarded development of larvae which stop eating (see Section 4.2.3.4). It has been argued that the number of moults can be affected by food, humidity and, in some cases,

Table 4.7: An analysis of the head measurements of larvae (in mm)

Instar	Statistics	Brooks' ratio	Crossby's ratio (%)
I	Mean ± SE: 0.41 ± 0.01 Range : 0.36 - 0.45 CM : 0.41 D : 0.00 CV : 0.29 N : 126	-	-
II	Mean ± SE : 0.54 ± 0.01 Range : 0.49 - 0.59 CM : 0.54 D : 0.01 CV : 0.20 N : 69	1.32	-
III	Mean ± SE : 0.71 ± 0.01 Range : 0.59 - 0.77 CM : 0.71 D : 0.01 CV : 0.32 N : 97	1.31	-0.8
IV	Mean ± SE : 0.95 ± 0.01 Range : 0.82 - 1.04 CM : 0.94 D : 0.01 CV : 0.30 N : 132	1.34	+2
V	Mean ± SE : 1.20 ± 0.01 Range : 1.04 - 1.36 CM : 1.25 D : 0.05 CV : 0.27 N : 206	1.26	-6
VI/ PP	Mean ± SE : 1.57 ± 0.01 Range : 1.36 - 1.82 CM : 1.58 D : 0.01 CV : 0.33 N : 425	1.31	+4
VII/ PP	Mean ± SE : 2.05 ± 0.01 Range : 1.82 - 2.91 CM : 2.08 D : 0.03 CV : 0.42 N : 328	1.31	0.0

PP : Prepupae, CM : Calculated Mean
D : Difference between calculated mean and actual mean
SE : Standard Error of Mean, CV : Coeficient of Variation
N : Number of larvae

Fig. 4.4 Number of instars of larvae U. cupressiana determined by head capsule measurement



temperature (Taylor, 1931; Gaines and Campbell, 1935; Rawat, 1959) and host condition and geographical location (Loerch and Cameron, 1983). In addition, larvae completing development in 6 instars may emerge as male or female beetles, while those completing in 7 emerge as female only.

Although the ranges for an instar may overlap with that of the succeeding instar, SEs and Coefficients of variation are very small indicate natural groupings around the mean measurements. These means follow Brooks' rule, and when the mean measurement for each instar is plotted against the corresponding instar numbers, a significant regression ($r=0.97$, $P<0.001$) is obtained (Fig. 4.5). However, inspection the figure suggests that the relation between the mean measurement of head capsule and the instar numbers may be curve-linear rather than linear. Deviation from a straight line would indicate an overlooked instar (Gaines & Cambell, 1935; Wigglesworth, 1972; and Loerch & Cameron, 1983). Crossby's growth rule provides additional evidence that no instar was overlooked, because all Crossby's ratios are less than 10% (Table 4.7)

It has been argued that differing environmental conditions may substantially alter the head capsule size for a species (Guppy, 1969; Maltais, 1980). However, in the present work for cypress twig borers when the means of head capsule widths cultured at 3 CT (15, 20, and 25°C) were compared, there was not much difference among them (see Table 4.8). This is in agreement with Nemjo & Slaff's (1984) statement that temperatures probably did not affect the head capsule sizes but the quality of food might have an effect, as in fact insects reared under laboratory conditions have smaller head capsules than those from field collection.

Conclusion

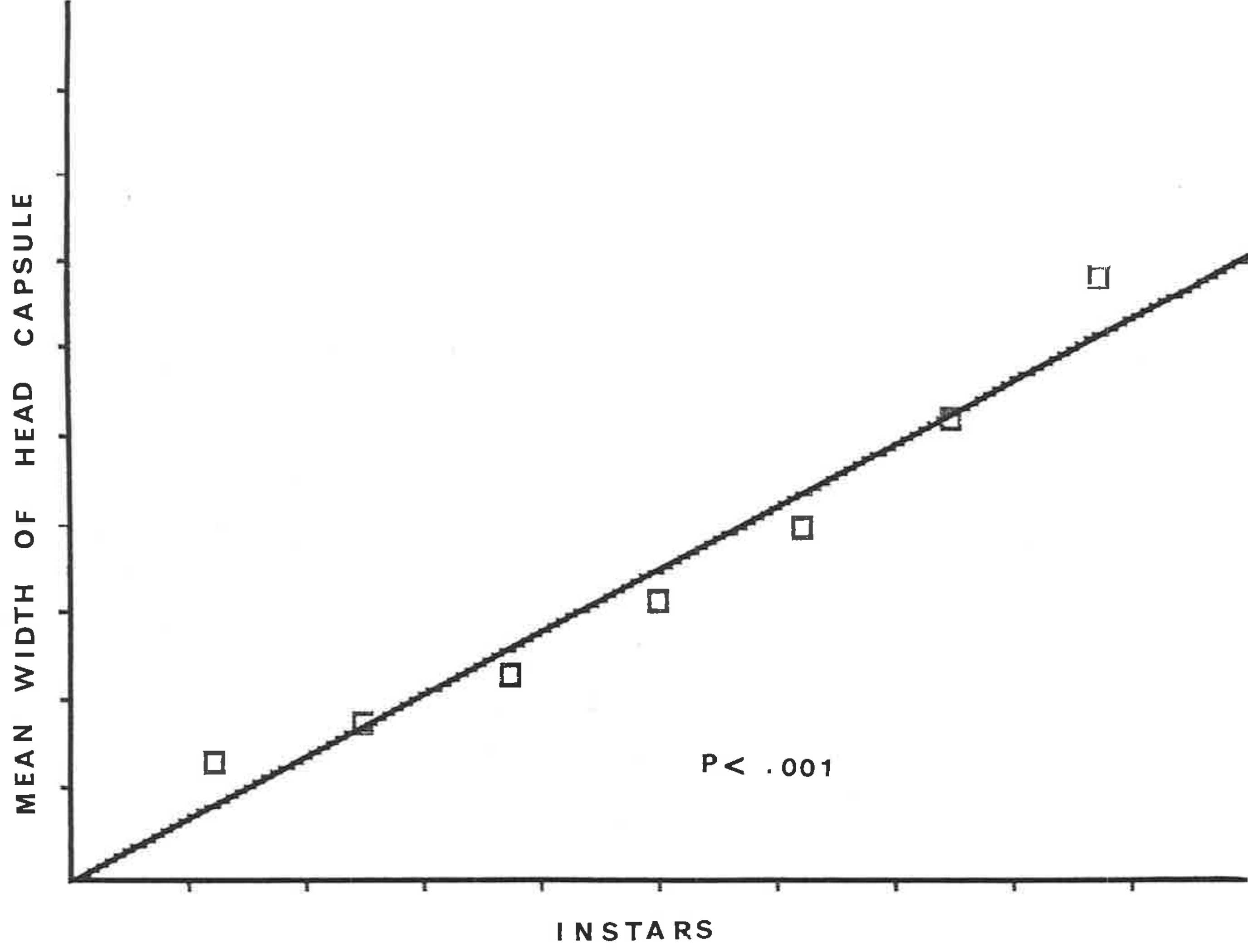
In the field the cypress twig borers may take 6 or 7 instars to complete their development, though in laboratory conditions only 6. The mean of the head capsule width of the 7 instars form a regular geometric progression and fit Brooks' (Dyar's) rule with growth ratio 1.31 (which is in agreement with Cole's growth ratio for the Cerambycids).

Table 4.8: Width of head capsule (mm) of larval Uracanthus cupressiana cultured at different constant temperatures

IR		Temperature (°C)		
		15	20	25
I	MSE	0.41 ± 0.01	0.41 ± 0.01	0.42 ± 0.01
	R	0.36 to 0.45	0.36 to 0.45	0.36 to 0.45
	N	32	40	50
II	MSE	0.54 ± 0.01	0.53 ± 0.01	0.54 ± 0.01
	R	0.50 to 0.59	0.50 to 0.59	0.50 to 0.59
	N	22	25	46
III	MSE	0.67 ± 0.01	0.68 ± 0.01	0.68 ± 0.01
	R	0.59 to 0.77	0.59 to 0.77	0.64 to 0.77
	N	43	44	37
IV	MSE	0.90 ± 0.01	0.94 ± 0.01	0.93 ± 0.01
	R	0.82 to 1.04	0.82 to 1.04	0.82 to 1.04
	N	52	41	42
V	MSE:	1.18 ± 0.01	1.19 ± 0.01	1.17 ± 0.01
	R	1.04 to 1.36	1.04 to 1.36	1.04 to 1.36
	N	53	80	83
VI	MSE	1.54 ± 0.01	1.47 ± 0.02	1.53 ± 0.02
	R	1.36 to 1.77	1.36 to 1.68	1.41 to 1.73
	N	42	34	36

IR : Instar
MSE : Mean ± Standard Error
R : Range
N : Number of larvae

Fig. 4.5: Mean measurements of head-capsule width and corresponding instars and linear regression relationship.



MEAN WIDTH OF HEAD CAPSULE
P< .001
INSTARS

Plate 5: Rearing containers with saturated salt solution at the bottom, and the layers of twigs on the plastic grid that was placed above the solution.

4.2.3.4 Larval growth and development

In the life history of insects, no prolonged arrest of growth occurs at any stage other than that caused by the direct action of adverse environmental conditions. Some factors affecting the growth and development of insects have been studied and discussed by many workers. Temperature appears to have a strong effect on insect development (Andrewartha & Birch, 1954; Wigglesworth, 1953; Howe, 1957; Matteson & Decker, 1965; Guppy, 1969; Taylor, 1981; Raynolds & Nottingham, 1984; Pershing & Linit, 1986; Ballou, et al., 1986 etc). In other cases food and water (Reynolds & Nottingham, 1985; Gaines & Campbell, 1935), nitrogen (White, 1978, 1984; Mattson, 1980; Scriber & Slansky, 1981; Lincoln, 1985), and secondary chemicals of the host plant (Rhoades, 1983; Johnson, et al., 1985; Lincoln, 1985, etc.), may affect the growth and development of the insect

Most of the determinations of growth have had reference to units of time (days, weeks, months or years), or to stages delimited by moults. The approximate duration of each stadium was determined using various methods by some authors. It was determined by calculating the distance in days (or half-day) from one mean to the next, or calculating the distance from the first date of one stage to the first date of the next, plus the distance between the last of the same 2 stages, divided by 2 (Taylor, 1930; Bedard, 1933). Prebble (Walters & McMullen, 1956) determined it by calculating the interval between the first date when that instar formed the majority of the population and the first date when the succeeding instar formed a similar proportion of the population, while Guppy (1969) defined it as the number of days from the time that 50% of the individuals of one stage reached the next stage.

In this present study the length of time spent in each instar larvae was determined by calculating the mean interval from the first to the last week appearance of a given instar.

The whole larval life of the cypress twig borer is spent in a tunnel within the host. Therefore the temperature and moisture content of the wood host might be important factors affecting larval growth and development. Experiments were carried out to determine their importance.

Experiment 1. Larval development in 4 different constant temperatures

At each of the selected temperatures (15, 20, 25. 30°C, and 14 hours daily photoperiod), 600 twigs of the C. sempervirens with 4 to 5

Table 4.9: Developmental times (weeks) of larvae at constant temperatures

Larvae Instar	Statistic	Temperatures (±C)			
		15	20	25	30
I	Mean	12	11	8	4
	Range	8-16	8-14	4-12	4
	MDR	8.3	9.1	12.5	25
	N	45	37	38	32
II	Mean	11	9	7	-
	Range	4-18	4-14	2-12	-
	MDR	9.1	11.1	14.3	-
	N	60	45	36	-
III	Mean	18	14	12	-
	Range	8-26	8-20	6-18	-
	MDR	5.5	7.14	8.3	-
	N	70	63	42	-
IV	Mean	18	16	12	-
	Range	8-28	8-24	4-20	-
	MDR	5.6	6.3	8.3	-
	N	74	63	47	-
V	Mean	22	16	12	-
	Range	4-34	4-28	4-20	-
	MDR	4.5	6.3	8.3	-
	N	72	78	45	-
VI &pp	Mean	38	32	24	-
	Range	16-60	12-52	16-32	-
	MDR	2.6	3.1	4.2	-
	N	90	132	71	-

MDR : Mean Development Rate (% per week)
N : Number of larvae recorded
- no observation

newly hatched larvae in each were placed in a plastic container (65x40x40cm) with saturated salt solution (NaCl), and kept there for the duration of the experiment. The length and diameter of the twigs were more less similar (30cmx0.7cm). On the bottom of each container 4 small plastic bowls full of salt solution, were placed. On the top of each bowl a plastic grid was laid and on the grid was spread a fine plastic gauze to prevent the frass falling down into the solution. The twigs were then placed horizontally in layers alternately at 90° to each other. This arrangement allowed enough space for air circulation within the container. Every month twigs were sprayed with 5% salt solution (Nacl) to protect them from fungus, and water was added to the humidifying solution. Observations were made of the generation time and rate of development by extracting 10 twigs at 2 week intervals. Development time and the number of instars were recorded for each larval instar (ecdysis to ecdysis).

The mean and range of development time and the mean of rate of development are given in Table 4.9. The reciprocal of the mean developmental time (the rate of development) was plotted against temperature. The threshold temperature and thermal constants were estimated using the method as given in section 4.2.2.4 (see Table 4.10).

It should be noted that figures given for the 6th instar included the prepupa, and the calculation was done for 6 instar using only larvae from laboratory rearing. The prepupa is distinguished by several behavioural and physical features: (1) feeding ceases, (2) the body contracts, (3) the colour changes, etc. However, apolysis does not occur in the 6th instar until formation of pupa. Therefore, the prepupa may not be considered as a separate instar stage.

At 30°C all larvae died by the L2 only, therefore the 30°C treatment was not included in the calculations. Linear regressions of mean development rate on temperature for first to 6th instar larvae were calculated (L1 to L6) see Fig 4.6).

L1 : $Y = 1.57 + 0.42\ X$ $(r = .94,\ P > 0.1)$

L2 : $Y = 1.10 + 0.52\ X$ $(r = .99,\ P < 0.05)$

L3 : $Y = 1.38 + 0.28\ X$ $(r = .99,\ P < 0.05)$

L4 : $Y = 1.33 + 0.27\ X$ $(r = .96,\ P > 0.5)$

L5 : $Y = -1.23 + 0.38\ X$ $(r = .99,\ P < 0.05)$

L6 : $Y = 0.10 + 0.16\ X$ $(r = .98,\ P > 0.05)$

The range of developmental times becomes greater for L5 and L6 perhaps because of the excessive desiccation of the twigs (food-wood).

Table 4.10: Developmental threshold temperatures (t) and heat unit (HU) for six larval instars of <u>U. cupressiana</u>

Larval instar	t °C	HU*
L1	- 3.7	244.8
L2	- 2.1	198.9
L3	- 4.9	365.3
L4	- 4.9	381.7
L5	3.2	280.1
L6	- 0.7	648.5

*HU is week degree.

Table 4.11: Development and larvae surviving in response to moisture content of wood

Month	dry wood		wet wood	
	stage	survivors	stage	survivors
1	I	8	I	9
2	I	6	I,II	8
3	I,II	4	I,II	6
4	I,II	4	II,III	6
5	II	3	III	6
6	II	3	III,IV	4
7	II.III	4	III,IV	5
8	III	3	IV,V	5
9	III	3	IV,V	4
10	III	2	IV,V	5
11	-	0	V.VI	4
12	-	0	V,VI	5

The figures are number of survivors per 10 extracted twigs
- no recorded larvae

Fig. 4.6: Linear regression of mean developmental rate on temperature for L1 to L6 of U. cupressiana:

L1: $Y = 1.57 + 0.42\ X$ $(r = .94, P > 0.1)$

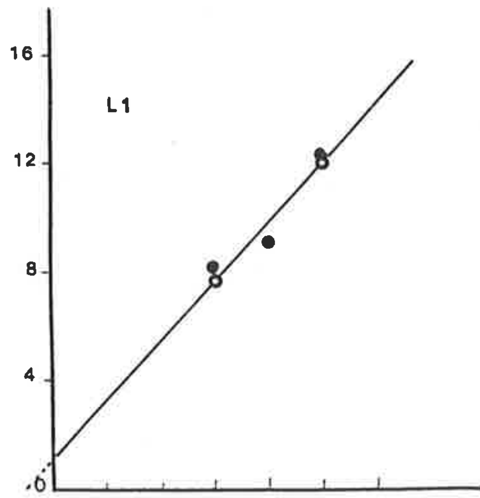
L2: $Y = 1.10 + 0.52\ X$ $(r = .99, P < 0.05)$

L3: $Y = 1.38 + 0.28\ X$ $(r = .99, P < 0.05)$

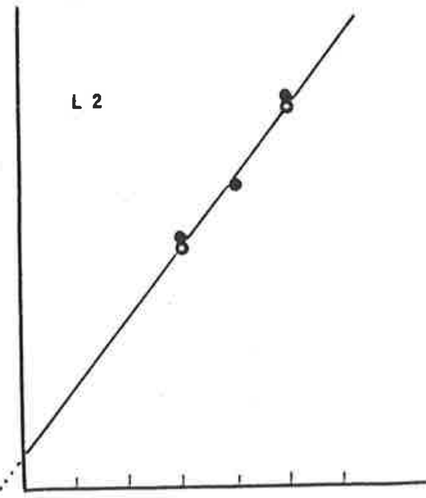
L4: $Y = 1.33 + 0.27\ X$ $(r = .96, P > 0.5)$

L5: $Y = 0.38\ X - 1.23$ $(r = .99, P < 0.05)$

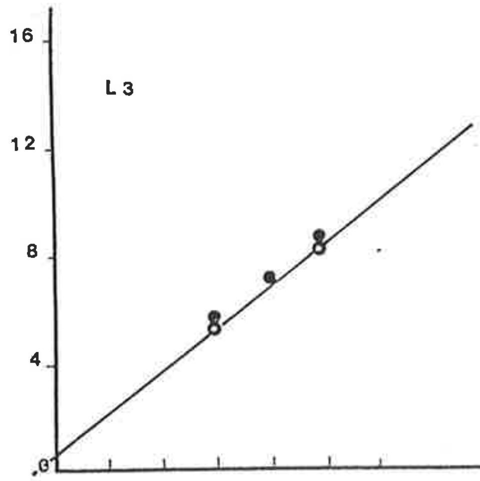
L6: $Y = 0.10 + 0.16\ X$ $(r = .98, P > 0.05$



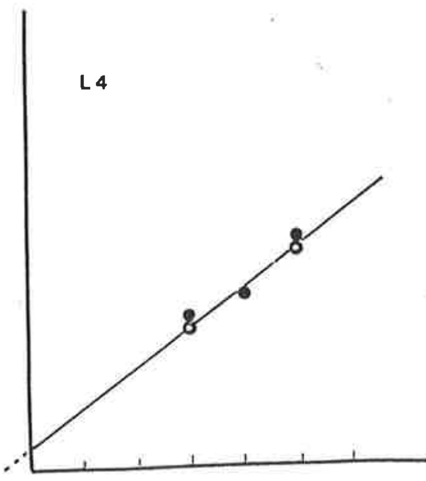
L1
16
12
8
4
0



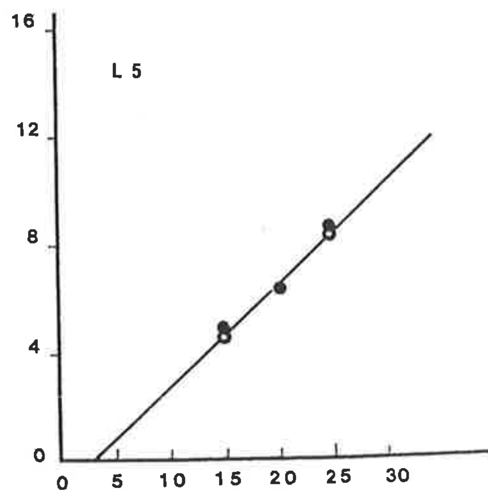
L 2



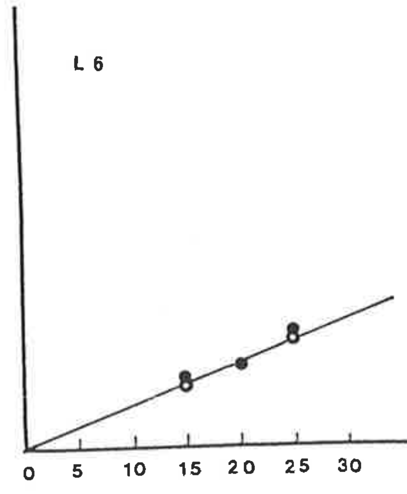
L 3
16
12
8
4
0



L 4



L 5
16
12
8
4
0
0 5 10 15 20 25 30



L 6
0 5 10 15 20 25 30

Both in the laboratory and in the field the prepupal larvae remain inactive for several months (2 to 4 months) or for about 12 months. From laboratory culture it was found that some prepupae still survived after 24 months, and a few from them pupated and emerged as adults.

Larvae of the cypress twig borer are extremely delicate and susceptible to bruising and other forms of injury. They will die within a few days if they are in any way bruised or injured. They are also remarkably susceptible to frost. A preliminary experiment in which 4 groups of 10 mature larvae were kept at a temperature of -6°C for 5, 10, 15, and 20 minutes demonstrated this susceptibility. When removed from the refrigerator they remained frozen solid for about 15 minutes. They were then placed in an incubator at 35°C, where the larvae that were subjected for 5 minutes all recovered in about half an hour. In the group subjected to 10 minutes chilling, just 2 larvae recovered, while those subjected to either 15 or 20 minutes all died, and their colour changed to dark brown or black after a few hours. This susceptible to frost indicates that larvae of the cypress twig borer are unable to withstand severe weather conditions.

4.2.3.5 Larval development in different moisture content of wood

For a developing insect, the rate of development depends mainly on the temperature regime in which it lives (Taylor, 1981). However, the rate may be altered by many aspects of the environment, such as humidity, nutrition, or disease. In the case of the cypress twig borer, larvae feed, grow, and develop within the food-wood; the moisture content of the wood might make a large contribution to the development of larvae. As mentioned in section 4.2.3.4, the wide range of developmental times for the mature larvae might be due to desiccation of food-wood. This section is intended to clarify this point.

Experiment 2. Effect of moisture content of food-wood on larval development and survival

The experiment was carried out at 20°C. CTR, 14°10 LD. 200 twigs with newly hatched larvae were placed in the plastic container with saturated salt solution, and sprayed with salty water at intervals of one month (as in exp.1). Another 200 twigs were placed in another container with neither salt solution nor salty water spraying. Each month

10 twigs were taken from each container and examined. The experiment finished when all larvae were dead or in the prepupal stage.

The results show that the development and survival of the larvae were much influenced by the moisture content of the twig. In moist twigs the larvae can survive and develop to maturity in 12 months, while in the dry twigs, larval development was retarded and none survived beyond the L3 (see table 4.11).

4.2.3.6 Larval development and behaviour in relation to moisture content of wood

In the previous section it is stated that in dry wood larval development was retarded, and larvae died. In this case the excessive desiccation of wood may cause the feeding behaviour of the insect to change. The following experiment was carried out to clarify this matter.

Experiment 3. Effect of moisture content of food-wood on the development and behaviour of larvae

The experiment was carried out in the Insectary at 20 to 25°C, 14 hours daily photoperiod, and with controlled relative humidity (65-75%). 200 twigs with mature larvae which were collected from the field were placed vertically in 10 cylindrical glass jars (12cm diameter and 20cm height), with 100 ml water. Prior to placing them in the jar, they were rubbed with 90% alchohol for half of the length to protect them from fungus. Another 200 twigs were placed in 10 jars without water. Beside these, 100 twigs were placed on a tray and were sprayed daily with water. Another 100 twigs were placed on another tray without water spraying. Larval development and behaviour were observed monthly by recording the dry weight of frass produced and the presence of emergence holes. Before weighing the frass was oven dried (70°C) for 2 week. At the last observation (8th) 20 twigs from each treatment were dissected and the larval development recorded.

The results show that in moist wood the larvae fed actively for the first 3 months (indicated by the amount of frass) and from the 4th to the 7th month the frass amount decreased while the number of emergence holes increased. The appearence of the emergence hole indicates that a larva has finished feeding and is about to become a prepupa. After 8 months all larvae ceased feeding. In dry wood the larvae fed actively for the first 2 months only. Feeding activity decreased until the 4th month,

Table 4.12: Development and behaviour of larvae in response to moisture content of wood

Obs.	Wood (Twigs)			
	VWT	VDT	HWT	HDT
1	13.7 ±0.23	9.40±1.46	5.86±0.17	5.60±0.50
2	12.57±0.23	8.26±0.21	5.66±0.44	3.70±0.06
3	11.75±0.12	7.85±0.32	4.96±0.08	2.86±0.36
4	8.10±0.49 ,33	5.21±0.08 ,1	3.97±0.10 ,15	2.56±0.36 ,0
5	3.66±0.12 ,42	2.36±0.27 ,3	2.23±0.25 ,23	0,0
6	3.03±0.07 ,43	0,3	0,25	0,1
7	2.30±0.56 ,54	0,3	0,35	0,3
8	0,56	0,4	0,36	0,3
LW	145.22±14.80	49.13±6.48	98.3±13.71	16.46±4.04
S	71.4	18	67.8	15

The figures in observations (Obs.) 1 to 8 are Mean weighing of oven dry frass ± Standard error, Number of emerging holes.
VWT : Vertical wet twigs
VDT : Vertical dry twigs
HWT : Horizontal wet twigs
HDT : Horizontal dry twigs
LW : Larval weight
S : Percentage of survivors

and then ceased without the appearance of emergence holes. Thus, in the dry wood, larvae cease feeding earlier and development becomes slow and retarded (see Table 4.12).

Much of the larval behaviour in seeking the site of a pupal chamber depends on the moisture content of the wood. All the larvae in the vertical twigs with water make the pupal chambers in the moist bottom part, while those in horizontal twigs with water spraying locate pupal chambers anywhere in the twig top, middle, or bottom. To elucidate this behaviour, 2 other experiments were carried out.

Experiment 4. Effect of moisture content of wood on position of pupal chamber

The experiment was conducted in the same place as experiment 3. Larvae were extracted from twigs and transferred to holes (5mm diameter) drilled longitudinally in pieces of dowel (10mm diameterx60mm long). The middle piece was drilled right through and the 2 end pieces just half way. There are 3 treatments: (1) 2 weeks oven drying (60°C); (2) daily water spraying; and (3) 2 weeks soaking or until saturated. Before putting the dowels together the wood moisture was measured using the Protimeter moisturemeter (see Chapter 2), and then all were carefully dipped into melted wax, while the end with hole was blocked by using cotton wool, so tunnel (drill made tunnel) was not blocked by wax, to keep the moisture content more or less constant during the experiment. The treated dowels were arranged as follows: 1-2-3, 1-3-2, 2-1-3, 2-3-1, 3-2-1, 3-1-2. The 6 arrangements were replicated 8 times, so 48 mature larvae were used. Each larva was released in the middle piece of dowel and facing in the same direction. After 7 days the larva were extracted and their position recorded.

Another experiment followed the same procedure, except that the larvae were released at one end of the set of dowels, all facing in the same direction through the tunnel. The releasing points of both experiments were compared.

The results show that the larvae prefer to construct their pupal chambers in the moist part of the wood ($P<0.05$, and $P<0.01$) (see Table 4.13). So it is clear that the moisture content of the wood influences greatly the behaviour of larvae in constructing the pupal chambers. About 70% of larvae moved around before settling in the preferred sites. Some of the larvae that chose the middle pieces of

Table 4.13: Position of pupal chamber within dowels of various moisture contents

Section	Wood moisture (%)	Number of larvae	
		Exp I	Exp II
dry	<15	9	10
wet	60	13	14
saturated	>90	26	24
N		48	48
X2		6.50	9.88
P		<0.01	<0.05

Exp: experiment
N: number of larvae

Table 4.14: Larval survival within frass of various moisture contents

Medium	Number survivors	Number pupate
moist	54	36
dry	16	2
X2	20.62	17.79
P	<0.001	<0.001

dowelling took wood from the wall of the tunnel and blocked it just in front of their heads before constructing the pupal chamber. The releasing points did not influence the preference of larvae in making the pupal chamber ($X2 = 0.1696$, $P>0.05$).

4.2.3.7 Larval survival and moisture content of wood

In the previous section it was mentioned that the length of the last instar of some mature larvae was prolonged. Some were found dead in their tunnels, and some moulted or pupated abnormally. All this may have been due to excessive desiccation of wood. This section is intended to clarify this matter.

Experiment 5. Effect of moisture content of wood on the survival of mature larvae

The experiment was carried out in the same place as experiment 2. 120 mature larvae were extracted and each was placed in a screw-lid vial (10x50mm) filled with frass. The frass had been oven dried for 2 weeks. Water (2ml) was added to each of 60 vials. The other 60 were left dry. Observations were done monthly for 8 months, and the number of survivals and pupations was recorded.

The results show that in the moist frass larval survival and pupation were significantly higher ($P<0.001$) than in the dry frass. In the moist frass more than 50% of treated larvae pupate, while in the dry frass few larvae pupate and, though some are still alive, their bodies are thin and weak and nearly dead (see Table 4.14).

General conclusion

The growth and development of larvae are greatly influenced by the temperature and moisture content of wood. More larvae survived in the moist wood than dry wood. In a suitable moisture content of wood and temperature more than 50% of larvae can develop and become adults. The larval period is about 14 months or 22 months or even more. Larvae chose the moist wood to construct their pupal chambers.

Plate 6: Rearing vials that were used after the larvae stop feeding (prepupae).

4.2.3.8 Larval mines

Cerambycid larvae attain maturity in a great variety of hosts, and their successful development depends to a great extent on the nature and condition of the wood. Many larvae exhibit a decided preference for a particular part of the tree. Very often a distinct preference is shown for wood in a particular condition (Duffy, 1953; Linsley, 1959). The mines themselves are in general broad, shallow excavations which are nearly always oval, seldom round in cross section, typically containing excreta and gnawed particles of wood but powdery in some cerambycinae (Duffy, 1953; Solomon, 1972 & 1974).

As mentioned previously, the larva of U. cupressiana, after hatching, immediately tunnels into the phloem and cambium, producing a spiral mine (0.5mm major diameter, and 10mm length) and then tunnels straight along the distal part of the twig until the twig is too thin for it to continue. Then it turns back (downward), widening and deepening the mine to the centre of twig. The mine is more or less oval in cross section and rather constant in size for each instar. For mature larvae the mines range from 1.8-3.18mm in cross section and 70-500mm in length (see Table 4.15). In the field the length of the mine is longer (100-510mm) than in laboratory cultures. It depends on the size of the twig or branch. The length of the mine from field collections is longer than those from laboratory cultures, perhaps because the larvae from laboratory cultures stop feeding early.

The mean length of larval mine was plotted against temperature as shown on Fig. 4.7.

The data show that there are no significant differences in cross section and length of mines within any temperatures. As mentioned previously, the cross sections of the mines are rather constant for any instar. They remain constant at different temperatures.

Linear regressions of mean length of mine on temperature for larval instar I to VI (L1 to L6), are as follows:

L1: $Y = 0.49 + 0.24X$ $(r = 0.97, P > 0.05)$

L2: $Y = 6.97 + 1.48X$ $(r = 0.93, P > 0.05)$

L3: $Y = 52.88 + 0.99X$ $(r = 0.95, P > 0.05)$

L4: $Y = 69.92 + 3.79X$ $(r = 0.96, P > 0.05)$

L5: $Y = 139.34 + 1.94X$ $(r = 0.98, P > 0.05)$

L6: $Y = 146.41 + 3.72X$ $(r = 0.65, P > 0.05)$

Table 4.15: Larval mines (cross section and length) in various constant temperatures

Larval Instar	Statistic	Temperature (°C)		
		15	20	25
I	Mean	0.67/3.9	0.68/5.57	0.82/6.28
	Range	0.45-0.90/ 1.80-9.55	0.45-0.90/ 2.95-8.40	0.68-0.90/ 3.86-10.90
	N	16	32	10
II	Mean	0.97/30.85	0.99/33.30	1.04/45.67
	Range	0.90-1.14/ 4 - 60	0.90-1.36/ 15 - 55	0.90-1.36/ 15 - 110
	N	10	20	10
III	Mean	1.27/ 66.70	1.28/74.54	1.32/76.56
	Range	0.90-1.59/ 15 - 125	1.14-1.59/ 33 - 195	1.14-1.59/ 15-150
	N	25	38	16
IV	Mean	1.59/124.33	1.64/150.81	1.69/162.27
	Range	1.36-1.82/ 40 - 290	1.36-2.05/ 70 - 260	1.36-1.82/ 80 - 300
	N	42	37	22
V	mean	2.01/167.3	2.03/180.57	2.04/186.73
	Range	1.59-2.72/ 70 - 300	1.36-2.72/ 80 - 300	1.59-3.18/ 80 - 350
	N	49	53	71
VI	Mean	2.5/215	2.4/195.43	2.6/252.24
	Range	1.8-3.18/ 70 - 340	1.8-3.18/ 80 - 400	2.17-3.63/ 120 - 500
	N	18	48	47

N : number of larval mines were recorded
The figures are cross section/length of mine (mm).

Table 4.16: The percentage of shreded wood in larval frass

Larva No.	Frass (mg)	Shreded wood (mg)	Shreded wood (%)
1	25.7	18.2	70.8
2	27.3	16.6	60.8
3	24.7	15.1	61.3
4	20.3	12.4	61.1
5	26.8	16.5	62.4
6	22.0	14.0	63.6
7	31.4	22.4	71.2
8	21.5	15.9	73.9

Table 4.17: Larval mine for L6 and L7 of *U. cupressiana* collected from field

Instar	length of mine (mm)	Width of mine (mm)
L6	Mean: 300.58 ± 16.04	3.01 ± 0.08
	Range : 180 - 440	2.05 - 3.64
	N : 26	
L7	Mean: 303.02 ± 11.05	3.48 ± 0.05
	Range: 130 - 510	2.5 - 4.55

Fig. 4.7: Linear regression of mean length of mines on temperature for L1 to L6:

L1: $Y = 0.49 + 0.24\,X$ ($r = .97$, $P > 0.05$)

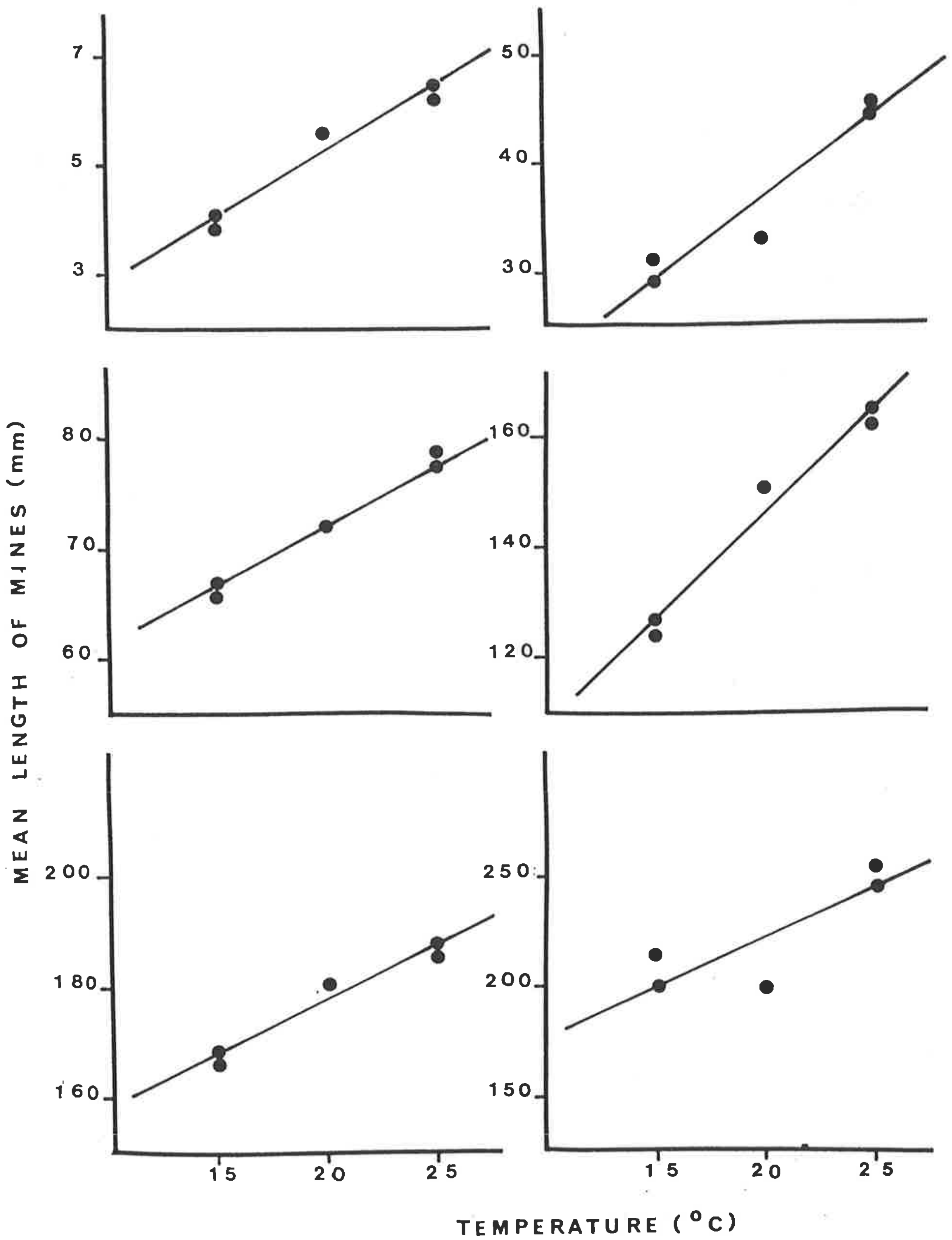
L2: $Y = 6.97 + 1.48\,X$ ($r = .93$, $P > 0.05$)

L3: $Y = 52.88 + 0.99\,X$ ($r = .95$, $P > 0.05$)

L4: $Y = 69.92 + 3.79\,X$ ($r = .96$, $P > 0.05$)

L5: $Y = 139.34 + 1.94\,X$ ($r = .98$, $P > 0.05$)

L6: $Y = 146.41 + 3.72\,X$ ($r = .65$, $P > 0.05$)


MEAN LENGTH OF MINES (mm)
TEMPERATURE (°C)
7
5
3
50
40
30
80
70
60
160
140
120
200
180
160
250
200
150
15
20
25
15
20
25

In the field, the length of mine and larval weight were significantly correlated with the diameter of the twig (P<0 05) (see Figs 4.8 & 4.9). This suggests that the bigger the twig the longer the larval mine. Apparently big twigs are usually longer than small ones. Thus the larvae have a chance to extend their mines towards the tip of the twigs or branches within those twigs whereas in small short twigs they are limited by the tip of the twigs. Sometimes within small short twigs the larval mine become irregular in width. However, there were no significant correlations of larval weight on length of mine (see Fig. 4.10 & App. 6). It might suggest that perhaps the larvae tunnel longer within wood of low nutritional quality (see Chapter 7). Observations of dried frass reveal that more than 50% is shreded wood and the remainder is faeces and discarded cuticle. It is clear that not all wood which is torn from the tunnel is eaten (digested). Eight active feeding larvae were used to examine the proportion of shreded wood in the frass. The result shows that the mean proportion of shreded wood was 65.64±1.90, range from 60.8 to 73.9% (see Table 4.16). The length of mine of L6 and L7 are almost similar but they differ in cross section (see Table 4.17).

Conclusion

The length of larval mine was strongly correlated with twig size but the larval weight was not correlated with length of mine.

4.2.3.9 Larval diapause

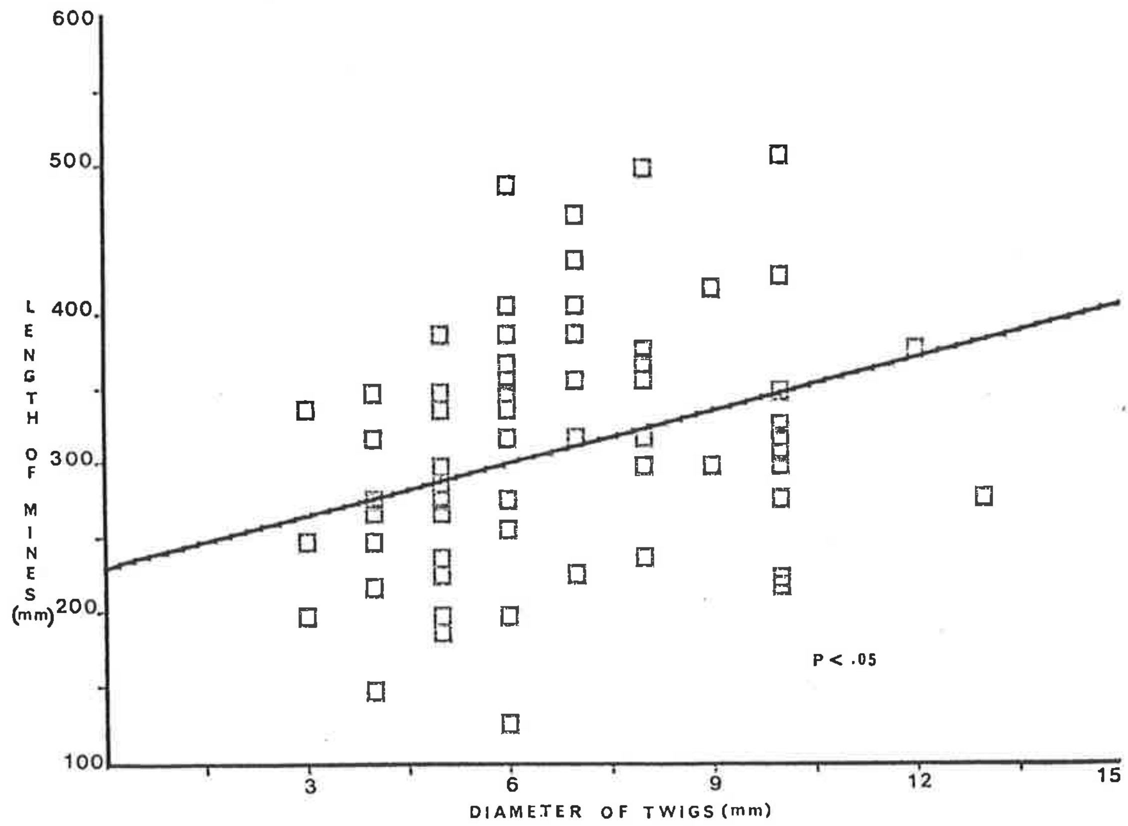
Introduction

The phenology of many insects is regulated by the phenomenon known as diapause. It is well known that diapause in insects serves to synchronise activity with favorable weather and available biotic resources such as food, mates, oviposition sites, and periods free from natural enemies. When it is in diapause, the insect is at that stage of its life when it is mostly able to survive under unfavourable weather.

The habitat of U. cupressiana has a Mediterranean climate characterized by hot dry summers and cool wet winters. U. cupressiana more likely responded to cool wet seasons by evolving the habit of spending about half of each year, largely during autumn and summer, in diapause

Fig. 4.8: Correlation between size of twig and length of mine ($P < 0.05$).

Fig. 4.9: Correlation between size of twig and larval weight ($P < 0.05$).


600
500
400
300
200
100
LENGTH OF MINES (mm)
3
6
9
12
15
DIAMETER OF TWIGS (mm)
P < .05

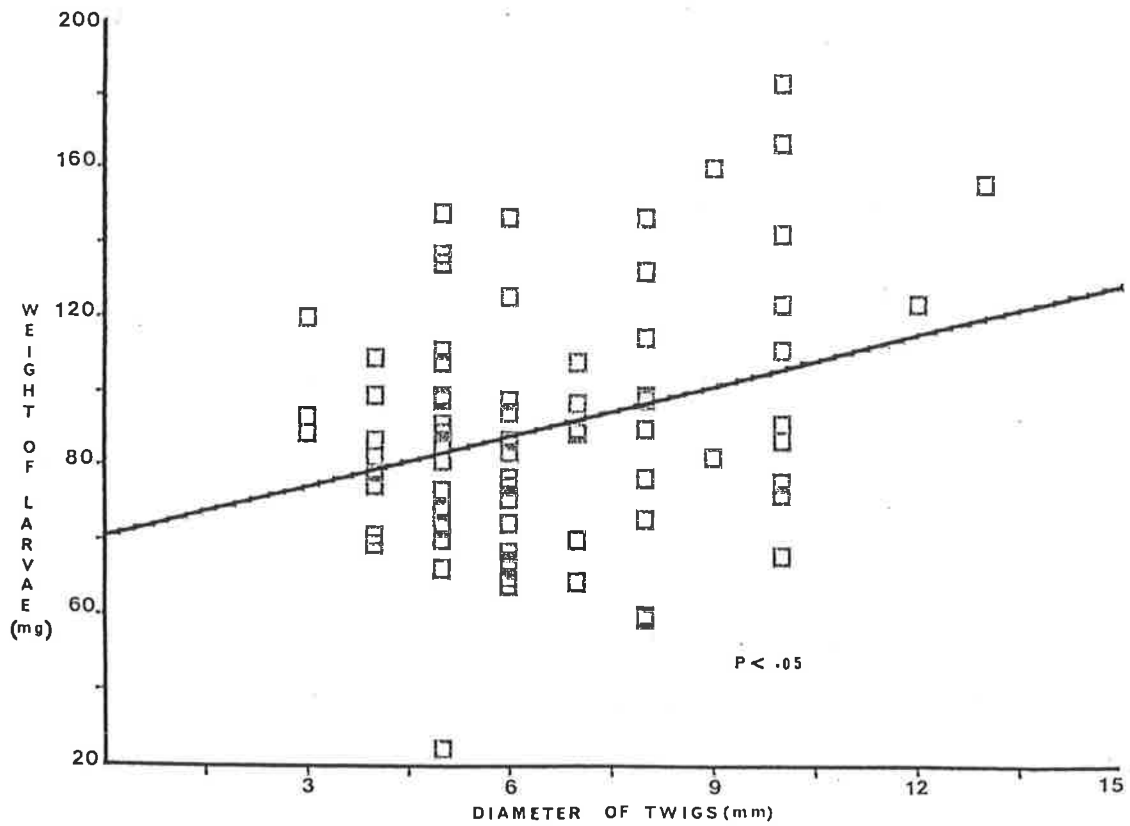
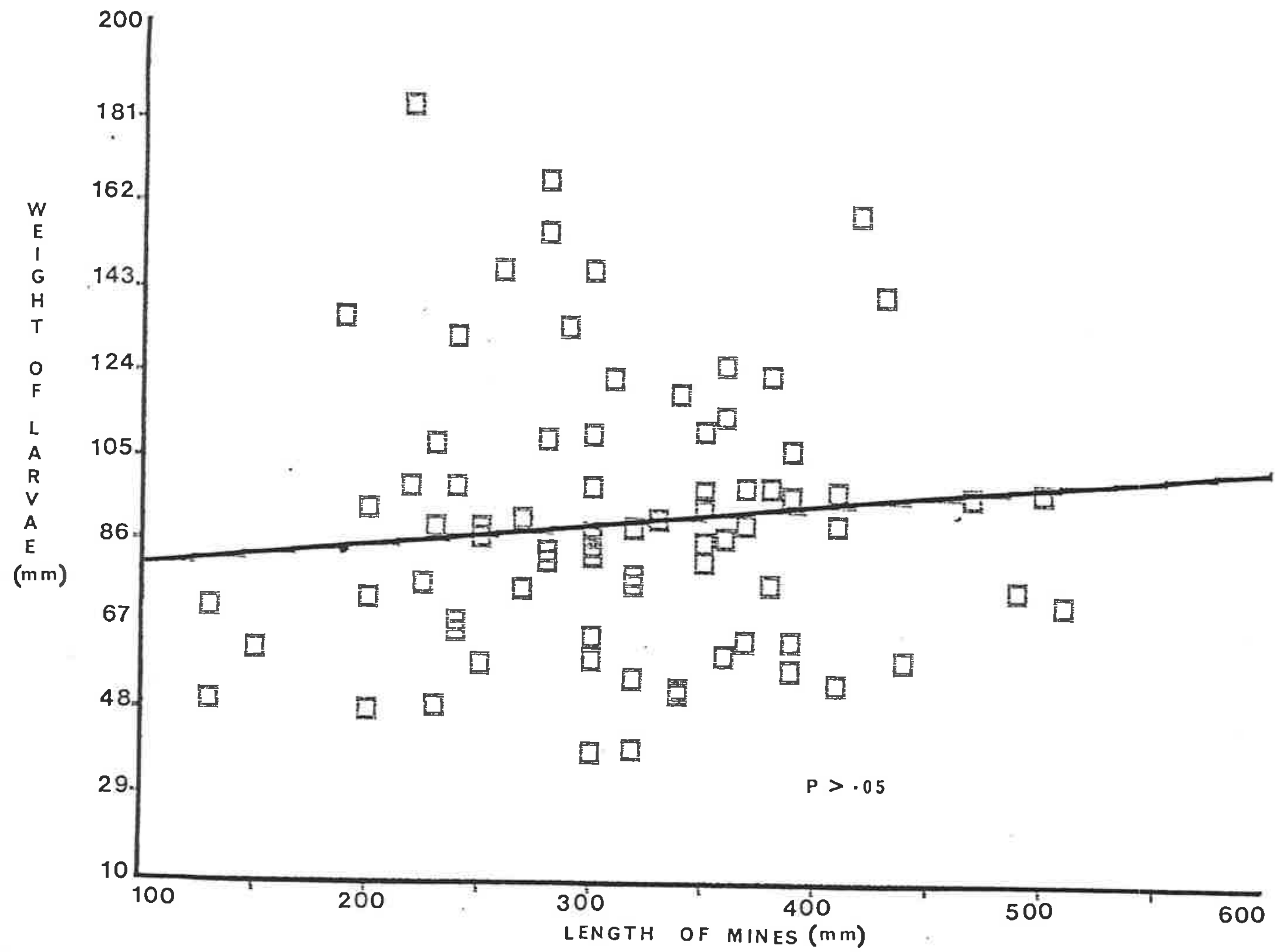

200
160
120
80
60
20
WEIGHT OF LARVAE (mg)
3
6
9
12
15
DIAMETER OF TWIGS (mm)
P < .05

Fig. 4.10: Correlation between length of mine and larval weight ($P > 0.05$).


200
181
162
143
124
105
86
67
48
29
10
WEIGHT OF LARVAE (mm)
100
200
300
400
500
600
LENGTH OF MINES (mm)
P > ·05

within their mine in the twigs or branches. The adults emerge in late summer, mate, and females deposit their eggs. Larvae hatch in autumn and become mature or full size in late summer of the following year. The mature larvae tend to diapause as prepupae during autumn and winter. Pupation begins in early or mid spring when the temperature level starts to rise. Adults start to emerge in late spring and summer. The insect is, therefore in synchrony with its environment.

In larval U. cupressiana, the diapause development apparently is a temperature-dependent process. A series of experiments was therefore devoted to examining the influence of temperature on diapause.

In the following sections, the words "high", "moderate" and "low" referring to temperature are used in a relative sense. Temperatures of 25°C are"high", 15-20°C are "moderate", and 10°C are "low". The terms "morphogenesis", "diapause stage" and "diapause development" are used in the sense defined by Andrewartha and Birch (1954).

Experiment 1. Mature larvae exposed to various constant temperatures

The test larvae were reared in the laboratory from nearly mature larvae in the field. The larvae had already constructed a pupal chamber and emergence hole of adults. They were extracted from the twig and put into a small vial (50x10mm) with moist frass and the vials were placed in the container with saturated salt solution (76% RH). 40 larvae were kept in each chosen CTR (10, 15, 20 and 25°C).

The results given in Table 4.18 show that at 10 and 25°C, all larvae entered a prolonged diapause throughout the Experiment (20 months). About 70 and 65% of those kept in 15 and 20°C respectively completed diapause development and resumed morphogenesis as indicated by the occurrence of some pupation after 6-10 months, with the remaining larvae pupating after 18-20 months (see App. 7). This finding suggests that development and apolysis of the prepupae and morphogenesis of pupae may occur at the moderate temperatures (15-20°C) but may not occur at 10 and 25°C. At 10 or below and 25°C and above apparently too cold and too high to permit morphogenesis.

Table 4.18: The percentage pupation (N = 40) and time required to complete diapause development at various constant temperatures*

Temperature (°C)	%age pupation	Time required (weeks) Range	Mean ± S.E.(N)**
10	-	-	-
15	75	24 - 76	37.17 ± 2.79 (30)
20	69	26 - 80	37.07 ± 2.90 (27)
25	-	-	-

* The experiment was terminated after 20 months
** N is number of survivors
\- no observation

Table 4.19: The percentage of pupation (N = 20) and time to pupate for larvae initially exposed to 10°C for three months and transferred to 15 and 20°C*

	Control		Initially exposed to 10±	
	15°C	20°C	15°C	20°C
%age pupation	70	65	65	60
Range of time required(weeks)	24-36	26-32	22-32**	18-26**
Mean ± S.E.	28.5±0.81	28.84±0.59	25.77±0.89	21.42±0.72

* The experiment was terminated after nine months
** values include time spent at 10°C (three months)

Experiment 2. Larvae initially exposed to 10°C for 12 weeks then kept at 15 and 20°C till pupation

40 mature larave were used. They were treated as those in experiment 1. They were initially exposed to 10°C for 12 weeks. After that time the lavrvae were divided into 2 groups of 20. The first group was transferred and kept at 15°C, and another group was at 20°C till they pupate.

The larvae were placed at 10°C in early winter (3 June) and they were kept for 12 weeks. They were transferred from 10°C to higher temperatures at a time of rising temperatures (in early spring) in the field. The experiment was terminated 6 months after the larvae were transferred from 10°C. The time of pupation was recorded.

The results are presented in Table 4.19 and App. 8. A T-test showed that there is a significant difference in mean length of time required to complete the diapause development ($P<0.05$ and <0.01). It is shorter for those transferred from 10°C to 15°C than those maintained continuously at 15°C. The larvae transferred to 20°C are also much shorter than those kept at 20°C. This finding suggests that diapause development was favoured by a low temperature. After exposing to a low temperature (10°C), the rate of diapause development and morphogenesis became fast at 15°C and even faster at 20°C. It is likely that 20°C is the optimal temperature of the diapause development and morphogenesis.

Experiment 3. Larvae initially exposed to 25°C for varying periods and then kept at 15°C until pupation

Larvae (N=60) were treated as in previous experiments and maintained at 25°C. After 6 months at 25°C, a group of 20 larvae (group 1) were transferred to 15°C, and another group of 16 (survival) (group 2) were transferred after 12 months. For control another group of 20 larvae (group 3) were maintained continuously at 15°C. The group 1 were taken from 25°C and transferred to the moderate temperature 15°C) in late winter (August) and the group 2 in early autumn (March). The time of pupation was recorded. The experiment lasted 6 months after the second group (16 larvae) were transferred to 15°C.

The results are presented in Table 4.20 and App. 9. A T-test shows that both groups of larvae (group 1 & 2) initially exposed either for 6 months or 12 months at 25°C required significantly longer at 15°C to complete the diapause development than those continuously

Table 4.20: The percentage pupation and time required to complete diapause development at 15°C after larvae were initially exposed to 25°C for six and 12 months*

	Control (Group 3)	Initially exposed to 25°C	
		6 months (Group 1)	12 months (group 2)
%age pupation	72	60	56
Range of time required (week)	24 - 72	60 - 72**	64 - 72**
Mean ± S.E.	37.14 ± 4.06 (N=14)	66.0 ± 1.13 (N=11)	68 ± 0.82 (N=9)

* The experiment was terminated
** Values include time spent at 25°C.

maintained at 15°C ($P<0.1\%$). The percentage of pupation of group 1 and 2 are lower than group 3. These suggest that high temperature (25°C) does not favour the diapause development or in other words, the high temperature reduces the rate of diapause development of U. cupressiana.

Discussion

Diapause in Cerambycidae is poorly understood. However, it had been recorded in Arhopalus ferus Mulsant by Wallace (1954). He found some larvae in diapause during the cold weather in winter, when the temperature was zero on several occasions. The larvae were bent double and were quite dormant. When they were taken from the stump, they were flaccid and gave no sign of movement but as the temperature increased in the laboratory where they were transferred, the larvae became active.

In U. cupressiana, diapause can be defined as the prepupal stage. There are changes in external features of the larvae. Body tends to incline. Thorax is swollen and head is bent down. When the larvae were extracted from twigs or branches, they made a response by moving or crawling. At the end of diapause (a few days before pupation), the larval body becomes straight again and quiescent.

Diapause development comprises the period from the formation of prepupae to the time when the larvae are competent to initiate development of pupae. This period varies depending on the temperature or possibly on individual factor or others. The finding showed that the larvae initially exposed to the low temperature have a decrease in the period of diapause development. On the other hand, those initially exposed to high temperature have an increase in the period of diapause development. This suggests that the low temperature may accelerate the rate of diapause development. High temperature is tolerated and even allows the diapause development but prolonged exposure to such temperatures are seemingly harmful. The percentage of pupation shows a decrease if larvae are initially exposed to 25°C for a long time.

Larvae maintained continuously at 25°C will not pupate and only a few will survive after 2 years. Apparently, in the high temperature, diapause is not terminated, therefore, the morphogenesis does not occur at 25°C. The morphogenesis is resumed at the lower temperature. The finding shows that larvae tend to pupate after being transferred to the lower temperature (15-20°C).

Larvae being continuously maintained at low temperature (10°C) will not pupate after 2 years. However, if larvae were initially exposed to this low temperature for a short period (3 months), the low temperature reduced the length of time spent at 15°C. It seems that at low temperature, the development of diapause proceeds but morphogenesis is not allowed to occur. The morphogenesis occurs at higher temperatures. Diapause in U. cupressiana is an adaptation to the environment where insect lives. By being in diapause, the insect's development synchronises with the cold wet South Australian winter. The animal is not only brought to an advanced stage of development in such temperatures but the development of diapause is also favoured by the low temperature. By the end of winter, the larvae are about ready to pupate. Adults start to emerge in mid-spring and the peak of emergence is in the late spring (November). At that time, field conditions favour substantially the reproductive activity of beetles.

From laboratory and potted tree cultures, it was found that larvae start entering diapause in early autumn and some larvae pupate in late winter. Most of them enter diapause in mid- and late autumn (April and May) and start to pupate in early- and mid-spring (September and October). It was also found that a few larvae are still actively feeding in early- and mid winter (June and July) and start to pupate in late winter and early spring and they tend to pupate in early summer. Such larvae apparently have a slow rate of development, so they will be late maturing. Another finding is that larvae may have a prolonged diapause development, particularly those maintained at 15 to 25°C continuously. The length of time spent by such larvae may extend to 36 weeks or even more than 80 weeks and some do not pupate at all. This might be influenced by the nutritional quality of twigs where larvae feed during feeding phase. It is believed that larvae in laboratory culture as well as those collected from the field before maturity may have low quality of nutrition because of the excessive desiccation of twigs. The effects of nutrition on the duration of insect diapause have been demonstrated in Chrysopa mohave (Tauber & Tauber, 1973 in Boyne et al., 1985) and in Platynota idaeusalis (Boyne et al., 1985; Boyne & Rock, 1985).

The RMC of twigs is unlikely to have direct effects on the duration of diapause development, because in experiments 1 to 3, the larvae tested were kept in vials with moist frass. Vials were placed in the container with saturated salt solution, 75% RH. In survival of larvae and

pupae, however, the RMC of twigs has direct effects (see Section 4.2.3.5 and Section 4.2.4.1).

In U. cupressiana, larvae which have annual life cycle (see Section 4.3), apparently have a short duration of diapause development. In laboratory culture, some larvae were found in diapause for 6 to 8 weeks before pupating. It depends on the temperature where they were kept. In 15°C they may enter diapause for 8 to 10 weeks and in 20°C 6 to 8 weeks before pupation.

Conclusion

The following features stand out from the preceding account of the factors involved in the induction and termination of diapause in U. cupressiana. First, diapause does occur on the Adelaide plain from autumn to winter or winter to spring. Second, diapause is not terminated at both high (25°C and above) and low (10°C and below) but it is at moderate temperatures (15-20°C). Third, the optimum temperature for diapause termination is about 20°C (still required further experiments for precise value). Fourth, the prolonged diapause under laboratory condition is more likely to be due to the nutritional quality of the wood food during feeding phase particularly in RMC.

4.2.4 The pupae

4.2.4.1 Pupal development and survival

When fully developed, the larva ceases feeding and enters the prepupal or pharate pupa stage, which lasts 2 to 6 months under normal conditions. From the full-grown larva to the inert prepupal stage the body contracts to about half the larval length, caused by the shrinkage of the intersegmental membrane and the ampullae losing their characteristic form. The head is gradually inclined downwards and the thoracic segments become swollen owing to the appendages beneath having become everted from their sacs. Prior to changing from prepupa to pupa, a considerable quantity of water is discharged through the anus. After the discharge, numerous fat deposits are aggregated, most of which pass on from pupa to the adult.

Towards the end of the prepupal period when the formation of the pupa is complete, the posterior part of the old larval cuticle is pushed backwards as a loose, contracted, and empty sac, by a series of

peristaltic contractions and expansions of the last abdominal segment. Pressure is thus brought to bear upon the anterior end of the larval cuticle. This pressure is further augmented by blood pressure. Consequently, the larval skin continues to be pushed backwards by rhythmic body movements and pushed to the end of the pupal chamber. It requires a few hours to one day or even more for the pupa to shed the larval exuviae completely. Pupation takes place at any time of the day and usually occurs in the pupal chamber.

Sometimes, in an abnormal moult, the larval cuticle splits along the dorsal thoracic region only, not extending to the head. The cephalic region of the pupa cannot free itself from the larval head capsule. The pupa remains attached to the larval cuticle at both ends and, despite its efforts, is unable to liberate itself. Such pupae die.

Three stages of pupal development were recorded: (1) The newly emerged pupa is yellowish or whitish and its eyes are partly pale purple dotted. The number and size of dots increases gradually until the eyes become fully dotted and the dots become dark. This stage lasts from one to 2 weeks or even more depending on temperature and other factors. (2) The spaces between the dots of the eyes gradually become dark, until the whole surface of the eyes become black. This stage lasts from about 2 to 3 weeks. (3) Some parts of the body (mandibles, claws, leg as a whole, elytra, head, thorax, and tip of abdomen) gradually sclerotise to full sclerotisation and to moulting. This stage lasts from about one to 2 weeks. Thus the pupal period varies from about 4 to 6 weeks, depending on temperature and other factors.

Experiment 1. Effect of temperature on the rate of development and survival of the pupae

Pupae were obtained from fully developed larvae that were extracted from field-collected twigs. The larvae were individually placed in a small screw lid glass vial (50x10mm), 3-quarters filled with frass. Before using the frass, it was kept in the oven (60°C) for one week, and before the larvae were placed inside the vials were filled with water and left for about 20 minutes until all the water had been absorbed by the frass. By mean of a needle handle (ca. 4mm in diameter) a hole was made in the frass just beneath the vial wall, for placing the larvae. In each chosen temperature (10, 15, 20, and 25°C) 30 vials were kept and were horizontally placed in the plastic container. The container was covered

with a piece of black cloth. To avoid the condensation in the vials, they were opened weekly. The observations were made every 2 days, until the pupae moulted as adults.

The results presented in Tables 4.21, 4.22, & App. 10 show that at 15°C pupal development is slow, the mean pupal period of male being 38.90±0.50 days (range 36-41, N=10); female, 44.08±0.89 days (range 40-49, N=13) and the number of pupations 78%. At 20°C the pupal development was significantly quicker than at 15°C, the mean development time for male being 19.63±0.42 days (range 18-21, N=8); female, 22,78±0.47 days (range 21-25, N=9) and the number of pupations 48%. There is no significant difference in developmental time of male and female (P=0.05). At 10 and 25°C none pupate (see Table 4.21). This suggests that the larvae of U.cupressiana can pupate just in a narrow range of temperatures. They need moderate temperature to pupate . The definition of low temperature here means below 15°C, moderate 15 to 20°C, and high 25°C. In the field, pupation starts in early Spring (Sept.), occurs mostly in mid to late Spring (Oct. and Nov.) with just a few pupating in early Summer (Dec.). This suggests that pupation occurred when the temperature started to increase from low Winter to moderate Spring temperature (see Section 4.2.3.9).

Experiment 2. Effect of moisture content of wood on the development and survival of the pupae

A group of 30 larvae was treated as in experiment 1. Another group of 30 larvae was placed in the vial with dry frass (no added water). The larvae were then kept continously in 20°C CTR until pupation and adult emergence. The numbers of larvae pupated and adults emerged were recorded.

The results presented in Table 4.23 show that in the dry frass condition the pupal development is retarded or abnormal. A few of them emerge as abnormal adults where the wings are shrunk or torn, and the remaining larvae die before completing development. In the moist conditions however, most pupae develop well, and the adults develop completely and emerge normally (see Table 4.23).

The abnormal pupation in dry condition might be due to the lack of moisture for insect development. It is well known that insect development is inhibited by the lack of moisture. Observations indicated that larvae lost weight drastically after one year maintained in the dry

Table 4.21: Pupal developmental time at different constant temperatures (days)

Stage - Sex		Temperature (°C) 10	15	20	25
I - Male	Mean:	-	13.40 ± 0.27	6.63 ± 0.18	-
	Range:	-	12 to 14	6 to 7	
	N :	-	10	8	
Fenale	Mean:	-	14.46 ± 0.27	7.33 ± 0.17	-
	Range:	-	13 to 16	7 to 8	
	N :	-	13	9	
II- Male	mean:	-	15.60 ± 0.43	7.50 ± 0.19	-
	Range:	-	14 to 17	7 to 8	
	N :	-	10	8	
Female	Mean:	-	16.54 ± 0.58	8.67 ± 0.53	-
	Range:	-	14 to 20	7 to 11	
	N :	-	13	9	
III- Male	Mean:	-	9.90 ± 0.28	5.50 ± 0.19	-
	Range:	-	9 to 12	5 to 6	
	N :	-	10	8	
Female	Mean:	-	13.08 ± 0.69	6.78 ± 0.15	-
	Range	-	10 to 17	6 to 7	
	N :	-	13	9	
Total, Male	Mean:	-	38.90 ± 0.50	19.63 ± 0.42	-
	Range:	-	36 to 41	18 to 21	
	N:	-	10	8	
Female	Mean:	-	44.08 ± 0.89	22.78 ± 0.46	-
	Range:	-	40 to 49	21 to 25	
	N:		13	9	

- no observation

Table 4.22: Developmental threshold temperature (t) and heat unit (degree day) for pupae

Temperature (°C)		MPP	ID	T	HU (D°)
15	male	38.90	2.57	9.9	198.4
	female	44.08	2.27	9.7	233.6
	Average	41.49	2.42	9.8	215.7
20	male	19.63	5.09	9.9	198.3
	female	22.78	4.39	9.7	234.6
	Average	21.04	4.74	9.8	214.6
Average				9.8	215.2

MPP : Mean pupal period
ID : Index of development
T : Temperature
HU : Heat unit.

Table 4.23: Pupal development and survival within moist and dry frass (after ten months)

Trial	N	No.survivors	% pupation	% emergence
moist	30	27	76.7	73
dry	30	6	10.0	6*

* abnormal (see text)

frass condition and just a few of them could survive and pupate. It is obvious that larvae lose their body water in dry condition, resulting in abnormal development or even death of the larvae before pupation. Such cases were also found in the field. Larvae dwelling in the distal dry part of twigs or branches were often found dead. Apparently the distal part of the branch can become too dry for insect development after the branch has been girdled by other larva at the proximal part of that branch (see Chapter 7).

Conclusion

The pupal development depends on the temperature and moisture content of wood. Pupation occurs in a narrow range of temperatures. Moderate temperature is needed for initiating pupation. In the high and low temperatures pupation does not occur. In the dry conditions most pupations are incomplete.

4.2.4.2 Pupal movements

In the field and under laboratory conditions the larvae pupate with their head directed either upward or downward, mostly upward. Some longicorn pupae are capable of ascending and descending their pupal chambers with ease and speed with the help of spines and stout structures on the abdominal tergite. However, in the case of the pupae of *U. cupressiana*, where they are almost quiescent, they appear to react by doing active movements with the tip of the abdomen when they are disturbed. The spines on the tergites might be simply for preventing the delicate pupal integument from becoming bruised by contact with the comparatively rough wall of the chamber.

4.2.4.3 Pupal eclosion

Two or 3 days before the eclosion of the imago, the pupal cuticle becomes loosened from the epidermis of the imago. By convulsive movements of appendages and body, the imago eventually succeeds in rupturing the pupal cuticle. The first rupture occurs at the front of the head, and gradually extends longitudinally along the thorax, the head being freed almost immediately. This is accompanied by similar tears in the cuticle of the legs in the region of the tarsi. At the same time the elytra begin to expand in the dorsal position. With the aid of the

mandibles the adult tries to tear the cuticle on the thoracic appendages. The cuticle is cleared from the pygidium by the hind legs.

The process of eclosion varies in duration, taking 2 to 24 hours. Sometimes in abnormal conditions it takes longer, with the process incomplete after several days. In such a case the adult dies. Within 2 or 3 weeks the adult has become fully pigmented and strongly sclerotised, depending on the temperature and other factors.

4.2.5 The adult

The 2 adult forms are present in both sexes and these forms have been described in the Chapter 3. Newly emerged adults (teneral adults) are still pale in colour and they become fully sclerotised after 2 to 4 weeks or more depending on individual or other factors. The adults remain in mines for 4 weeks or more depending on the teperature and other factors and then emerge after all these processes are complete and all ova mature.

4.2.5.1 The activities of adult beetles

The onset of dusk appears to be a cue for adult activities. Flight, mating, and oviposition take place in the period between dusk and dawn. However, in the captive condition mating can occur any time if male and female contact each other. The activities of the adult U. cupressiana were examined.

The adult emergence

Adults emerging from their mines within the twigs or branches were recorded by using a video-camera. This was done during the peak month (November) of the emergence season. Two sets of recordings were made, firstly with fluorescent light (Philips 36/33 white) (during the day time) and with red light at night; and secondly with red light only provided. The number of emergences was recorded daily. The recordings were carried out under fluctuating temperatures. Ambient temperature and humidity were recorded during observations.

The recording with white and red light provided shows that beetles start emerging from 1700 to 2300h, with the peak hour between 2000 and 2100h. However, in the red light only the beetles emerged early. If the temperature for the previous day was high they started to emerge before noon (1000 to 1100h), around noon, and in the afternoon from 1500 to 2200h,

with peak emergence from 1700 to 2100h (see Fig. 4.11). The number emerging during 1984/1985, 1985/1986, and 1986/1987 is shown in Apps. 11 & 57. The beetles respond to the bright and sunny day. The number emerging increases if the ambient temperature for the previous day is high. More beetles emerge on sunny days with intermediate to low relative humidities. On the other hand, few beetles emerge on cloudy and humid days and very few or no beetles emerge on rainy days.

Males begin to emerge 2 weeks or even more before female beetles, few females appear in the early period of emergence. This might be due to the longer development period of immature stage for the female. In the later part of the period, the number of females is more than males. However, the average ratio is about one to one for U. cupressiana (see Section 4.2.5.3).

During the emergence season no adult beetles were caught in the light trap, even though there were some infested trees around the trap. This suggests that the beetles do not respond positively to the light even on emergence. Ovipositing females also fly very little (see Section 4.2.5.5) suggesting that the species is not vagile. Linsley (1959) pointed out that the infestations of some cerambycids are often characterised by brood trees, i.e. the trees from which the beetles emerge or on which they feed as larvae, and on which they deposit their eggs. Once the trees become infested the borer population builds up rapidly and heavy re-infestation occurs until the host is no longer suitable for larval development.

Laboratory experiments were carried out to discover some aspects of adult emergence.

At each constant temperature room (10, 15, 20, and 25°C) a group of 50 fully developed larvae was kept. They were extracted from twigs and each was put in a screw lid vial (45x10mm in diameter) filled with moist frass. They were kept until they had molted and emerged as adults. Development, molt, and emergence time were recorded every other day. Before emerging the lids of the vials were replaced with a cotton wool plug which was easy for adults to push out.

The results are presented in Table 4.24. This revealed that in 10 and 25°C neither pupation nor emergence occured. In 15°C adults remained in tunnels for longer period (male, 24.63 ± 0.98; female, 51.5 ± 1.72) than those in 20°C (male, 14 ± 0.42; female, 28.13 ± 0.55). There was a large variation in times that beetles remained in the tunnels

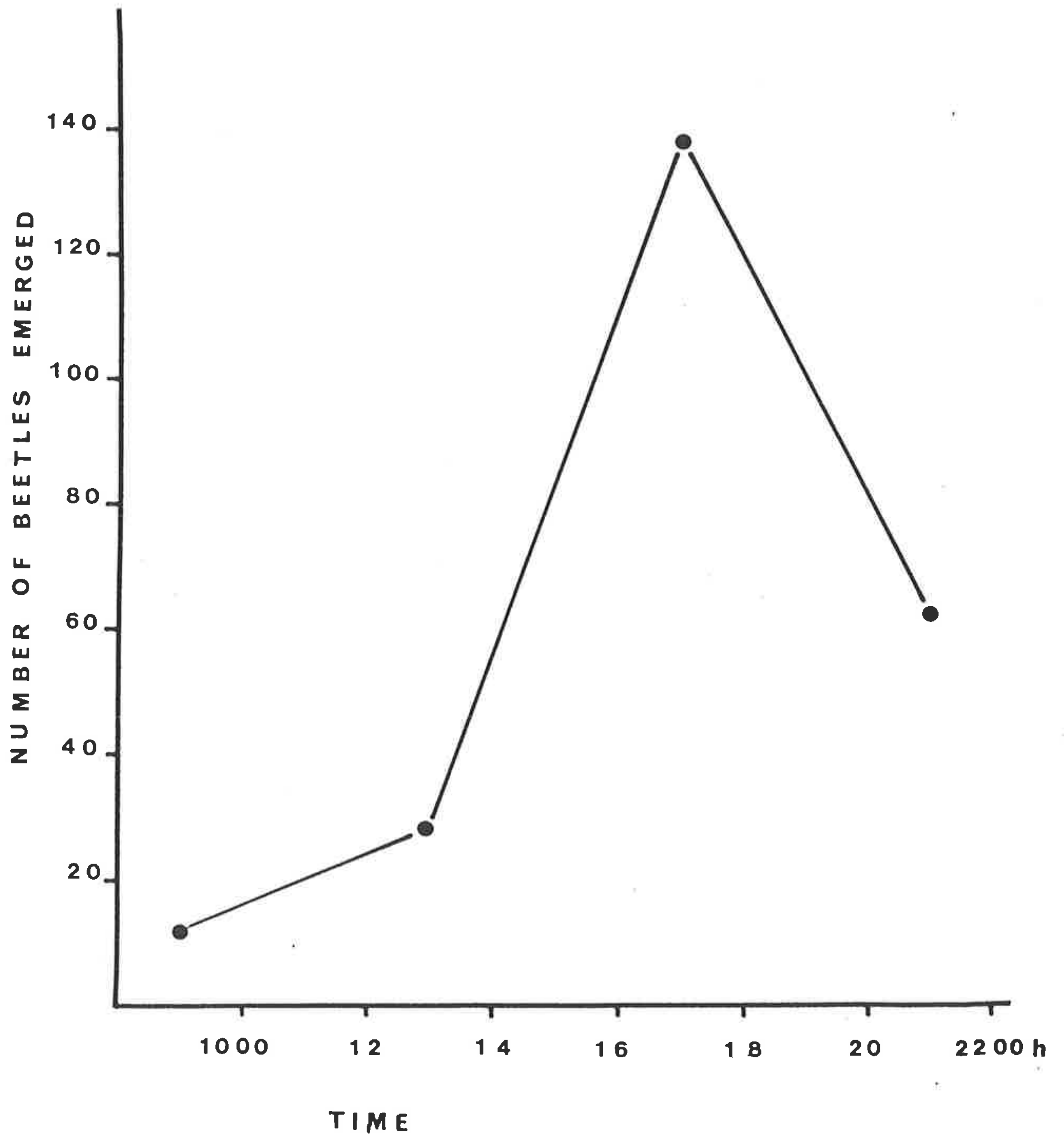
Table 4.24: The period that adult remain in the tunnel at different temperatures

Temperature (°C)	Male (days)	Female (days)
15	Mean: 24.63 ± 0.98	51.50 ± 1.72
	Range: 20 – 28	46 – 60
	N : 12	12
20	Mean: 14.00 ± 0.42	28.13 ± 0.55
	Range: 12 – 16	26 – 30
	N : 12	12

Table 4.25: Longevity of adult beetles on different diets

Diets	Male		Female	
	Mean	Range	Mean	Range
Honey+water	21.3	4-63	12.5	6-18
Water	17.8	14-21	17.2	15-19
Twigs+water	21.2	8-33	11.5	6-16
Twigs	20.0	18-33	10.5	8-12
Pollen	8.0	6-10	10.0	8-14
No diet	6.1	2-11	9.0	2-18

Fig. 4.11: Cumulative number of beetles emerged daily during 1984/1985.


NUMBER OF BEETLES EMERGED
140
120
100
80
60
40
20
1000
12
14
16
18
20
2200 h
TIME

existing in the cool and intermediate temperatures. The length of the period the beetles remained in tunnels decreased sharply from 15 to 20°C. This suggests that temperature significantly affects the emergence time of the beetles. It was mentioned above that beetles respond to temperature in that the number of emerging beetles increases if the temperature increases. Females remained in the tunnel for about twice longer period the males. This suggests that females require a longer time to complete their sexual develoment. The beetles, upon emergence, walk a short distance, make a few flights, and ready to accept mate.

Diel activity

Diel activities of U. cupressiana were examined. The observations were carried out under field conditions in a back yard at Myrtle Bank, very close to the Waite Institute. Ten gravid and mated female beetles were individually placed in a cage with thin nylon mosquito netting covering. They were provided with fresh cut host twigs for laying eggs. The activities were recorded at 30 minute intervals for 24 hours by using a red light torch at night. The observations started when the beetles began to walk, about 1900h. The ambient temperature and humidity were recorded.

The results presented in Fig. 4.12 show that the beetle activities such as walking, probing, and laying eggs started around 1900h and continued non-stop for about 3 hours. The beetles tended to be inactive about 2300h for half an hour and active again by 0100h. The beetles kept still until about 1900h the next day. Activity declined when the ambient temperature was going down and the humidity going up.

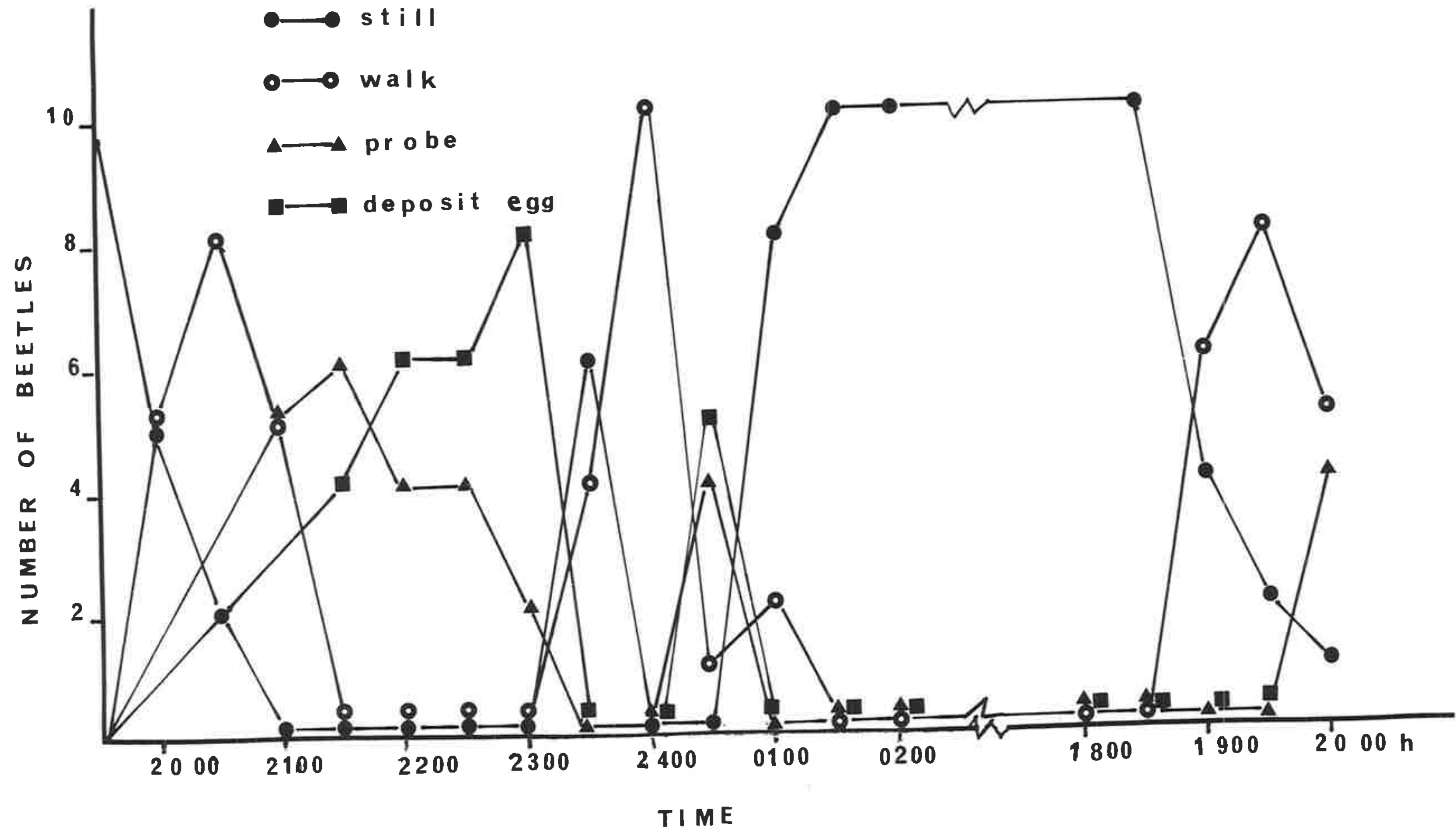
Conclusion

The activity of adult CTB was strongly influenced by temperatures. Beetles are inactive at low temperature.
Male beetles emerged earlier than females.

4.2.5.2 Adult longevity

Little is known of the natural longevity of the emerged adult longicorns. The limited feeding of many species suggests that they are probably short lived. In this Section the longevity of adult beetles of U. cupressiana was examined under laboratory conditions.

Fig. 4.12: Diel activities of adult CTB, for 30 minute interval during 24 hours.



still
walk
probe
deposit egg
NUMBER OF BEETLES
10
8
6
4
2
20 00
2100
2200
2300
2400
0100
0200
1800
1900
20 00 h
TIME

Experiment 1. Longevity and dietary requirements

In each plastic vial a couple of newly emerged beetles were placed. The diet with which they were provided was as follows: Sweet solution (honey+water), water, cypress twigs with sprayed water, twigs only, and pollen (flowers). A control group was given nothing. Each diet was given to 10 couples of beetles. The adult feeding behaviour and life span were observed daily and dead beetles were discarded. The diet was replaced daily. The experiment was carried out under fluctuating temperatures.

The results are given in Table 4.25. The Table shows that beetles given either the sweet solution on cotton wool or water sprayed on twigs, live longer than those on other diets. Male longevity is longer than female. Those with a pollen diet provided spent their time just sitting under the petals during observations and the longevity of both males and females was not significantly different from the control. This suggests that U. cupressiana is neither a pollen feeder nor anthophilous. Gosling (1984b) has listed the flower records for anthophilous cerambycids mostly from Lepturinae and a few tribes of Cerambycidae and Laminae. Tragardh (1930) pointed out that the pollen feeder has head and prothorax tapering gradually forward so as to allow the beetles to insert them into the flowers. It is clear that U. cupressiana beetles are not that type (see Chapter 3). Beetles sipped either water or sweet solution that was provided. This indicates that under field conditions beetles perhaps sip the dew on the twigs in the early morning.

In reviewing the feeding habits of Cerambycidae in general, Duffy (1953) states that the extent to which feeding is necessary, either for survival or for the attainment of sexual maturity, is still an open question. In so far as U. cupressiana is concerned, copulation was observed to commence just postemergence, and females deposit viable eggs within a few hours. Adult of both sexes are, therefore, sexually mature on emergence. Feeding certainly affects survival. As mentioned above, beetles live longer with the addition of either sweet solution or water. It follows that in U. cupressiana: (1) adult feeding is neccesary for survival but not for the attainment of sexual maturity; (2) the main intake is water or dew during the summer. In this last respect, the species would tend to modify Tragardh's (1930) classification, which groups Longicorn feeding habits into 3 groups, i.e. (1) food consisting of pollen and other parts of flowers; (2) food consisting of the green parts of

plants; (3) food consisting of the bark of twigs and branches and leaf-rib; (4) not feeding during their short adult stage. The 4th group might be those feeding on water only.

Experiment 2. Adult longevity in different temperatures

15 couples of beetles were kept in each constant temperature room (15, 20, and 25°C). They were placed in 15 plastic vials, one couple per vial, and provided with fresh cut twigs of Cupressus. The twigs were sprayed with water, beetle life spans recorded, and the dead beetles discarded daily.

The result presented in Table 4.26 show that beetles kept under low temperature lived longer than those kept under higher temperature. Males lived longer than female beetles at 15 and 20/C. At 25/C, however, there is no difference between male and female longevity.

Experiment 3. Adult longevity in different humidities

Ten female beetles were kept in each humidity (32, 42, 56, 74, 80, and >90% RH). They were placed in plastic cylinders 1/3 filled with saturated salt solution and were provided with fresh cut twigs. For supporting the twigs and keeping the beetles from the solution, a circular wire gauze was placed about 3cm above the surface of the solution. The experiment was carried out at 15 and 25°C. The beetle life spans were recorded daily.

The results presented in Table 4.27 show that at both 15 and 25°C the low and high humidities, are unfavourable for the beetles. Adult longevity was just one to 2 days in 32 and >90% RH. However,in the favourable humidity (74%) the adult longevity ranges from 6 to 14 days.

Conclusion

The male longevity is about one 4th of the female longevity. Beetles live longer at low temperatures and suitable relative humidities. Beetles live longer if they are provided water or solutions.

4.2.5.3 Sex ratio

Estimations of the male to female sex ratio are based on the number of emerged beetles under laboratory conditions. The beetles emerged from twigs that were collected in the field during the course of

Table 4.26: Longevity of adult beetles at different temperatures

Longevity (days)	15		20		25	
	M	F	M	F	M	F
Mean	19.7	11.6	14.8	10.2	5.3	6.5
Range	5-39	2-34	3-32	3-18	3-8	2-14
N	15	15	15	15	15	15

M: male
F: female
N: number of beetles were recorded

Table 4.27: Longevity of adult beetles in different relative humidities

Temp. (°C)	L	Relative Humidity					
		31%	43%	61%	74%	80%	>90%
25	Mean	2.2	3.2	4.8	7.2	5.1	1.8
	Range	1-3	2-4	4-7	6-12	4-8	1.2
	N	10	10	10	10	10	10
15	Mean	2.8	4.7	5.9	8.2	5.5	1.6
	Range	2-3	3-5	5-8	6-14	2-8	1-2
	N	10	10	10	10	10	10

L: Longevity in days
N: Number of beetles were recorded

this study (1983 to 1987) (see App. 11). The ratios were: 1983/1984, 0.98:1 (n=240); 1984/1985, 1.22:1 (n=513); 1985/1986, 1.05:1 (n=738); and 1986/1987, 0.86:1 (n=640).

-Test of the sex ratio data

Sex ratio data were tested by using Snedecor's method (Snedecors, 1962) and heterogenity X2 (Zar, 1984). The results show that the ratio males to females was significantly different within any season and during 1984/1985 and 1986/1987 (see Tables 4.28-4.31). Within any season there were significantly more males than females in the early season (September and October) while there were more females in the late season (December and January). As mentioned previously, males emerge earlier than females. During 1984/1985 there were more males than females, and during 1986/1987 there were more females. This suggests that perhaps the population regulates its own numbers by producing more males and more females alternately. It has been argued that sex ratios vary within and between populations, sometimes in such directions and circumstances as to be advantageous to the population (Landahl & Root, 1969; Giesel, 1972; Walker, 1984; etc). The sex ratio in natural populations may alter with numerous factors such as climate, host species, nutritional status (Marshall, 1981), population density (Leigh, 1970; Anderson, 1961; Marshall,1981; Walker, 1984 etc). Regarding sex ratio and population density, Walker (1984) put forwards 3 assumptions, i.e. (1) sex ratio is a population adaptation that stabilizes the population at a favorable density, (2) sex ratio is a population adaptation that produces maximal population growth, (3) sex ratio is a result of selection of genes that maximize individual reproductive success. In the case of the sex ratio of U. cupressiana, however, when the male to female ratios were ploted against the total numbers of the beetles, there was no significant correlation (r=.38, P>.05). This revealed that population density had no effect on the sex ratio of U. cupressiana. It was possibly altered by other factors such as climate and nutritional status. This agrees with Anderson's (1961) statement that in animals with chromosomal and random sex determination and heterogametic males the investigated species (mostly Coleoptera and Diptera) showed no effect of crowding on sex ratio.

Table 4.28: Number of male and female beetles emerged during 1983/1984 and sex ratio *

1983/1984	Sep.	Oct.	Nov.	Dec.	Jan.	Feb	Total
Males	5	36	54	14	9	1	119
Females	0	19	45	36	18	3	121
Total	5	55	99	50	27	4	240
Percentage males	100	65.5	54.5	28	33.3	25	49.58
Ratio males to females	-	1.89	1.2	0.39	0.5	0.33	0.98
Ratio males to 100 females	-	189	120	39	50	33	98

Sept. value not include in calculation
Average percentages of males, 41.26 % which is divergent from the correct 49.58 %
Heterogenity, X2 = 21.117, P < 0.001
* Number of beetles recorded emerged from twigs under laboratory conditions.

Table 4.29: Number of male and female beetles emerged during 1984/1985 and sex ratio *

1984/1985	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
Males	3	96	132	21	30	0	282
Females	0	42	96	51	42	0	231
Total	3	138	228	72	72	0	513
Percentage males	100	69.5	57.9	29.2	41.7	0	54.97
Ratio males to females	-	2.28	1.38	0.41	0.71	0	1.22
Ratio males for 100 females	-	228	137	41	71	0	122

Sept. value not include in calculation
Average percentages of males 49.58 % which is divergent from correct 54.97 %
Heterogenity X2 = 36.244, P < 0.001
* Number of beetles emerged from twigs under laboratory conditions.

Table 4.30: Number of male and female beetles emerged during 1985/1986 and sex ratio *

1985/1986	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
Males	-	90	142	84	63	0	379
Females	-	36	147	103	71	2	359
Total	-	126	289	187	134	2	738
Percentage males	-	71.4	49.1	44.9	47.0	-	51.35
Ratio males to females	-	2.5	0,97	0.82	0.89	-	1.06
Ratio males for 100 females		250	97	82	89	-	106

Sept. and Feb. values not included in calculation
Average percentage of males 53.1 % which is divergent from the correct 51.35 %
X2 = 25.389, P < 0.001
* Number of beetles emerged from twigs under laboratory conditions.

Table 4.31: Number of male and female beetles emerged during 1986/1987 and sex ratio *

1986/1987	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
Males	0	4	214	50	26	2	296
Females	0	0	186	64	84	10	344
Total	0	4	400	114	110	12	640
Percentage males	-	100	53.5	43.9	23.6	16.7	46.25
Ratio males to females	-	-	1.15	0.78	0.31	0.20	0.86
Ratio males for 100 females	-	-	115	78	31	20	86

Sept. and Oct. values not included in calculation
Average percentage of males, 34.43 % which is divergent from the correct 46.25 %
Heterogenity, X2 = 36.000, P <0.001
* Number of beetles emerged from twigs under laboratory conditions.

Conclusion

Sex ratio varied within any seasons. There were more males in the early season and more females in the late season.

4.2.5.4 Potential fecundity

The potential fecundity of adult beetles of U. cupressiana was examined. The potential fecundities were determined from the total number of deposited eggs and from the mature eggs remaining within the abdomen. The latter were counted by dissecting the abdomen of both parous and non-parous females shortly after the day of death. The body weight and size of the beetles were recorded. Size was measured as length and width by means of a pair of vernier calipers (accurate to 0.05mm).

The eggs remaining within the abdomen of the dead female beetles are always in mature condition, so it is possible to determine the actual potential of the species. The mean potential fecundity of the U. cupressiana is 47 eggs (range 16-96). This correlated with body weight and size ($P<0.01$) (see Table 4.32, Figs. 4.13-4.15, & App. 12). The larger the beetle the higher the potential fecundity. Every milligram increase in weight produces 2 more eggs. The mean actual fecundity (the mean number of eggs deposited by a female) is 22.60 ± 2.40 eggs (range 0-94).

4.2.5.5 Oviposition

Typologies for cerambycid oviposition have been grouped by Tragardh (1930) and have been developed by Butovitch (Duffy, 1953; Linsley, 1959). It is stated that there are 2 major types of oviposition habits. The first is: oviposition exclusively with the aid of the ovipositor, either (a) on the bark or outer surface of the host or (b) in the bark cracks or under bark scales or (c) in cracks and crevices in the wood or (d) in entrance, emergence or ventilation holes of other insects or (e) in the soil or (f) on the surface of various objects other than the host. The second type is: oviposition with the aid of the ovipositor and mandibles, either (a) in egg niches without special preparation of the substrate or (b) in egg niches cut by the mandibles or drilled with the ovipositor with special preparation of the substrate. In the case of U. cupressiana, the females deposit their eggs on the bark. This behaviour places the U. cupressiana in the oviposition category (a) of the first type

Table 4.32: Potential fecundity in relation to body size and weight

Statistic	Number of eggs	BW (mg)	BL (mm)	BWth (mm)
Mean	46.92	58.03	16.9	2.8
Range	16-96	20.5-122.0	12-22	1.5-3.8
SD	18.769	22.769	1.951	0.549
N	34			

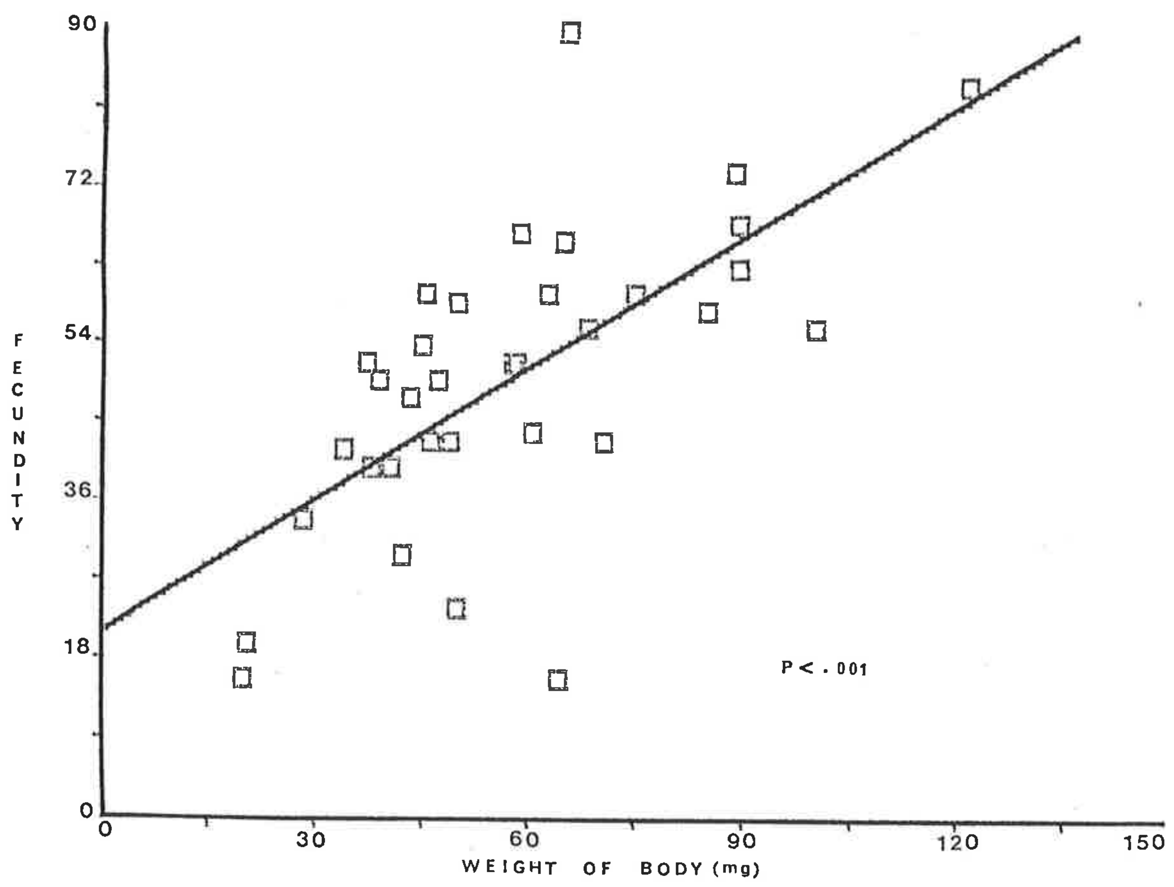
BW : Body weight
BL : Body length
BWth : Body width
N : Number of beetles were recorded
SD : Standard deviation.

Table 4.33: Larval density and survival within potted tree of C. sempervirens

Density (no. of larvae)	N	No. of survivors	Percentage
1	10	9	90
2	20	12	60
3	30	10	33

Fig. 4.13: Correlation between potential fecundity and body weight ($P < 0.01$).

Fig. 4.14: Correlation between potential fecundity and body length ($P < 0.01$).


90
72
54
36
18
0
F E C U N D I T Y
0
30
60
90
120
150
WEIGHT OF BODY (mg)
P < . 001

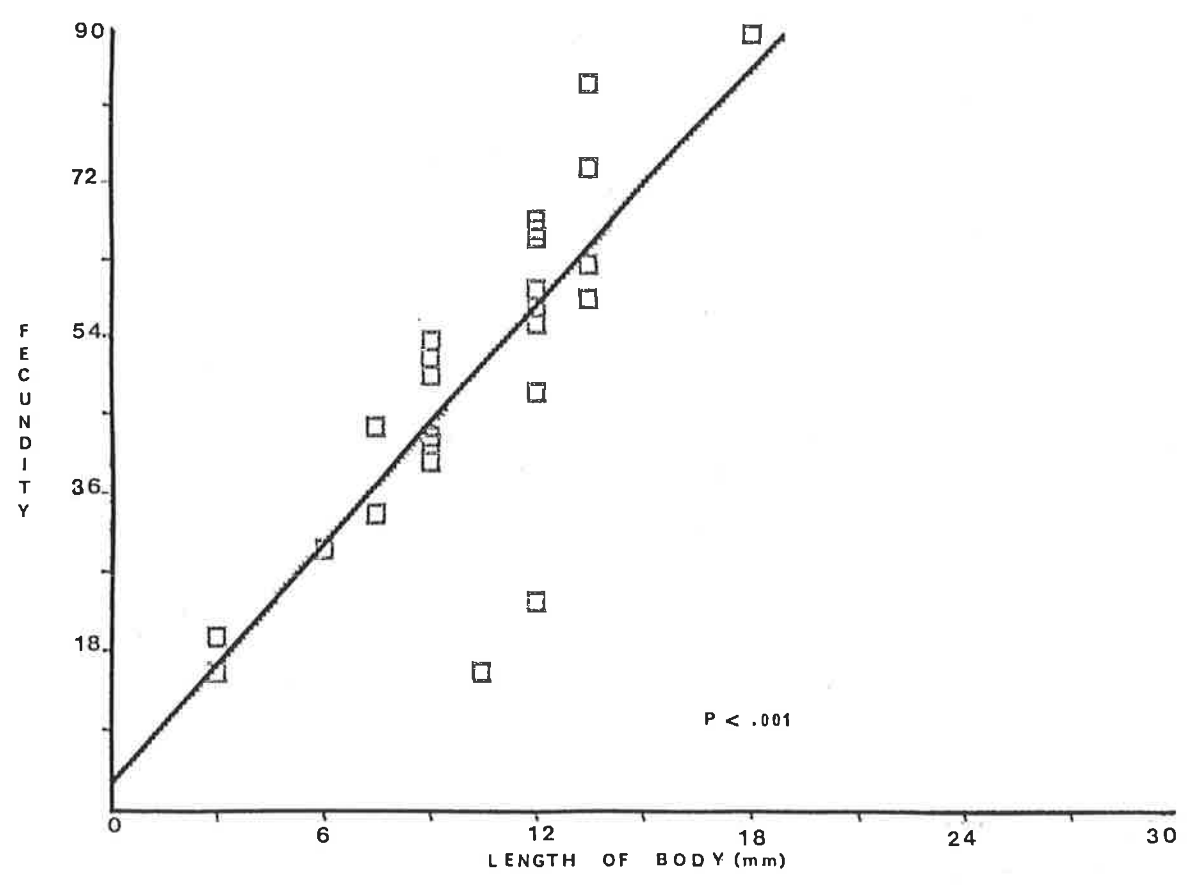
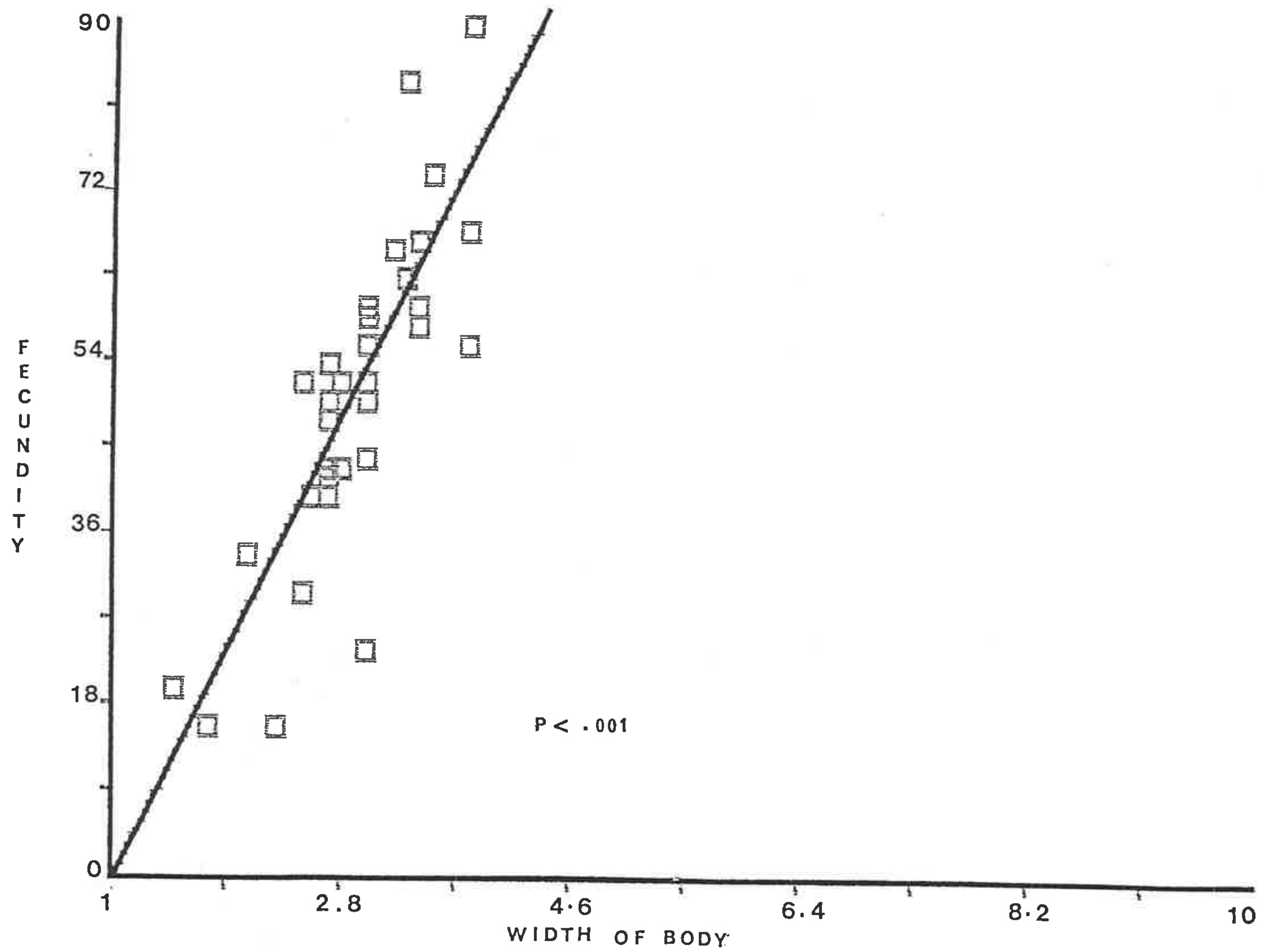

90
72
54
36
18
F E C U N D I T Y
0
6
12
18
24
30
LENGTH OF BODY (mm)
P < .001

Fig. 4.15: Correlation between potential fecundity and body width ($P < 0.01$).


90
72
54
36
18
0
FECUNDITY
P < .001
1
2.8
4.6
6.4
8.2
10
WIDTH OF BODY

where eggs are deposited on the bark or outer surface of the host by the ovipositor.

Temporal pattern of oviposition

Both laboratory and field caged pairs of U. cupressiana were used to study various aspects of the temporal pattern of oviposition. In the laboratory each pair was kept in a cylindrical plastic container (25x15cm in diameter) after copulation. They were provided with fresh cut twigs of Cupressus sempervirens for egg oviposition. Beetles were obtained by rearing from infested twigs that were collected from the field. In the field, pairs of beetles (one to 2 h after copulation) were transferred to field cages. Each pair was placed in the one cage which was provided with 4 Cupressus potted trees. The cages used were plastic gauze cages about 1.5x1.5x1.5m. The number of eggs was counted daily and the oviposition periods and temperature were recorded.

Observations revealed that females mate and deposit eggs shortly after emergence. The oviposition period varies from 2 to 7 days depending on temperature and individual variation. Normally it ranges from 2 to 3 days at about 20 and 25°C. At the peak of oviposition eggs are deposited in quick succesion at intervals of less than a minute (30-45 seconds) to 2 minutes. Without exception, eggs are deposited at night (see Section 4.2.5.1). The highest number of eggs deposited by a female was 94 and the minimum one, or even none, depending either on temperature or individual variation or failure to copulate effectively (see Chapter 5). Usually beetles deposit a high number of eggs on the first night, most of the remaining eggs on the second night, and just a few on the third night. Occasionally, a beetle will deposit a very few on the first night and the remaining eggs on the second and third nights.

Dick (Blake, 1961) has grouped the oviposition cycles of Coleoptera into 4 distinct types:

(1) species which live only a short time as adults and deposit all their eggs within a few days,
(2) species of which the adults live a long time and produce eggs continuously,
(3) species which during one season deposit eggs in batches of fairly short intervals of time,

(4) species which deposit more or less continuously in 2 or more seasons separated by a period during which oviposition ceases. As mentioned above the oviposition period of U. cupressiana ranges from 2 to 3 days after emergence. This indicates that U. cupressiana is an example of the first group.

Spatial pattern of oviposition

The spatial pattern of oviposition of U. cupressiana was investigated from field potted trees of C. sempervirens that were exposed to the beetles as mentioned above. Observations revealed that females responds to small twigs. The favored site for egg deposition was either the angle between the petiole of needle and twig or the angle between twig and stem, or between twig surface and bark scale like leaves. Eggs were also deposited on the twig surface only, usually singly but occasionally in groups of 2 or 3. My observations on 135 twigs on 24 potted trees indicated that females deposit almost all their eggs singly, primarily on twigs 2.10$\pm$0.05mm (range 1.4-2.7mm) diameter, between 7 and 30cm (14.91$\pm$0.33) below the tips of the twig. Apparently the area more than 30cm below the twig tip is difficult for the larvae to bore into. This is because also, the larvae usually tunnel distally about 8.06cm (see Chapter 5) after penetrating, where they turn back and tunnel downwards to the stem or main branches. On the potted trees females deposited significantly more eggs at mid and lower parts than at upper parts of the trees ($P<0.01$; Tukey Test) (see App. 13). Apparently the females deposited their eggs more frequently and rapidly at the lower parts, the peak of oviposition being where the eggs were deposited in quick succession at mid parts of the trees. The interval of oviposition becomes longer and egg-depositing less frequent until the female ceases to deposit eggs at the upper parts of the trees. There is evidence that beetles released in the centre of the cages flew immediately to the trees. From the twig or branch they walked downwards to the stem and continuously walked to the base of the tree. Occasionally they walked on the ground and came back again to the base of the tree. They crowled upwards slowly, touched either the stem or the twigs which were encounted from the base to the tip of the tree with their ovipositor, and also with the long bristles on the tip of their abdomen. Apparently the beetles walk upwards and touch the twig surface while depositing eggs. Sometimes the searching procedure takes up to 30 minutes or more, depending on the how quickly the first egg deposition occurred.

Conclusion

The mean potential fecundity of U. cupressiana is 47 eggs ranging from 16 to 96. Potential fecundity is correlated with body size and with weight. Oviposition is on the bark, normally 2 to 3 days after beetle emergence. Twig size preferred for oviposition is about 2mm and between 7cm to 30cm below the tip of twigs.

4.2.5.6 Scent emission

Apparently several species of the cerambycinae emit a powerful scent. The aromatic glands are located on the metasternum near the coxa (Linsey, 1959, Duffy, 1953). The adult beetles of U. cupressiana can emit or produce scent or a strong smell when suddenly disturbed or taken from the rearing container, so it may be a defensive action unassociated with sex attraction.

4.2.5.7 Sound production

Adult beetles, both male and female, of U. cupressiana posess the power of stridulation. When a pair of beetles was kept in a mating container, often the male would stridulate, raising his body to the full extent of the legs, before courting. The sound may be produced by rubbing the posterior femora against the edges of the elytra.

4.3 SEASONAL OCCURRENCE

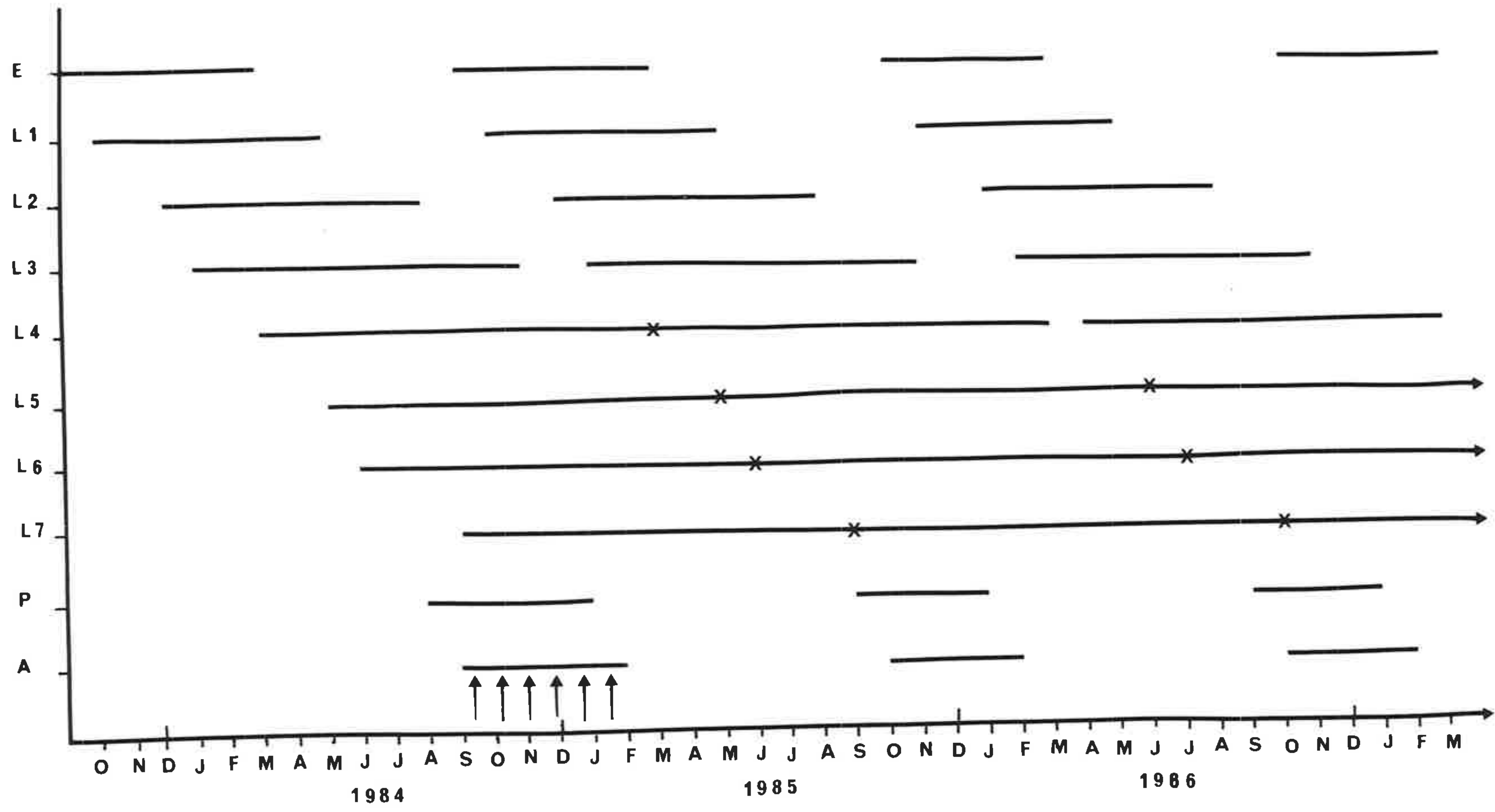
U. cupressiana has a 1-year (annual) and 2-year (biennial) life-cycle, and the times of occurrence of the different stages during the year are rather similar (see Fig. 4.16).

Adults - Adult activity takes place in spring and summer (late September or early October to early February). They start emerging in late September or early October. The peak of emergence is in November. The number emerging decreases sharply in December and January, and just a few emerge in early February.

Eggs - As mentioned previously, shortly after the beetles emerge they mate and lay eggs. The incubation period of eggs is about one month, so the eggs could be found from October to early March.

Fig. 4.16: Seasonal occurence of U. cupressiana (eggs, larvae (L1 to L7 including prepupae), pupae, and adults) from 1983 to 1987.

[A, adults; E, eggs; L1 to L7, larval instars 1 to 7 including prepupae; P, pupae; arrows indicate population derived from current generation (N1)].


E
L1
L2
L3
L4
L5
L6
L7
P
A
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
1984
1985
1986

Larvae - First instar larvae (L1) are found from November to early May. Second instar larvae (L2) could be found from late December to late August, and the third (L3) from late January to November. There is a 2 month gap between L3 of successive generations. The L4 could be found from March to March of the next year, i.e. with no gap (or a gap of less than one month) between generations. L5 could be found from May to July of the next year, overlapping with L5 of the next generation. L6 runs from June to November of the next year, overlapping with the L6 of the next generation by 6 months. L7 runs from September to May over the next 2 years, overlapping with the same instar of the next generation. Therefore L1 to L3 could be found from January or February to May, while L4 to L5 could be found any time of the year. The larval period lasts from 12 to 22 months or even more, depending on the moisture content of the wood.

Pupae - Pupation begins in late August or early September, i.e. lasts one month for individual but this is the population. Pupae could be found from late August or early September to January the following year (see Figure 4.16). Both L6 and L7 may pupate.

Length of development - In laboratory conditions, eggs deposited in November 1984 gave rise to 9 adults in December 1985. The other 47 survivors emerged as adults between November 1986 and February 1987. From eggs deposited in December and January 1985/1986 no adult emerged during the emergence season in 1986. In the field cage eggs deposited on the potted trees in October and November 1984 gave rise to 3 adults in December 1985 and another 29 in November and December 1986. Eggs deposited in December 1985 and January 1986 develop into 22 L5 , 36 L6, and 37 L7 in March 1987. All larvae were still actively feeding (not fully developed). Thus, part of the population appeared to have a one-year life cycle and the other, a 2-year life cycle. The proportion with the one-year life cycle was rather small (9-16%).

Evidence was found that the time of oviposition is important in determining whether a larva can develop in one or 2 years. Data showed that the oviposition period was quite long, spanning a period from late September or early October to early February. Some of the larvae from eggs deposited early in the period pupated after one winter's feeding, and emerged in early summer. Those from eggs deposited later in the period did not. The latter required one more summer feeding and prepupated in

the second autum to late winter. Most larvae, from eggs deposited either earlier or later in the period started pupating early in the second spring and emerged in mid to late spring or summer. Perhaps both spring and summer temperatures are the key factors which determine the proportions of the population with one- and 2-year life cycles. Spring temperature may determine the time of pupation and emergence, which would in turn affect the time of oviposition. Extended periods of cold and warm weather any time in spring could also slow down or speed up development of the first year.

Conclusion

The length of the life cycle seemed to depend on when the egg was deposited during the long oviposition period. Some larvae from eggs deposited early in the period emerged in the following spring or summer (one year). The rest of the larvae emerged in the second spring or summer (2 years). The current growth (N0) population is derived from current generation (N1) and previous generation (N2) (counting backwards).

4.4 FACTORS AFFECTING THE BIOLOGY

4.4.1 Natural factor control

Before considering the natural agencies which exercise control over this species in South Australia, it was necessary to review the observations of other workers on cerambycids. Nothing has been recorded on this or any other species of the genus Uracanthus.

Mortality in cerambycid populations from biotic and physical causes may be high although published quantitative data are relatively few. Linsley (1959) noted that 25% mortality of eggs of Saperda calcarata Say was caused by infertility, climatic conditions, and other physical causes; 18% loss was attributed to parasites (Iphiaulax and other Braconids). 29% loss occurred among L1 and L2 as a result of climatic conditions, unsuitable or insufficient food, predators, and excessive sap flow. Further, mortality in L3 and L4 was caused by a combination of hymenopterous parasites, and wood-peckers. In S. inornata (Grimble & Knight, 1970), Enderus lividus (Ashmed) (Eulophidae) is the principal parasite of the early stage of the larvae. Of the Braconids, Meteorus cognatus Muesebeck, Iphiaulax eurygaster Brulle, and Cenocoelius sanguineiventris Ashmed are solitary ectoparasites and Bracon spp. are gregarious ectoparasites of larval S. inornata (Grimble & Knight, 1970) and

S. concolor (Mecleod & Wong in Grimble and Knight, 1970).

Duffy (1953) and Linsley (1959) recorded a number of parasites and predators, but among the most effective natural enemies of the cerambycids are predaceous Coleoptera such as Cucujus (feed upon adults and larvae); Tenebroides and Temnochila (ostomids); numerous clerids (Cymatodera, Thanasimus, and Chariessa); and elaterids (Alaus, Hemirhipis and Stenagostus).

Little is known of the role of parasitic Diptera and Hymenoptera in reducing the longicorn population. However, Elliot and Morley, Kleine in Linsley (1959) have listed a number of parasitic Hymenoptera which were reared from various European cerambycids and Chittenden (Linsley,1959) has recorded a number of parasites of North American species. Most of them are in primitive groups such as members of the Braconidae (Xordini and Acaenithini) and several groups of Ichneumonids. Of the Ichneumonids, 3 species have been recorded by Grimble and Knight (1970) as solitary ectoparasite of S. inornata, i.e. Dolichomitus messor perlongus (Cresson), D. populneus (Ratze burg), and Xylophrurus bicolor (Cushman). In addition, 3 other species as well the species as mentioned above have been recorded by McLeod & Wong in Manitoba and Saskatchewan, the remaining 3 species, i.e. Cubocephalus contiaclus Townes and Gupta, C. prolixus, and Dolichomitus sp. (Grimble & Knight, 1970). Parasitic and predatory Diptera such as Asilids and Rhagionids feed on larval cerambycids: Sarcophagids and Tachinids parasitise both adults and larvae. Two species of flies have been recorded parasitising S. inornata (Grimble & Knight, 1970) and S. concolor (McLeod & Wong in Grimble & Knight, 1970), i.e. Lixophaga sp. (Tachinidae) and Odinia sp.

Among the Hemiptera, the ambush bug (Phymata) (Balduf, 1939 in Linsley, 1959), the reduviid Arilus cristatus (Hahn), Margasus afziela Stal, and Rhinocorus nitidulus (Fabricus) (Linsley, 1959) all feed on adult cerambycids.

The nematode, Bradynema strasseni Wulker, has been reported as a larval parasite of Rhagium and adults are commonly infested with mites and pseudoscorpions (Linsey, 1959).

Among the birds, woodpeckers, creepers, flycatchers, nighthawks, vireos, nuthatches, and warblers have been recorded feeding on adult cerambycids (Duffy, 1953; Linsley, 1959; Solomon, 1972 and 1974, and Grimble & Knight, 1970).

Apparently little has been recorded of diseases of cerambycids. However, some fungi have been recorded that can attack living individuals, such as Beauveria bassiana (Linsey, 1959), Isaria and Entomophthora (Duffy, 1953).

The objective of the work reported here was to determine the identities and impact of the natural control agents on the cypress twig borer in South Australia.

Attacked twigs of C. sempervirens were collected from several locations in the Adelaide Plains at various times from 1983 through to 1986. They were placed in the rearing containers (plastic garbage bin) and were kept in the insectary, where they were sprayed with 5% salted water once a month. During the emerging season the emerging parasites and predators were removed from the bin and identified, and their actions were recorded. After the emerging season the insects remaining in their mines were extracted and cases of parasitism were recorded. Observation on acts of parasitsm or predation were made in the laboratory. Larvae and adults suspected to be predators or parasites were caged with various stages of U. cupressiana and observed. Diseased larvae and pupae were observed. Also once a month some sample twigs and branches were also collected from the field and immediately dissected, cases of parasitism were recorded.

During the course of this study the following records of natural agencies that may have a direct or indirect effect in controlling population numbers:

Insect parasites: - Three parasitic Hymenoptera were recorded from rearing. Braconids (Heleoninae: Cenocoelini, unidentified genus and species) (Austin, per. comm) were found by extracting them from the Uracanthus mines. The species attacks the L3 To L5 and pupates in prepupae or pupae of Uracanthus. From one host 3-6 parasitic pupae were found. Their size varies depending on the number of pupae within a host and the small pupae tend to become male adult parasites. The pupal stage lasts from January to October, and pupal periods vary from 6 to 10 months. The adult parasites under laboratory conditions emerge from July to October, and adult longevity varies from 3 weeks to 2 months when fed with honey. The sex ratio of male to female was 1:2. In the field the mortality of U. cupressiana caused by this parasite was about 6%. Cleonymus sp. (Pteromelidae) was found in the rearing bin and emerged during the emergence season of the Uracanthus. They were caged with eggs and various stages of Uracanthus larvae, but nothing happened during

observations. When the twigs from which they had emerged were extracted, the larvae or pupae of Uracanthus still survived or had emerged as adults with the emergence hole as evidence. It suggests that Cleonymus sp. are not parasites of Uracanthus, but might be parasitising the associated cerambycids (Bethelium tillides Pascoe and 2 unknown species). Bethelium tillidae were numerous in the rearing bins as a secondary pest on the dry twigs of cypress after the twigs had been cut by U. cupressiana (Morgan personal communication).

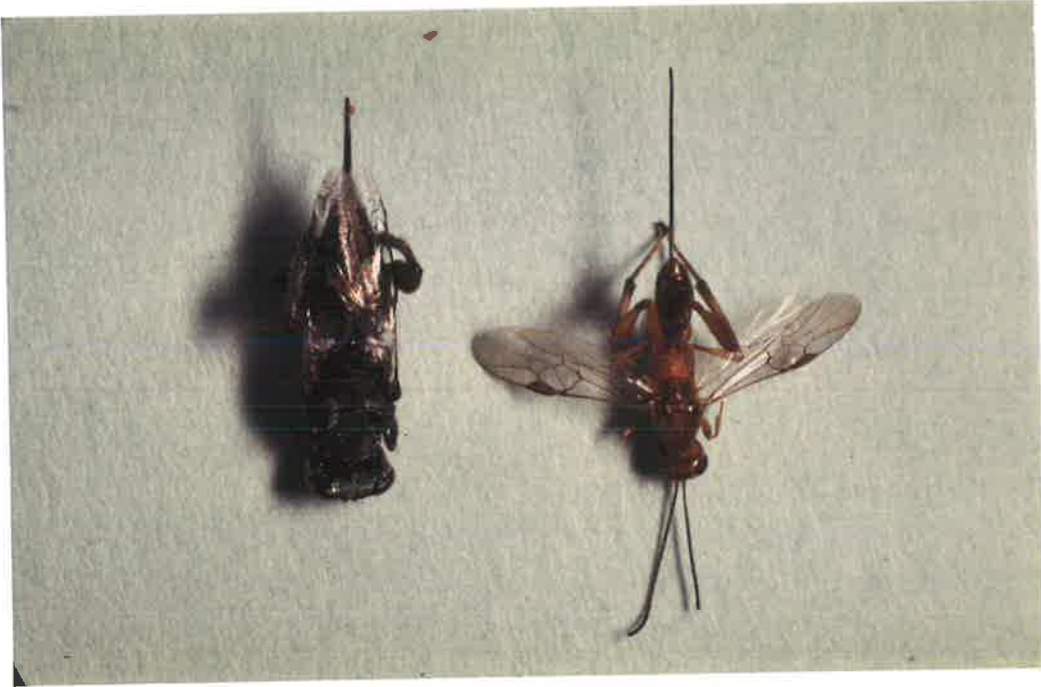
Another wasp parasite (Chalcidoidea) was found by dissecting the twigs and the mines of L3 and L4 instar larvae of Uracanthus. The parasitic female deposits her eggs in a mass within the Uracanthus mine. The egg mass blocks the mine, and the eggs develop to larvae and parasitic adults within the mine while the host is still actively feeding within the same mine. The role of this parasitic insect upon Uracanthus population is still not known. According to Morgan (personal comm.), it is a parasite of a woodboring weevil in Cupressus.

Predators: - Two species of clerid predators were found. The emerged adults were found in the rearing bin, and the mature larvae were walking around in the container or sitting in the mine of Uracanthus. Mature larvae of the predators were caged with L3 and L4 of Uracanthus that were still in their mines. Once a predator larva had eaten one or 2 Uracanthus larvae, it became quiescent with a swollen abdomen for about a month, and it did not respond to the presence of prey until its abdomen was back to normal. It does not feed on mature instar (L6 and L7) of prey. Young instars of predator larvae perhaps feed on young instars of prey. The adults feed on associated cerambycid beetles or they feed on each other if caged together.

In the field, the mortality of U. cupressiana caused by the clerids predator was about more than 10%. This figure is based on extracted twigs collected from several locations in the field.

Other predatory insects such as earwigs and black ants were found wandering within the mines of the cypress twig borer. The earwigs, when fed with Uracanthus larvae, immediately hold the larvae and feed on them. They can eat 2 of the L3 to L5 a day but if they are fed a mature larvae (L6 or L7) just one larva is eaten or sometimes only half of the larval body. As with the predatory clerids, once the earwigs have enough feeding they become quiescent for a long time (one to 2 months) and do not respond to the presence of prey. It is evident that earwigs have a role

Plate 11: Parasitic wasps: Braconids, Heleoninae, Cenocoelini, unidentified genus and species; and _Cleonymus_ sp, Pteromelidae. Predator clerids that associated with _U. cupressiana_.



in decreasing the population of *Uracanthus*. In the field, loss due to this predator is still unknown. There is still no evidence relating to the role of the black ants in decreasing the population of the borer.

The role of birds as predators is still unknown, although several species of birds nested on the trees that were attacked by the cypress twig borer.

Disease: - During the course of these studies no pathogens which play an important role were recorded. Under laboratory conditions, very few dead larvae were found covered by fungus or other pathogens. The fungus may have grown after the larvae died because the fungus not only covered the larva but had also grown along the mine. Eggs kept in high humidity (90%) all died covered by fungus. Such conditions would not occur in the field because the eggs are deposited by females in spring and summer, when the humidity is very low in South Australia (Adelaide). Dead larvae covered by fungus are very rarely found in the field.

In terms of numbers, voracity, and searching abilities, clerid predators are obviously the most important natural enemies of the cypress twig borer.

Cannibalism: - The tendency towards cannibalism among larvae of the species was very low in the field. Even on the severely attacked trees cannibalism was about one to 2% because, of course, the female beetles deposit their eggs individually on the bark. However, in the captive condition where they were provided with young potted trees for oviposition sites, they deposit their eggs in groups or individually but only a short distance apart. Cannibalism frequently happens when the larval mines connect to each other. Sometimes larvae died with damaged heads, and sometimes larva with only the head left were found.

Physical factors: - The influence of physical factors, particularly temperature and humidity, have been partly discussed in the previous Section on immature stage development. Their effect on the adult stage, particularly on their activity, will be discussed in Chapter 5.

4.4.2 Moisture content of wood

Studies of the ways in which the moisture content of wood influences the biology of *U. cupressiana* have been discussed in the previous Section (4.2.3.5, 4.2.3.6, & 4.2.4.1).

4.4.3 Density of larvae

Infestations of cypress twig borer, as in other species of Cerambycidae, are often characterised by brood trees, i.e. the trees from which the beetles emerge or on which they feed as larvae, and on which they deposit they eggs. Once such trees become infested, the borer population builds up, and heavy reinfestation occurs. The larger the tree size, the larger the population (see Chapter 6).

In infested twigs that were collected from the field from such trees, 2 to 3 larvae were often found in one big twig or branch. Usually the larvae in the upper part of the twig do not survive because the wood dries out after the larva in the lower part of twig has girdled the twig. The effect of larval density on the biology of the cypress twig borer was examined.

Experiment 1. Effect of larval density on larval survival of Uracanthus.

30 young potted trees of C. sempervirens were exposed to the female beetles for depositing their eggs. After 2 months, the trees were grouped into 3 groups of 10 trees. In each tree of the group 1 the wilting twigs that had been cut by the young larvae were removed except one infested twig which was left on the tree. On each tree of the group 2, 2 twigs were left on mid- and upper parts of the tree. In the group 3, 3 twigs were left, respectively at upper, mid and lower parts of the tree. After 6 months all the dry parts of the twigs were taken and the larval survivors were counted. The trees were grown in the Rockpile (20-25°C, 14/10 L/D).

The results (Table 4.33) show that in trees with 3 larvae few can survive, while in trees with one larva only, most larvae survive. One died covered by oleoresin. These figures suggest that the density of larvae can directly affect the mortality of larvae by cannibalism, as indicated by interconnecting larval mines with no dead larvae except some parts of larval heads. Furthermore density affects mortality indirectly when the larvae have girdled the proximal parts of twigs or stem of young potted trees, hence causing unfavourable conditions for larval growth or even the death of the other larvae as indicated by a few dead larvae in dry conditions at the upper parts of the stem.

4.4.4 Host plant defence

This subject will be broadly discussed in Chapter 7.

4.5 THE DEVELOPMENT OF LIFE TABLES FOR U. CUPRESSIANA

The method used to develop the life tables of U. cupressiana was essentially the same as that of Morris and Miller (1954), Morris (1963) and Harcourt (1963). In these studies 2 life tables of U. cupressiana were obtained (see Tables 4.34 & 4.35). They were based on laboratory, field cage, and field studies. Population was recorded on the 112 potted trees from peak of oviposition (November) to emergence season (Oct., Nov., and Dec.) over the next 2 years. The potted trees were exposed to the beetles for depositing eggs in the field cages. Four potted trees were placed in each cage and 2 pairs of newly emerged beetles were released. After completing the oviposition, the cage covers (made from plastic gauze) were removed. So, the eggs and remaining stages were exposed to parasites and predators. In the field (Adelaide Plain) the population was sampled on the trees on the all permanent ecological plots (in zone 4, see Chapter 6). Six developmental stages were recorded on the potted trees and as well those which were sampled from field for construction of the life tables of U. cupressian: (1) eggs on potted trees and eggs to L1 on the field trees, (2) larvae, L1 to L2, (3) larvae, instar L3 to L5, (4) larvae, L6 to L7 include prepupae, (5) pupae, and (6) adults. The remaining periods within the life tables are not true age intervals but subdivisions developed within the life table to account for certain variables that have an effect on the population trend. The variables: (a) sex ratio, when the proportion of female is less than 0.50; (b) fecundity, when the mean fecundity is less than 22 (mean actual fecundity); (c) adult mortality.

The method of studying each age interval may be outlined briefly as follows:

- Eggs

lx was based on direct sampling of the population at the completion of the oviposition. The proportion that fail to hatch due to desiccation or infertility was not difficult to determine either by rearing about 200 eggs for each generation or observing the eggs laid on the potted trees. The dx value was obtained from the percentage that were infertile, desiccated and hatched but which had failed to bore the twig because, for example, the eggs had been deposited on an unfavorable site, or because they were covered by oleoresin when the young larvae had just started to bore the bark of the twigs. In the field, the lx value of the eggs to L1 was obtained by adding the total value of dx from potted trees (it is

assummed that dx value from potted trees equal to that from the field) with lx value of L1 to L2. It is difficult to record the numbers of eggs on the field trees since they were deposited individually by female.

- Larvae, L1 to L2

lx was presented simply by the number of eggs which hatched successfully (L1) and the number of small larvae that (L2) had established in the twigs after a 2 month hatching. It was not difficult to determine by counting the dry twigs on trees. The survival rate during this age interval was low, indicating that the excessive oleoresin flow can have an important role in decreasing the population. No mortality was caused by parasites or predators during this age interval.

- Larvae, L3 to L5

lx, the number of larger larvae was based on the sampling of the population that had established in the branches or stem of the potted trees after about 3 months of the establishment of the L1 (March to June). Mortality (dx) due to cannibalism was obtained by collecting and extracting the twigs. Loss of larvae (in twigs or branches) blown down by the wind could be found by counting the fell of twigs or branches. Furthermore, the excessive oleoresin flow was considered to be a more important agent. For parasitism by insect parasites and predators, 100qx was obtained by collecting and rearing them from host larvae.

- Larvae, L6 to L7

The value of lx for this age interval was obtained by direct population sampling. On potted trees the value was determined by counting the number of emergence holes that had been constructed by the fully developed larvae before prepupation. Total dx value was found by substacting lx value of pupae from lx value of L6 to L7. The establishment of dx value for the individual dx factor operating during this period was obtained by either collecting and rearing larvae in the laboratory or collecting and extracting the infested dry twigs after the emergence season.

- Pupae

The value of lx was established by the direct population sampling of the pupal cases in March after the emergence season. Examination of the cases supported by data from collections and rearing of pupae before emergence provided the value of dx. Parasitism had occurred from L6 and L7, but the effect was obviously seen in this period.

- Beetles

lx was represented by the number of pupal cases showing that successful adult emergence and sex could be determined from the same cases. In this example the abnormal sex ratio was applied. It was distorted in favor of males, so it is considered to be a mortality factor.

- Females

lx was the percentage of females applied to lx for beetles. The result was doubled, of course, to maintain balance in the life table. Reduced fecundity either due to reduced body size or mating failure might be considered to be a mortality factor.

- Normal females

lx, represents the number of normal females capable of depositing a normal complement of eggs. It was a hypothetical figure but in the present example correspond to the actual number of females.

- Expected eggs

lx, the number of normal females (in this case 9 and 3.67) is multiplied by 22 (mean oviposition per female).

- Actual eggs

lx was determined by direct population sampling at the beginning of the next generation. 100qx attributable to adult mortality was based on the difference between actual and expected eggs.

- Trend index

This was simply lx for eggs of the new generation expressed as a percentage of lx for the old. In this present example, mortality factors had combined to cause a decline or incline in the population trend.

- Generation (survival within generation)

The generation survival with the effects of adult (female) mortality could be obtained by rearing the beetles in the laboratory to determine some factors affecting the beetles, such as mating failure, or female mortality either before oviposition or after a portion of the eggs were deposited.

The construction of the life tables of U. cupressiana can be seen in Table 4.34 and 4.35. The survival rate (lx), death (dx), and death-rate curves were made, based on the life table in Table 4.34. along with supplementary information on the rate of development (see Fig 4.17). In studying these Tables it can be noticed that survival rates of both populations were varied within any developmental stages. The greatest

mortality was in young larvae (L1 to L2) when the newly hatched larvae started to penetrate the host. It was obvious that there was a key factor (see Chapter 8) operating in each developmental stage. These following key factors were considered to play a role in decreasing the population of U. cupressiana:

- Key factor in young larvae (L1 to L2)

The major mortality factor operating in young instar larvae, i.e. excessive oleoresin flow, operated when the newly hatched larvae started to bore the bark and oleoresin covered the larvae and chorion. The factor also operated when L1 have already penetrated and started girdling the twigs. The examination of this factor can be found in Chapter 7.

- Key factor in larger larvae (L3 to L5)

It was obvious that excessive oleoresin flow also plays a role in this period when the larvae are tunneling to the larger twigs or branches or stems on the young potted trees. Other factors such as predators and cannibalism have been examined in Section 4.4.1. However, cannibalism rarely occurred in the field population.

- Key factors in mature larvae (L6 to L7) and pupae

It was considered that parasitism and desiccation of wood play an important role in these stages. Both factors have been examined in Section 4.4 & 4.2 respectively.

- Key factor in adult stage

Sex ratio and failure mating that can be concluded as factors operated in this stage. Both factors had been discussed in Section 4.2.5.3 and 5.2.5 respectively.

Weather influences are expected to play an important role in favoring the key factor operation. Variations in weather, particularly in rainfall can cause fluctuation in the establishment of young instar larvae by increasing and decreasing the excessive oleoresin flow. Low temperatures during spring and early summer may affect the mating and oviposition activities. Under certain conditions parasites (Braconids wasps) and predators (clerid beetles) could constitute key factors.

Although there were some mortality factors operating in decreasing the population, the trend index of the population was on the increase in successive generations. The trend index of the field population was 145%. This suggests that there was a slow increase in

population. This result is consistent with the results obtained from other aspects of the study (see Chapter 6).

Conclusion

Survivorship curves plotted from life-table data can sometimes be useful in deciding on the best time for evaluating an infestation or predicting future population levels. Survivorship curves, plotted from sampling field data during the period of 1984 to 1986 (Fig 4.17) show that the highest mortality rate occurs in the late spring and early summer on early instar larvae.

Key factors cannot be clearly identified from life-tables covering only few generations no matter how complete or accurate the tables. However, key periods in life cycles, within which key factors operate, are sometimes identifiable. For U. cupressiana populations the most likely key periods are: (1) The establishment period of the L1 and L2 in late spring and early summer, because that is when most larvae die and the rate of mortality might be variable from year to year and between sites. Most of this mortality is caused by excessive oleoresin flow. (2) The adult stage, because the egg depositions under natural condition are highly variable. It was indicated that far greater egg deposition is possible than is actually found. Sex ratio and mating failure play an important role.

Table 4.34: Life-table for Uracanthus cupressiana on potted plant of Cupressus sempervirens that were placed in the orchard of WARI, from 1984 to 1986

SD (x)	NE (1x)	PB & MF dxF	ND (dx)	dx as percent of 1x (100qx)	PRM 100xdx/n	S (Sx)
Egg	210	Fail to hatch	5	2.38		
		Fail to tunnel	5	2.38		
		Infertility	5	2.38		
		Sub total	15	7.14	7.14	.93
Larvae (L1 to L2)	195	Establishment in host, host factor interacting with weather or other factors, particularly excessive oleoresin flow	58	29.74		
		Unknown factors	12	6.15		
		Sub total	70	35.89	33.33	.64
Larvae (L3 to L5)	125	Host factors (oleoresin)	20	16.00		
		Cannibalism	23	18.14		
		Mechanical (twigs fell-down by the wind)	17	13.60		
		Sub total	60	48.00	28.57	.52
Larvae (L6 to L7)	65	Twigs (wood desiccation)	17	26.20		
		Unknown causes	8	12.30		
		Sub total	25	38.45	11.90	.62
Pupa	40	Unknown causes	15	37.50		
		Sub total	15	37.50	7.14	.63
Adult (SR 13:12)	25	Sex	2	8.0	0.95	.92
Female x2	23	Size	0	0	0	0
		Failure mating	3	13.04		
		Sub total	3	13.04	1.43	.87
Normal-female x2	20	Adult mortality	2	0.1	0.95	.90
Actual-female x2	18					
Generation		–	192	91.42	91.42	.09

Expected eggs: 198
Actual eggs: 454
Index of population trend Expected: 94 %
Actual: 216 %

–

SD: State of development, NE: Number entering each x.
PB: Predominant behaviour, MF: Mortality factors,
ND: Number dying in each x, PRM: Percent real mortality,
S: Survival rate within x, SR: Sex ratio.

Table 4.35: Life-table for Uracanthus cupressiana in zone 4 Adelaide Plain, from 1984 to 1986

SD	NE (lx)	PB & MF dxF	ND (dx)	dx as percent of lx (100qx)	PRM 100xdx/n	S
Egg	247.86	Fail to hatch	-			
		Fail to tunnel and other factors	-			
		Infertility	-			
		Unknown causes	-			
		Subtotal	17.68	7.14	7.14	.93
Larvae (L1toL2)	230	Establishment in host, host factor interacting with weather and other factors, particularly excessive oleoresin flow	84.73	36.84		
		Unknown causes	12.09	5.26		
		Subtotal	96.82	42.10	39.09	.54
Larvae (L3toL5)	133.22	Host factors (oleoresin)	18.1	13.59		
		Cannibalism	6.05	4.55		
		Mechanical (twigs fell-down by the wind)	12.1	9.09		
		Predators	14.17	10.64		
		Unknown causes	10.1	7.58		
		Subtotal	60.52	45.45	24.43	
.55						
Larvae (L6toL7)	72.66	Twig desiccation	6.05	8.33		
		Parasites	6.05	8.33		
		Mechanical (twigs fell-down by the wind	12.1	16.66		
		Unknown causes	12.1	16.66		
		Subtotal	36.3	49.98	14.65	
.50						
Pupae	36.36	Twigs desiccation	6.05	16.66		
		Parasites	6.05	16.66		
		Unknown causes	12.01	33.33		
		Subtotal	24.02	66.66	9.72	
.34						
Adults	12.34	Sex	2	16.21	0.81	
.84 (SR 6.34:6)						
Female x2	10.34	Size	0	0		
		Failure mating	2	19.34		
		Sub total	2	19.34	0.81	
.81						
Normal- .88 female x2	8.34	Adult mortality	1	11.99	0.98	
Actual- female x2	7.34					
Generation .03		-	240.34	97.03	97.03	

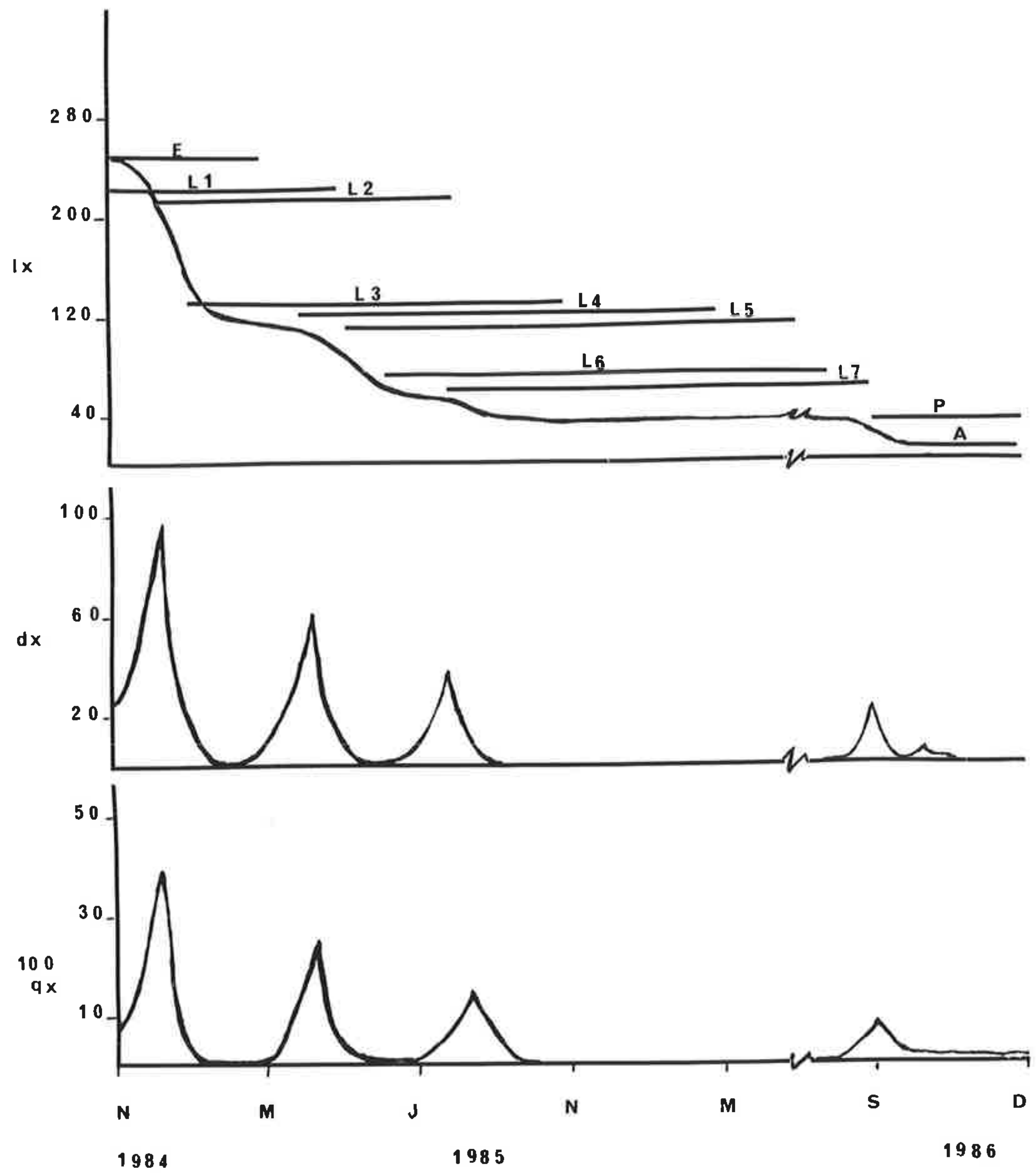
continued.

continued.

Expected eggs: 80.74
Actual eggs: 360
Index of population trend, Expected: 33 %
Actual: 145 %

SD: Stage of development, NE: Number entering each x,
PB: Predominant behaviour, MF: Mortality factors,
ND: Number dying in each x, PRM: Percent real mortality,
S: Survival rate within x, SR: Sex ratio.

Fig. 4.17: Survivorship (lx), mortality (dx), and percentage of mortality (100 qx) curves for 1984-1986 generations of U. cupressiana on zone 4, the Adelaide Plain.


280
200
120
40
lx
E
L1
L2
L3
L4
L5
L6
L7
P
A
100
60
20
dx
50
30
10
100
qx
N
M
J
N
M
S
D
1984
1985
1986

CHAPTER V

CHAPTER 5

REPRODUCTIVE STRATEGY

5.1 INTRODUCTION

Reproduction is an essential function of the individual, with certain exceptions such as the worker bee. It is well known that in insects, following their moult to the stage in which they carry out reproductive functions, there is usually a period during which the genital products mature. In some insects there is no pre-reproductive period at all, e.g. some aphids and some tipulids (Laughlin, R. personal comm.). This pre-reproductive period may be very short, as in Ephemeroptera and Lepidoptera (Bombycidae, Saturnidae, etc), or relatively long, as in Odonata (Richard, 1974). When the period is long, genital maturation is preceded by a compulsory feeding phase (Traqardh, 1930; Linsey, 1959; Richard, 1974; Duffy, 1953, 1957, 1960). In some insects (e.g. Odonata, Diptera, Homoptera, Heteroptera, ect.), this pre-reproductive period is one of intense wide ranging locomotor activity which results in migration (Richard, 1974).

As mentioned previously, cerambycids can be divided into 4 groups with respect to feeding: pollen feeders, leaf or needle feeders, bark feeders, and feeders on unknown substances (Traqardh, 1930; Duffy, 1953, 1957, 1960). U. cupressiana probably belong to the 4th group. It is not known whether there is a feeding phase. Females removed from the pupal chamber 3 to 4 days before normal emergence when their bodies are still not strongly sclerotized, could receive males. As mentioned previously, however, shortly after emergence from their pupal chamber, adults walked a short distance, made short flight, and were capable of receiving a mate. The beetles sipped water or a sweet solution if it was provided but it seemed to be for survival and not for sexual reasons. When the dead beetles were dissected, their hindguts were found to contain numerous particles of wood. This is not evidence that beetles feed when they make their way from the pupal chambers that usually are blocked with shredded wood by the larvae before pupating because, when beetles emerged from glass vials that were plugged with cotton wool, particles of wood were also found in their hindguts.

Insects display characteristic sequences of reproductive behaviour. The sequence varies among orders, families, or even species.

In cerambycids the sequences of reproductive behaviour are not well-known. In this section the reproductive strategy of the *U. cupressiana*, including mate location, courtships, mating, oviposition and host selection, is investigated and discussed.

5.2 MATING BEHAVIOUR

5.2.1 Introduction

Mating behaviour in cerambycids, as in other insects, generally involves a complex series of behaviours initiated by corresponding stimuli. Males of some cerambycids respond to olfactory stimuli to search for females within short range, using other stimuli for the final contact (Linsey, 1959; Akutsu and Kuboki, 1983; and Iwabuchi, 1985). The mating behaviour takes place in 2 phases: first the flying female approaches the resting male guided by a male sex pheromone (the active female phase); second, the male approaches the alighting female and copulates with her (the active male phase) (Iwabuchi, 1982, 1985). In other cerambycids the female is not active (Linsey, 1959; Akutsu and Kuboki, 1983). These statements raise questions concerning where mating occurs and the age of the mating insects.

Previous works on cerambycids such as that of Kuboki *et al.* (1985) and Akutsu and Kuboki (1983) found that the sequences in mating behaviour in *Acalolepta luxuriosa* Bates include male wandering, orientation in the approach to the female, grasping, mounting, licking, and copulation. In the same species Akutsu and Kuboki (1983) have demonstrated that vision does not play an essential role in recognition of the female by the male. Males recognized sexually mature females through the contact chemoreceptors of the antennae. In *Cerambyx dux* also, males recognized females on antennal contact.

In this study, the mating behaviour of *Uracanthus cupressiana* was investigated to determine the sequences of mating behaviour, including mate location, mating stimuli, and mating; some factors affecting mating; and impact of mating on reproduction or oviposition pattern.

5.2.2 Mate location

This section describes how male and female *U. cupressiana* recognize each other and find their mate. A series of experiments were carried out.

Wind tunnel bioassay

Experiment 1. Sexual response of U. cupressiana to male and female stimuli

The experiment was carried out in fluctuating temperatures between 1800 & 2300h, the period during which the beetles are very active. Two wind tunnels were made from plastic tubes, diameter 2.5cm, length 200cm. At one end of the tunnel a compressed air line was connected. At the other end an anemometer was placed, covered by a piece of mosquito net to keep the beetles out. The wind velocity used was 1.5 to 2.1 meters per second. Temperature range during the experiment was 24 to 25°C and relative humidity range was 48 to 50%. The experiment was carried out in 2 phases over 2 successive nights. Four groups of 15 pairs of beetles of different ages were used. Group 1 beetles were newly emerged from twigs. Group 2 beetles had emerged 1-3 days previously; group 3, 4-7 days; and group 4, > 7 days previously. The experiment was carried out in 2 stages. (1) male vs female- In each trial one male was placed at the anemometer end of the tunnel and one female at the other. Each insect was used once only. For control a male was placed at each end. (2) female vs male- Positions were reversed with the female at the anemometer end of the tunnel. The controls in this series of trials used female vs female.

The sexual responses of the insects (antennae raising, walking, and abdomen bending) were observed for a maximum of 15 minutes after release. Between release and the insect's response, the distance travelled and time was recorded. The insects were categorized 'no response' if, in the 15 minutes, they did not raise their antennae or walk or bend their abdomen. In the dark, observations were made under red light. Data were analysed by using a 2-way ANOVA with replicates in cells.

The results are presented in Tables 5.1, 5.2, 5.3 and Apps. 14 & 15. Most males and females respond to the stimuli. After having contact with stimuli, they raised the antennae and walked with bent abdomens towards the stimuli. Some males even ran with bent abdomens and raised antennae, and came into contact with the sources. But some males raised the antennae, walked a short distance, were still then for few seconds, and continued to walk with antennae raised. Some males and females walked for short distances with antennae raised and then remained

Table 5.1: Sexual response of adult U.cupressiana to stimuli from males and females of different ages (days)

Sex and age (days)	No.of tests	No.of response	no response
Male vs female			
0 vs 0	15	11	4
0 vs 1-3	15	14	1
1-3 vs 1-3	15	15	0
4-7 vs 1-3	15	15	0
>7 vs 1-3	15	8	7
Male vs male			
0 vs 0	12	0	12
1-3 vs 1-3	12	0	12
Female vs male			
0 vs 0	15	10	5
1-3 vs 0	15	15	0
1-3 vs 1-3	15	15	0
4-7 vs 1-3	15	12	3
>7 vs 1-3	15	2	13
Female vs female			
0 vs 0	10	0	10
1-3 vs 1-3	10	0	10

Table 5.2: Length of time spent responding to the stimulus of male or female of different ages

Sex and age tested	Means (secs)	F	P
Male	49.71	6.36	> 0.1
Female	76.71		
0 vs 1-3	92.68a	28.92*	< 0.05
1-3 vs 1-3	19.23b		
4-7 vs 1-3	40.2b		
>7 vs 1-3	180.0a		

A Two-way ANOVA replicates in cells
Means followed by the same letters are not significantly different.

still. Observations suggest that both sexes emit scent that can stimulate the sexsual response. In other words, both male and female of U. cupressiana may produce a sexual pheromone. Analysis of data revealed that there were no significant differences in response times and travel distances from stimuli between males and females. Within groups in both sexes, however, there were significant differences. Both males and females from groups 2 and 3 responded quickly to the stimuli. Shortly after they were released, they raised the antennae and walked with bent abdomens until, in a few seconds, they were close to or in contact with the source of stimulus. Those from groups 1 and 4 take a longer time to respond. Sometimes they travel just half way from the stimuli (see Tables 5.1 & 5.2 and Apps. 14 & 15). This suggests that male and female become very active when they are physiologically ready to accept a mate. The older the beetles are the less they respond. A homosexual response did not occur in either sex although, when the males were kept together in a small vial, it often happened. It never happened among females kept in a vial. In this case perhaps other stimuli affect the male (see exp. 4).

Experiment 2. Sexual response of mated and parous beetles to stimuli

In this experiment the methods used were the same as in experiment 1. The beetles used were more or less the same age, but different in reproductive status, i.e. unmated (UM), mated (M) and parous (P). They were treated as follows: (1) UM males vs M females, (2) UM males vs P female, (3) M males vs UM females, (4) M males vs M females, and (5) M males vs P females.

The differences between treated pairs of beetles were quite clear (see Table 5.4). The data show that unmated males respond to mated females less often than mated ones do. This might be due to lower stimulus being produced by the mated females resulting in failure to stimulate the unmated males, but stimulating the mated ones. Perhaps the mated males were more capable of detecting the weak stimulus emitted by the mated females than the unmated males were. The lower response to P female might be because P female produced much less stimulus than mated females.

For females, UM or M females were not much different in their responses to M or UM male stimuli. P females, however, did not respond at all to the male stimuli. Perhaps it is not nessesary to copulate when most of the eggs have been deposited.

Table 5.3: Distance travelled from source of stimuli of male and female

Sex and age tested	Means (cms)	F	P
Male	76.73	.869	> 0.5
Female	73.93		
0 vs 1-3	115.63a	20.07*	< 0.05
1-3 vs 1-3	30.50b		
4-7 vs 1-3	71.17c		
>7 vs 1-3	127.0a		

A Two-way ANOVA replicates in cells
Means followed by the same letters are not significantly different.

Table 5.4: Sexual response of mated, unmated, and parous adults

Sex and age tested	Number of tests	Number responding	No response
Male vs female			
1-3 UM vs 1-3 M	12	2	10
1-3 UM vs P	12	1	11
1-3 M vs 1-3 UM	20	15	5
1-3 M vs 1-3 UM	20	16	4
1-3 M vs P	15	10	5
Female vs male			
1-3 UM vs 1-3 M	12	12	0
1-3 M vs 1-3 M	12	10	2
P vs 1-3 M	12	0	12

UM : unmated
M : Mated
P : Parous females

Conclusion

Adults of U. cupressiana emit a powerful olfactory sex attractant that can guide them to locate their mates. Both male and female become very active when they are physiologically ready to accept a mate. The older the beetles, the lower their responses. Mated males are more aggressive than unmated ones. The sequences of mating behaviour of U. cupressiana is presented in Fig. 5.1.

5.2.3 Mating stimuli

In this section the existence of female sex pheromone was tested. Two experiments were carried out to investigate whether the female of U. cupressiana produces a sex pheromone that triggers the male copulatory response.

Experiment 1. Female sex pheromone in vials that had contained female beetles

Two groups of 20 newly emerged males and one group of 20 newly emerged females were sexed and kept separately, one beetle per vial, in plastic vials (3cm in diameter, 8cm in height) for 24 hours. Female beetles were taken out and were kept in other vials. The males of group 1 were put (one per vial) in the vials which had held the females while each male of group 2 was put in clean, washed vials that had never been used for keeping females. The behaviour of the males was observed for 15 minutes in a temperature of about 23°C, under fluorescent light (Philips 36/33 White).

The differences between the 2 groups of males were clear cut. In group 1 most of the males behaved as follows: shortly (4-10 sec.) after placing in the vials the male always stops on the bottom of the vial, bends his abdomen and attempts to mount or copulate on the surface of the bottom of the vial. This act can last for a long time, sometimes 15 minutes or even more if the male is not disturbed. On the other hand, those that were placed in new, washed vials just wandered around in the vials (see Table 5.5). It is obvious that the female of U. cupressiana can produce a sex pheromone that elicits a copulatory response from the male. The existence of a female sex pheromone has been reported in some cerambycids, e.g. the short distance acting pheromone of Hylotropes bajalus, contact pheromones of Megacyllene robine and M. caryae (Iwabuchi, 1985), and Acalolepta luxuriosa (Akutsu and Kuboki, 1983;

Table 5.5: Number of males responding to female pheromone in a vial that had contained female beetles before the males were introduced

Treatment	N	Number responding	no response
vial with female	20	18	2
vial no female	20	0	20

Table 5.6: Sexual response of male to female stimuli

Treatment	Trial	Before washing	After washing
Water	150	150	98
Ethyl alcohol	150	150	0

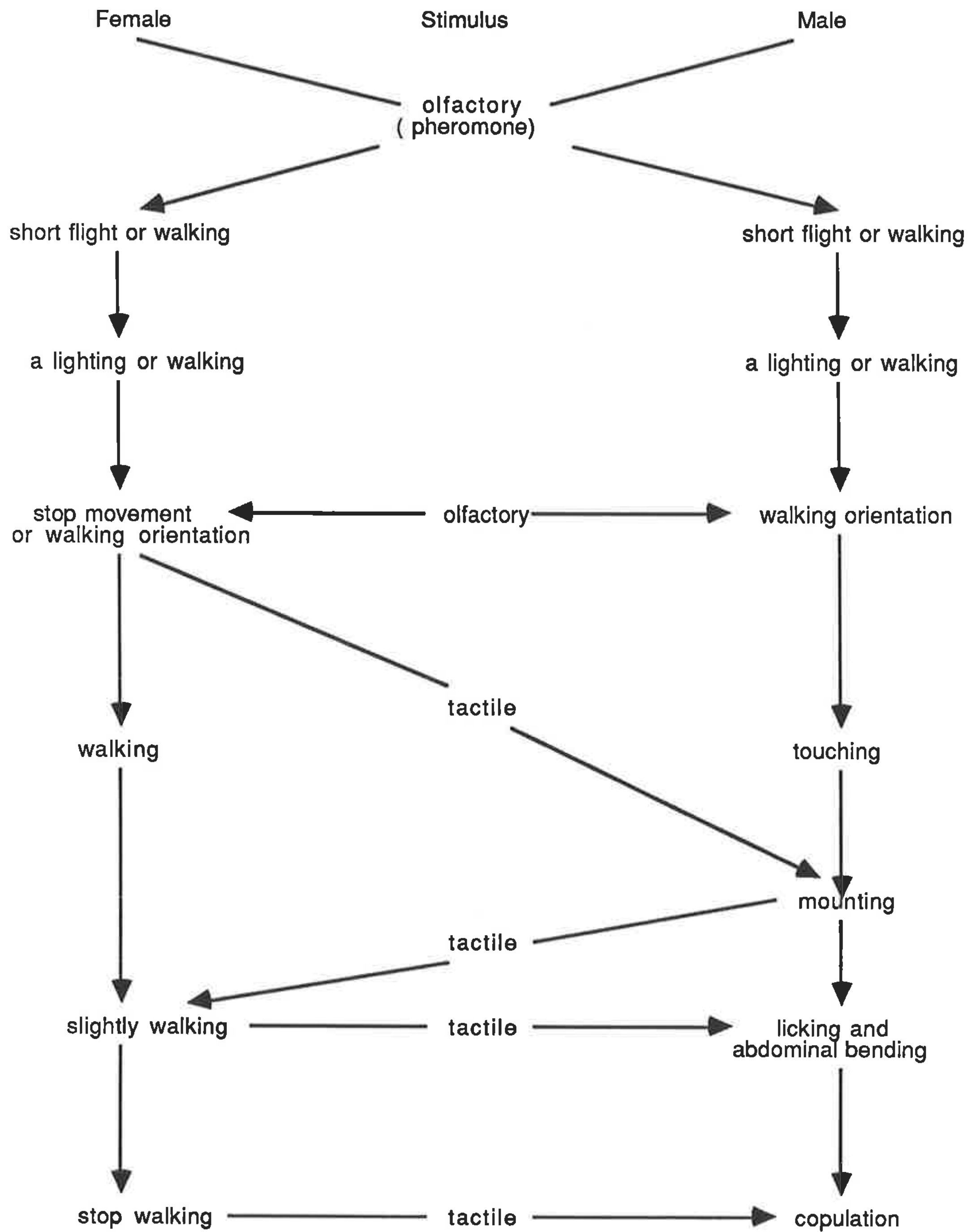


Fig. 5.1 The Sequence of Mating Behaviour of U. cupressiana and Stimuli Involved in it, Both Male and Female were Active

and Kuboki et al., 1984). The sexual contact pheromone was effective only within a short range but it functioned as a stimulus for recognition and appeared to be a trigger to start the second phase of the mating behaviour (Iwabuchi, 1985).

This study also indicated that vision does not play an essential role in the recognition of the female by the male, since the male directly mounted the surface of the bottom part of the vial without either female or dummy. The same fact has been demonstrated in A. luxuriosa (Akutsu and Kuboki, 1983; and Kuboki et al., 1984).

Experiment 2. Existence of sexual contact pheromone on the surface of female of U. cupressiana

Two groups of 20 newly emerged females were killed in a jar with a piece of cotton wool that was wet with ethyl acetate. One hour after the females had been killed, each was put on a petridish. Then the response (contact and mounting) of each of the 10 newly emerged males was tested by putting them in the petridish with a dead female. The females were then grouped into 2 groups. The first group of females was immersed in ethyl alcohol, and the second group in destilled water for about 18 hours. One hour after evaporation of the ethyl alcohol, the dead female was individually placed in a petridish. Each of the previous 10 males was released in the petridish with a female of group 1. Releasing time was 5 minutes, and each male was re-released with another female of group 1. Males then were transferred individually in the petridish with a female of group 2, and each male was re-released with another female of group 2. Male response was observed. The experiment was carried out in the laboratory at temperature 24-25°C, relative humidity 48%, and from 1800 to 2200h with fluorescent light (Philips 36/33 White).

The results show that all males responded to the stimuli of untreated dead females, 65% of males responded to the females of group 1 (immersed in distilled water) (see Table 5.6). Shortly after releasing the male walks around, contacts the female with his antennae, and attempts to mount her. On the other hand, none of the males responded to the females of group 2 (immersed in ethyl alcohol) or in other words none females extracted with ethyl alcohol triggered a male response. These males just walked around and passed the females, making no attempt to mount.

These reactions suggest that on the surface of the female body a contact sex pheromone is present. The presence of contact sex pheromone in the cuticular wax has been established in other cerambycids such as Acalolepta luxuriosa Bates (Kuboki, 1984) and Xylotrechus pyrrhoderus Bates (Iwabuchi, 1985).

5.2.4 Mating pattern

In this section the courtship and mating behaviour of the U. cupressiana are discussed.

Experiment 1. Single pair mating

108 pairs of newly emerged beetles (0 day) were used. Each pair was placed in a mating vial (8x3.5cm in diameter). Mating behaviour of insects and duration of mating from contact or mounting to completion of copulation were recorded. The insects were observed for 30 minutes. The experiment was carried out in the laboratory at temperature 24-25°C, relative humidity 40-50%, with fluorescent light (Philips 36/33 White).
Insect behaviour - 3 steps of sexual behaviour were observed, namely:
(1) Pre-copulation - Most males of U. cupressiana could pass the female at a very short distance. It was obvious that males recognize females only by contacting them with the antennae. The male after has a contact with female, mounts on her back, clasps her with foretarsi on her thorax or basal part of the abdomen (if the male is smaller than the female), grasps her hindlegs by his middlelegs, and holds both sides of her pygidium by his hindlegs, and begins to stimulate her. The female usually attempts to throw the male off or actively walks, carrying the male on her back if she is not yet ready to receive him. On the other hand, if the female is ready to be copulated, she becomes very active, walks around, she passes the male and the male touches her with his antennae and mounts her while she is in the stationary position. Sometimes if the male is very active, after he has made contact with the female, he raises his body to the full extent of his hindlegs and stridulates.
(2) Copulation - When the female become restless, the male then tries to establish copulation. He bends down his abdomen to contact the ovipositor of the female and the male genitalia (aedeagus or penis) may be inserted. When copulation is established the male becomes motionless for a few second. When the copulation has been established, some males perform a 'licking' (movement with his mouthparts; i.e. palps exert a stroking action

on the back or thorax of the females. Sometimes licking is combined with 'tapping' (downward movement of head where the mouthparts come to hit against the thorax or the back of the female).

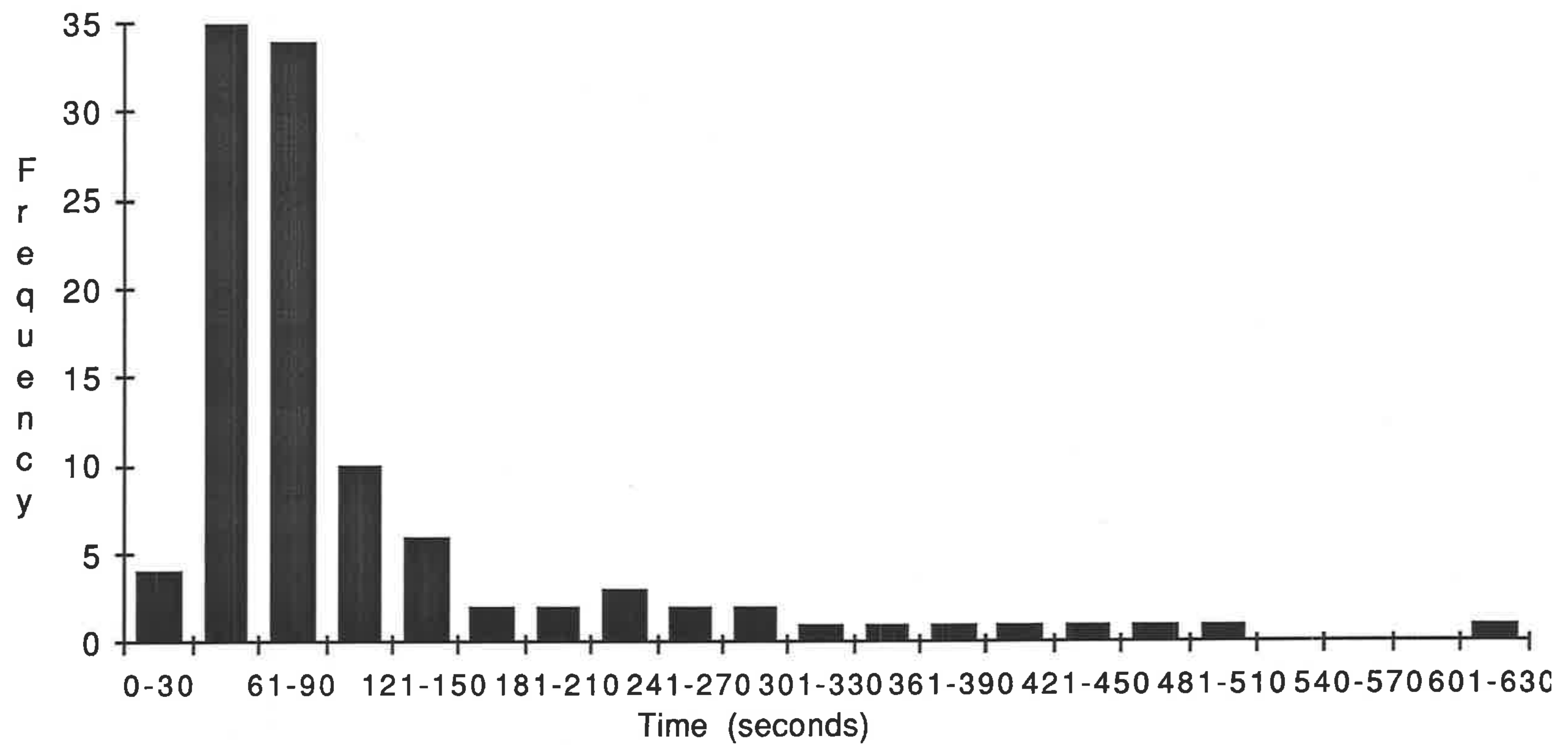
(3) Post-copulation - At the end of copulation some males perform a few tappings, then are motionless. They later then make slow pygidial movements, performed at regular intervals for a few seconds, before withdrawing the sexual organ. After finishing copulation, most males move aside and walk away. Some males move backwards on the back of the female, raise their bodies with fully extended hindlegs, and fly away. Some males leave the females after some time without any previous efforts by the female to dislodge them. Some females, however, attempt to be free from male grasping by kicking the male legs with their hind legs and then running away.

Duration of mating - From the beginning of courtship to the end of copulation (dismounting) lasts from 3 to 630 seconds, and the mode of mating time falls within 31-60 seconds (see Figure 5.1A and App. 16). It usually takes long time if the female is not yet ready to be copulated, since she rejects or avoids the male that attempts to copulate her, or walks around while carrying the male on her back so the copulation cannot be established. But if no interruption occurs or, in other words, if the female is ready to be copulated, the period from the beginning of courtship to the end of copulation lasts from a few seconds to 1.5 minutes.

It has been argued that the duration of courtship and copulation appears to be extremely variable in cerambycids, or even within species. It has been observed that some species such as _Xylotrechus rusticus_ Linneus require only about 1.5 minutes; in _Hoplocerambyx spinicornis_ copulation lasts only a few seconds; _Hylotropus bajulus_ Linneus requires about 5.5 to 6 minutes; in _Stromatium fulvum_ Villiers about 10 minutes is required; _Stenocorus meridianus_ Linneus, _Aromia moschata_ Linneus, and _Saperda carcharias_ Linneus remain in copulation for at least an hour at a time (Duffy, 1953); and in _Acalolepta luxuriosa_ copulation lasts about 20 seconds to 10 minutes, with an average 4 minutes (Akutsu and Kuboki, 1981).

Mounting position - Usually a male mounts a female from behind but sometimes, when a female is walking towards a male, he mounts her from the front or side and subsequently tries to copulate in an incorrect position without turning around. This also happens when the female approaches the male from behind. The male attempts to mount her.

Fig. 5.1a Frequency of single pair mating time of adult U. cupressiana (Maximum observation time 30 minutes, N=108)



He turns around while the female keeps on walking, resulting in his being in the opposite direction. Such behaviour have been demonstated in other cerambycids, i.e. in Xylotrechus pyrrhodrus (Iwabuchi, 1985). It was also observed that when a male attempts to copulate with a female while she is walking the male is carried by the female, not sitting on the back, but clinging to the ventral side of her abdomen while he keeps on attemping to mate.

Multiple mating - Both sexes have been observed to copulate several times at short intervals from a few to 30 minutes. Most females, once they have been copulated, become more aggressive. One male could copulate successfully one to 6 times.

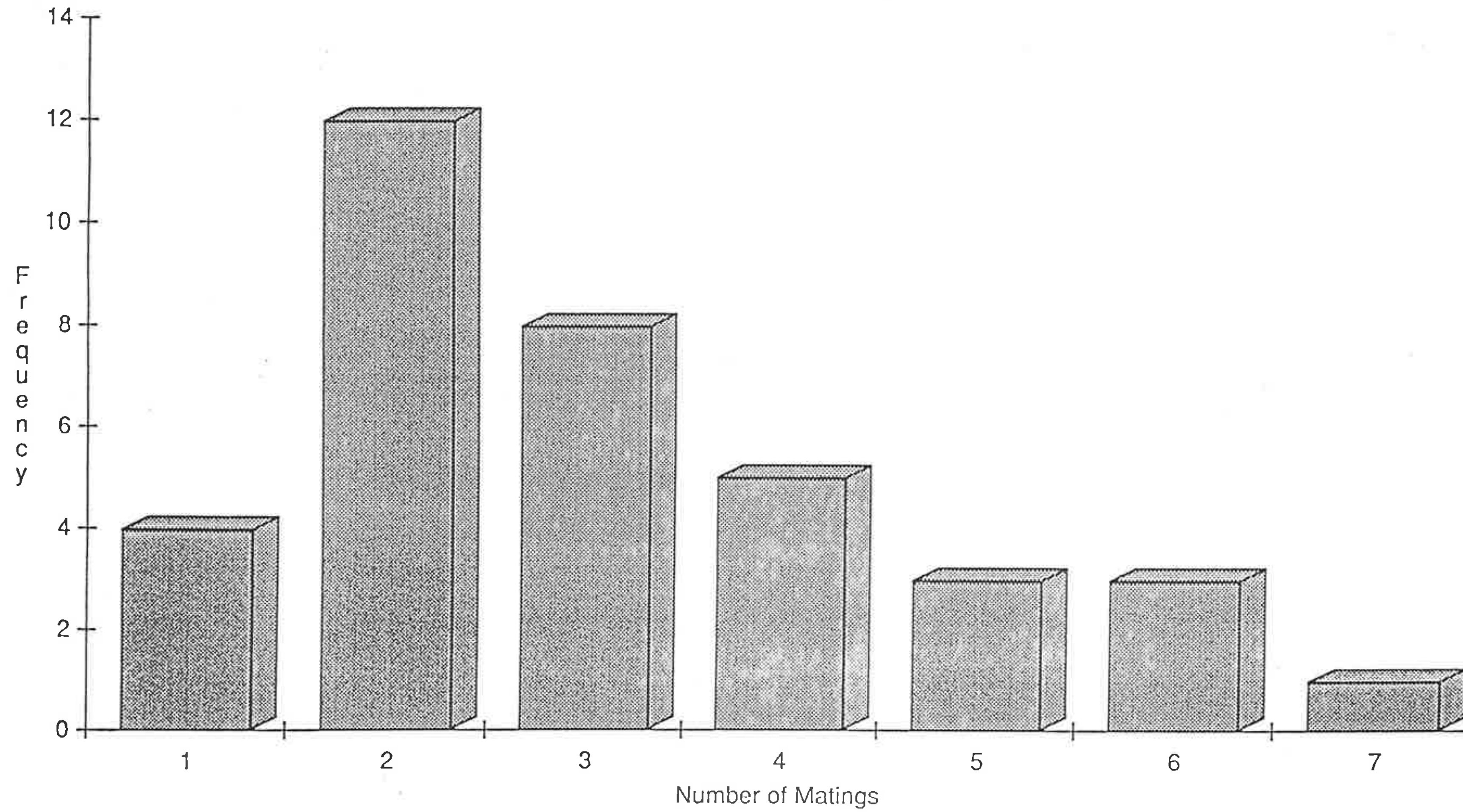
Experiment 2. Multiple mating of a male on one female

The experiment was set up as in experiment 1. 36 pairs of newly emerged beetles were used. Each pair was placed in a plastic mating vial (8x3.5cm in diameter). Repeated matings for each pair were recorded in 30 minutes. Each mating was indicated by mounting, copulation, and copula establishment. Unestablished copula was not included in recording.

The 36 couples mated from one to 7 times, average 3.11 ± 0.26 times within 30 minutes (see Fig. 5.2 and App. 17). It was observed that males whose copulation lasts just a few seconds or minutes are able to repeat the mating several times within a short period. Those that copulate for a long period repeat just a few times, perhaps not even finishing one copulation. The length of the mating periods might depend on the fitness or vigour of the male himself and the unwillingness of the female. This agrees with the copulation-latency times in Drosophila melanogaster proposed by Van der Berg (1985). In his model, it was stated that copulation-latency time is thought to be the quotient of 2 normally distributed variables: female reluctance and male vigour. Robertson (Van der Berg, 1985) stated that long courtship durations were due to female unwillingness. Most females need a certain time after introduction to the mating chamber to calm down before responding to male courtship. When a male starts courting immediately upon introduction, the courtship time will be long because no success will be achieved before the female is ready. If the male does not begin courtship before the female is ready, this effect will be absent, resulting in a short courtship.

Fig 5.2

Frequency of Males on
Mating with one Female (N=36)



Experiment 3. Multiple mating of a male on different females

Two groups of 15 males were used, the first group with males 0-3 days of age and the second with males aged >3 days. Females used were 0-3 days old and each female was used twice. Each male was placed in the mating vial with a female. After finishing one copulation the female was replaced with another one. Copulation was repeated within 30 minutes. The number of matings for each male was recorded. The experiment was set up as in experiment 1.

The 0-3 day age group was able to copulate with 2 to 7 different females, average 3.8 ± 0.37 females. The >3 day age group managed one to 3 females, average 1.7 ± 0.16 females (see Table 5.9, Fig. 5.3 & App. 18). It is obvious that the age of a male affects his fitness for mating. It has been argued that age (e.g. Kennedy, 1971) or physiological state (e.g. Mead-Briggs & Vaughan (Hinton, 1981) of the male affects fertility.

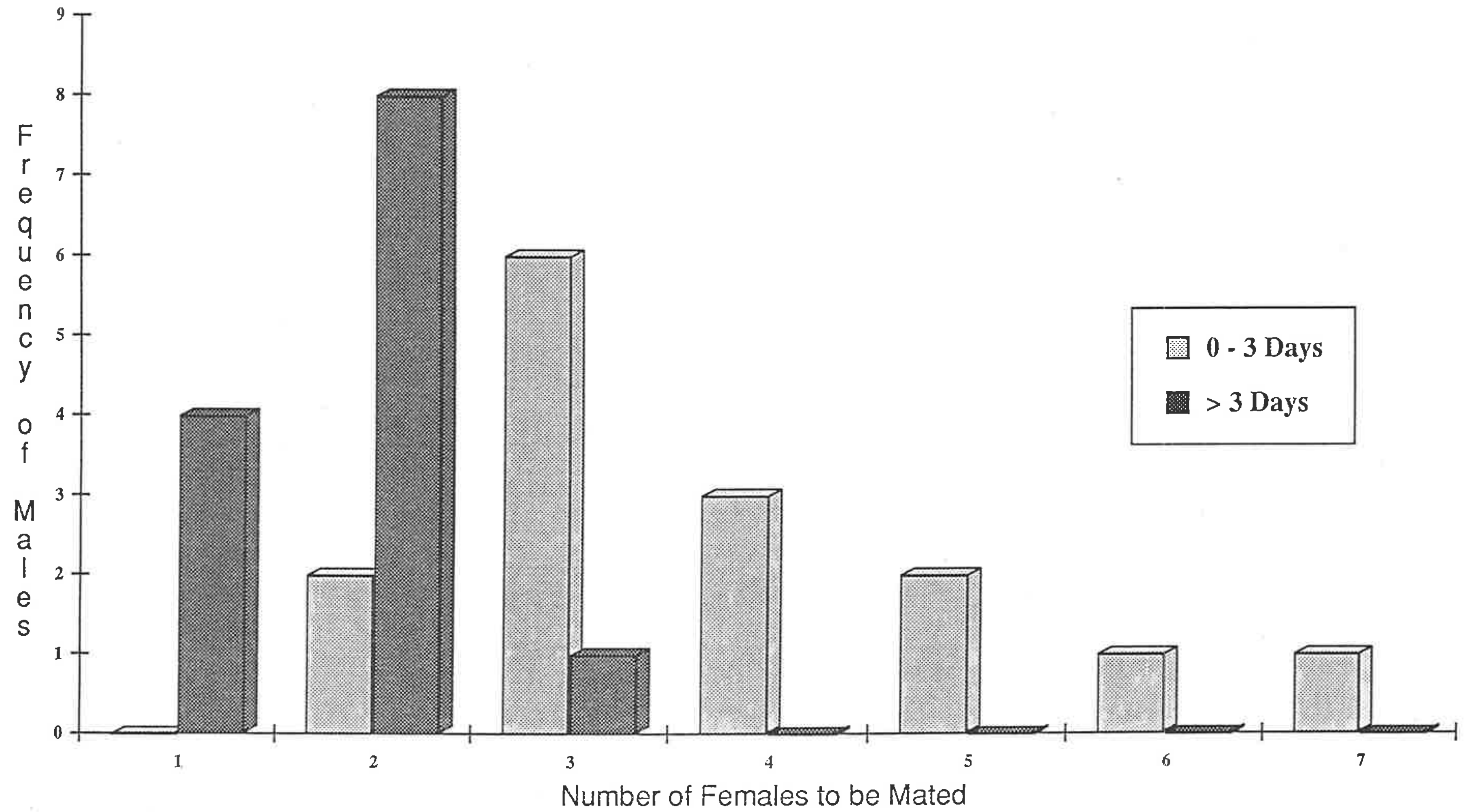
Experiment 4. Multiple choice mating

80 pairs of newly emerged beetles were used. They were grouped into 16 groups of 5 pairs. Each male of a group of 5 was marked individually on its elytra, and then the group was placed in a plastic mating vial (11x15cm in diameter) with transparent lid. The experiment was set up as in experiment 1. The behaviour of insects and mating periods were recorded. Males tending to be homosexual were separated, placed in another vial and replaced with other males. Matings of a female with more than one male (in the same time) were excluded in time recording. Each pair male and female was quickly removed and placed in the small mating vial (as in experiment 1) and timed until the end of copulation.

Observations revealed that there are 2 sexual behaviours:

Sharing behaviour - There was no fighting among males during observations but sharing behaviour always occurred. A male attempts to copulate a female and a second male mounts the back of the first male. Sometimes a third, a 4th, or even a fifth male joins the first 2. The 4th and fifth cling to the sides of the female, one may even cling to the ventral side. The cluster of beetles may stay together for several hours, a day or even longer. The female or one of the males may even die during this time. They are difficult to separate because they hold each other tightly with their legs. Such behaviour has not yet been recorded in any other cerambycids. Duffy (1953) stated that, in certain species, it is common for the large sized males to monopolise several females such as in

FIG. 5.3 FREQUENCY OF MALES (IN DIFFERENT AGE GROUPS) ON MATING WITH DIFFERENT FEMALES



Hoplocerambyx spinicornis; and the males of many species are ferocious fighter such as in Arhopalus ferus Mulsant. Such is also the case in Monochamus scutellatus (Hughes, 1981), and Acalolepta luxuriosa (Akutsu & Kuboki, 1983). In Uracanthus cupressiana such a behaviour was never seen during this study; instead, sharing behaviour always happened if a female was put with several males. Perhaps this behaviour is a characteristic of this species.

Homosexual behaviour - Between males this behaviour was occasionally found when males were kept together in a vial. Thus copulatory behaviour may be elicited by tactile stimuli. A female sex pheromone may simply increase the likelihood of a copulatory attempt by males under field conditions. Homosexual behaviour has been observed in other cerambycids such as Xylotrechus pyrrnodorus (Iwabuchi, 1985) and Cerambyx dux Fulderman (Saliba, 1974). Females did not display homosexual mounting during this course of study. However, in certain cerambycids female beetles did (Iwabuchi, 1982 and 1985).

Duration of mating - Mating lasts one to 20 mins., average 4 mins. (245,6±29,42 seconds). It lasts longer than 20 mins. if the female walks around or is interrupted by other females or males before establishment of copulation (see Fig. 5.4, and App. 19). Such cases have been observed in mass mating of Drosophila melanogaster, where the females can avoid the males easily and more effectively the bigger the mating chamber. When a female moves away, male courtship stops. In this case more time is needed before the female reaches her threshold level (Van der Berg, 1985).

5.2.5 Impact of mating on reproduction

A series of experiments was carried out to measure the impact of mating on reproduction or the oviposition pattern of U. cupressiana.

Experiments 1 to 7 were carried out at 25°C, 45±10% RH for 14 hours photoperiod. The beetles were kept in oviposition chambers, cylindrical plastic containers (25x15cm), with 6 fresh cut twigs of C. sempervirens (20cm in length) for depositing eggs. The number of eggs deposited was recorded daily. They were removed from the twigs and placed in a petridish with filter paper. At the end of the experiment the females were killed and dissected under saline solution (0.9%). In order to observe the presence of sperm the spermatheca was removed and placed on a concave microscope slide with a drop of saline solution. The

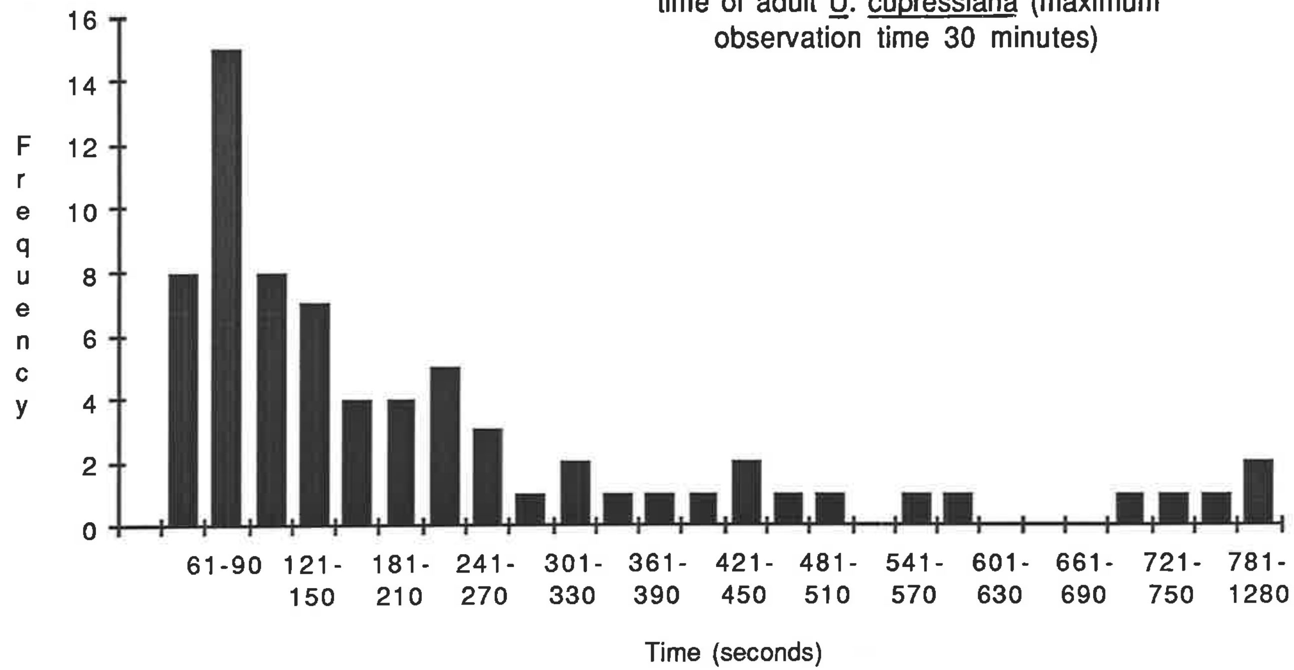


Fig . 5.4 Frequency of multiple choice mating time of adult *U. cupressiana* (maximum observation time 30 minutes)

Plate 7: Mating behaviour and position, showing the sharing mating of beetles U. cupressiana: mating of one female with two males (top), and mating of one female with three males (bottom).

spermatheca was crushed with fine forceps and the cloud of material coming out was teased to separate the sperm in the drop of saline solution which was then examined under a light microscope. In order to observe ovary (egg) development the abdomen was opened and the ovarioloes examined. The presence and quantity of sperm and mature ova were indicated by symbols: + (a great amount of sperm), ± (not many sperm), and 0 (none).

Experiment 1. Mating and oviposition

Two groups of 10 newly emerged females were used. Each female was placed individually in an oviposition chamber. In the first group, each female was paired with a male during the experiment. The other group was left unmated.

Females paired with males deposited eggs, while those without males deposited none. All females with sperm in their spermatheca deposited eggs. In both groups of females, all had mature ova (see Table 5.7). These results indicate that eggs are fertilised and laid only when there is sperm in the spermatheca. This result agrees with observations on Cimex lectularius (Davis, 1965), and on alfalfa weevil (Lecato & Pienkowski, 1972a, b).

In some insects, mating activates the corpora allata and thus stimulates oocyte or egg maturation (Gerber, 1967; Davis, 1965; Gordon & Toher, 1968) or egg production (Gordon & Bandal, 1967) or production of viable eggs (Turnipseed & Rabb, 1963); Burt & Fischer, 1967). In U. cupressiana, mating appears to induce egg deposition and viable egg production since the unmated females had mature ova (egg) in their abdomen but did not deposit eggs. The same has been observed in other insects (Gerber, 1967).

Experiment 2. Multiple matings of single male and different males of different ages and oviposition

Two groups of 15 newly emerged females were used. Each female was individually placed in an oviposition chamber. The first group of females was paired throughout with a single male of the same age group. The second group was paired with different males every day, or the male was replaced with another virgin male daily until the end of the oviposition period.

The results are presented in Table 5.8. The data showed that females which have multiple matings daily with different males of

Table 5.7: Mating and oviposition

FN	With male			Without male		
	NED	PMO	PS	NED	PMO	PS
1	45	+	+	0	+	0
2	23	+	+	0	+	0
3	27	+	+	0	+	0
4	67	+	+	0	+	0
5	0	+	0	0	+	0
6	35	+	+	0	+	0
7	28	+	+	0	+	0
8	63	+	+	0	+	0
9	0	+	0	0	+	0
10	21	+	+	0	+	0

FN: Female numbers
NED: Number of eggs deposited
PMO: Presence of mature ova
PS: Presence of sperm.

Table 5.8: Multiple mating of a female with a single or different males and oviposition

Female no.	Single male			Different males		
	No.eggs	No.ova	Sperm	No.eggs	No.ova	Sperm
1	14	26	+	79	2	++
2	23	15	+	46	5	++
3	16	26	+	63	3	++
4	26	24	+	49	4	++
5	17	35	+	42	3	++
6	2	52	+	76	5	++
7	58	12	+	93	2	++
8	45	13	+	82	4	++
9	2	38	+	63	4	++
10	5	41	+	72	2	++
11	6	39	+	24	2	++
12	18	31	+	31	4	++
13	0	48	0	45	2	++
14	0	45	0	76	2	++
15	84	6	+	58	4	++

different ages deposited more eggs (mean±SE: 61.93±5.49 eggs) than those with a single male (mean±SE: 21.07±6.22 eggs) (T=4.92, P<0.1%). The former had a lower number of remaining ova in their abdomen (mean±SE: 3.2±0.30) than the latter (mean±SE: 30.60±3.60 ova) (T=7.59, P<0.1%). They also had longer oviposition periods (range 4-8 days; females with single male, 3-5 days). This suggests that females mated with different males daily have an increasing store of sperm and higher fecundity than those mated with a single male. It is unlikely that the presence of sperm itself plays the dominant role. Frequent and long-lasting copulations are more likely to be the factors which maximise fecundity. Similar results were observed on *Rhinocoris marginatus* (Ambrose & Livingstone, 1985) and on *Oncopeltus fasciatus* (Gordon & Loher, 1968).

Experiment 3. Single and multiple mating of one male and oviposition

Newly emerged beetles were kept under the following conditions:

(1) 15 once-mated females placed individually and without a male in an oviposition chamber.

(2) 15 females each continuously maintained with a male in an oviposition chamber.

The results are presented in Table 5.9. Females receiving single mating laid a lower number of eggs (mean±SE: 10.13±3.97 eggs) than females receiving multiple mating (mean±SE: 55.93±6.72 eggs) (T=6.69, P<0.1%). This result indicates that females receiving a single mating stop ovipositing after sperm is depleted, or when suffering a shortage of sperm late in the oviposition period. Remating increased fecundity and fertility. Some females did not deposit eggs at all and had no sperm in their spermatheca. This may have been because the male was incapable of transfering his sperm to the female, or in other words, the male copulated but did not ejaculate since the females were already mated before they were placed in the oviposition chamber. As mentioned before, the presence of sperm in the spermatheca activates oviposition.

It has been argued that the number of sperm present in the spermatheca plays a major role in controlling oviposition and fertility. A reduction in sperm lowers oviposition and fertility (LeCato and Pienkowski, 1972a,b; Drea, 1969).

Observations on plum curculio revealed that the average sperm content per female increased as the number of matings increased. So

Table 5.9: Single and multiple mating of a female with one male and oviposition

Female no.	No.eggs deposited		Sperm presence	
	Single	Multiple	Single	Multiple
1	0	0	0	0
2	52	84	±	+
3	0	94	0	+
4	0	87	0	+
5	10	49	±	+
6	31	58	±	+
7	6	45	±	+
8	5	42	±	+
9	28	29	±	+
10	15	26	±	+
11	0	76	0	+
12	0	78	0	+
13	0	58	0	+
14	2	45	±	+
15	3	68	±	+

females that mated 2 or 3 times produced more eggs during their life span than those that mated only once (Johnson & Hays, 1969). Repeated mating seems to stimulate productivity long before the store of sperm is exhausted. Anderson suggested that a second mating may replenish sperm depleted by fertilization and allow a female to produce more fertilized eggs (Turner & Anderson, 1982).

In general, males who mate repeatedly leave more offspring than those who mate less frequently (Bateman in Turner and Anderson, 1982). Parker pointed out that repeated mating is clearly an important part of the selection which takes place in natural populations, and it is important to understand the evolution of the mating behaviour which underlies it (Turner & Anderson, 1982).

Experiment 4. Various numbers of males and oviposition

Two groups of 15 females were kept under the following conditions:

(1) 15 females each continuously maintained with a male in an oviposition chamber.

(2) 15 females each continuously maintained with 2 males in an oviposition chamber.

The observations are presented in Table 5.10. A T-test showed that there were no significant differences between the mean number of eggs deposited ($T=1.12$, $P>5\%$) and degree of presence of sperm between females re-mated with a single male and those with 2 males. This suggests that both groups of females received more or less the same number of matings. As mentioned before, males placed together in one container often show either homosexual or sharing behaviour. Such behaviour might cause interruptions to ovipositing or copulating females. The results of this experiment are very similar to observations recorded for alfalfa weevil (LeCato & Pienkowski, 1972a).

Experiment 5. Male status and oviposition

Two groups of 15 females were kept under the following conditions:

(1) 15 females each continuously maintained with a virgin male of the same age group (newly emerged) in an oviposition chamber.

(2) 15 females each continuously maintained with a mated male and not of the same age group in an oviposition chamber.

Table 5.10: Mating of a female with various number of males and oviposition

Females no.	No. eggs deposited		Presence of sperm	
	1 Male	2 Males	1 Male	2 Males
1	22	63	+	+
2	6	27	+	+
3	70	71	+	+
4	41	2	+	+
5	18	16	+	+
6	3	2	+	+
7	34	21	+	+
8	25	6	+	+
9	17	41	+	+
10	9	53	+	+
11	18	43	+	+
12	75	50	+	+
13	26	33	+	+
14	10	58	+	+
15	6	29	+	+

Table 5.11: Male status and oviposition

Pairs no.	Mated			Virgin		
	No.eggs deposited	Sperm female	Sperm male	No.eggs deposited	Sperm female	Sperm male
1	8	–	+	22	+	+
2	31	U+	+	36	+	+
3	2	±	±	70	+	+
4	0	0	0	41	+	+
5	0	0	0	38	+	+
6	0	0	0	37	+	+
7	3	±	+	34	+	+
8	48	±	±	65	+	+
9	3	±	±	37	+	+
10	5	±	±	29	+	+
11	2	+	+	84	+	+
12	0	0	±	94	+	+
13	0	0	±	87	+	+
14	6	±	±	76	+	+
15	5	±	±	58	+	+

Both females and males were killed and dissected under saline water (0.9%). For females the procedure is as mentioned above. For males the testes, together with the vasa deferentia were removed and put onto a concave microscope slide with a few drop of saline solution (0.9%) and examined under the microscope for the presence of sperm. The amount of sperm was indicated by symbols: +, ± and 0.

The results are presented in Table 5.11. A T-test showed a significant difference between the mean number of eggs deposited (P<0.1%). Females kept with virgin males deposited more eggs (mean±SE: 53.87±6.11) than those remated with mated males (mean±SE: 7.53±3.51 eggs). 30% of females kept with mated males did not deposit eggs at all and had no sperm in their spermatheca. 20% of males contained no sperm at all. These results suggest that some males become exhausted or sexually depleted after re-mating with one female. They either did not copulate or did not ejaculate. Similar observations have been made in *Aedes aegypti* (Jones, 1973).

Experiment 6. Male size and oviposition

Two groups of 12 females were kept under the following conditions:

(1) 12 females (>= 20mm length of body) were kept each with a small male (=< 15mm body length) of the same age group in an oviposition chamber.

(2) 12 females (>= 20mm body length) were kept each with a larger male (> 15mm body length) of the same age group in an oviposition chamber.

At the end of the experiment the eggs were recorded as fertile and infertile.

The results are presented in Table 5.12. A T-test showed significant differences between the mean number of eggs deposited (P<1%) and the mean of infertile eggs (P<0.5%). Females with small males deposited fewer eggs (mean±SE: 26±4.17 eggs) than those kept with larger males (57±8.37 eggs). The former also deposited more infertile eggs (8.5±2.38 eggs) than the latter (0.58±0.23 eggs). The results suggest that large males have more success in mating than small ones. This might be because the small males have difficulties in mounting display. Since they would not be able to grasp the thorax and legs of a large female they could easily be carried by the walking females. If they were able to grasp the female's thorax their pygidium might not reach the genitalia of the females. Thus it would be difficult for copulation to be established

Table 5.12: Male size and oviposition

Female no.	Small		Large	
	No.eggs deposited	No.eggs infertile	No.eggs deposited	No.eggs infertile
1	58	27	72	1
2	36	12	78	0
3	41	15	64	0
4	32	7	89	2
5	32	4	35	0
6	21	0	25	0
7	0	0	38	0
8	21	4	46	1
9	32	18	56	0
10	14	8	0	0
11	25	7	94	2
12	0	0	87	1

Table 5.13: Successful mating of one male with several females

No. of females copulated	Male frequency	NFCEM/NFDE
1	0	0
2	0	0
3	3	3/2, 3/3, 3/3
4	4	4/1, 4/2, 4/3, 4/4
5	3	5/2, 5/3, 5/4
6	3	6/2, 6/4, 6/5
7	2	7/3, 7/5

NFCEM: No. of females copulated by each male
NFDE: No. of female deposited eggs (successful mating).

though they could copulate well if the females kept still. Similar observations have been made in some insects such as on Lytta vulnerata LeConte, Epicauta ochrea LeConte and Tegrodera erosa LeConte Meloidae (Pinto & Mayor, 1986); Nezara viridula (Mclain, 1985); and on Brachinus lateralis (Juliano, 1985). It has been argued that fecundity and male mating success are both interrelated. Large males are more likely to mate than small ones (Juliano, 1985; Pinto & Mayor, 1986). In a natural population larger males mate more frequently than small ones (Mclain, 1985). In other cerambycids, this was observed in Monochamus scutellatus (Say) by Hughes & Hughes (1982). They found that large males were far more successful than moderate and small ones in mating and antagonistic encounters with other males.

Experiment 7. Mating success

The experiment was carried out in the laboratory (temperature 22-24°C, 48% RH, under fluorescent light (Philips 36/33 White) at 1700-2300h the time when the beetles are very active. 15 newly emerged males were used and treated as follows:

- Each male was placed in a mating vial (80x35mm in diameter), a female in the same age group introduced, and the couple allowed to copulate. After completion of copulation, indicated by the male moving away from the female or the female from the male, the female was removed and replaced with the second virgin female of the same age group. The previous male and introduced female were again allowed to copulate. This procedure was repeated until the male lost energy or was not keen to copulate for 30 minutes.
- Each female, after being copulated was maintained in an oviposition chamber.
- After the experiment, the females were dissected as usual. The mating success of the male was indicated by the presence of deposited eggs and sperm in the females' spermatheca.

The results are presented in Table 5.13. Data showed that one male is able to copulate with 3 to 7 females in a short period (in a few hours). The average number of matings was 4.8±0.35. However, the females that were mated were not all inseminated. Of the 15 males, 2 were able to inseminate 5 females, 3 inseminated 4 females, 5 inseminated 3 females, 4 inseminated 2 females and one inseminated one female only (mean 3.07±0.30). The results suggest that there was a variability in the

mating success of the males. This might be due to the individual fitness of the males. It was noticed during the experiment that some males, after the first or second mating, became more eager to re-copulate the virgin females that had been newly introduced. On the other hand, some males after the first or second mating became passive or were not keen to mount the females, even though the females were more active in order to be copulated. The results suggest that some males are capable of re-copulating different females, but only one or 2 females could be inseminated. In other words, males were capable of re-copulating but were incapable of ejaculating or transferring sperm into the female genitalia. Ejaculation could be inferred from the presence of sperm in the female's spermatheca. Such behaviour might be due to individual or other factors. Some factors affecting mating will be examined and discussed in the succeeding section.

5.2.6 Some factors affecting mating success

Mating success in sexually reproducing animals is of interest in evolutionary biology due to its potential role in determining the magnitude of variability in natural populations (Pinto & Mayor, 1986). I found during the course of this study that quite a high proportion of males have unsuccessful mating or in other words either they did not copulate or did not ejaculate. In this section some factors that may affect mating success are considered and discussed.

Experiment 1. Mating and temperature

The experiment was carried out at 4 constant temperatures (15, 20, 25, and 30°C; 14 hours daily photoperiod). 40 newly emerged females were used. One group of 10 females was kept at each temperature, and each female was continuously paired with a male of the same age-group within an oviposition chamber that had fresh cut twigs of C. sempervirens for oviposition. At the end of the experiment (7 days) mating occurrence was recorded by counting the number of eggs deposited and observing the presence of sperm in female's spermatheca and male's vasa deferentia. The presence of sperm was indicated by symbols: +, ± and 0.

The observations are presented in Table 5.14. Data showed that females deposited eggs at any temperature except at 15°C. Those which did not deposit eggs had no sperm in their spermatheca. This indicates that successful mating did not occur at 15°C. At 15°C also, the

Table 5.14: Effect of temperature on mating (eggs deposited and the presence of sperm)

Pairs no.	Temperature °C											
	15			20			25			30		
	ED	FS	MS	ED	FS	MS	ED	FS	MS	ED	FS	MS
1	0	0	±	10	+	+	25	+	+	64	+	+
2	0	0	0	9	+	+	35	+	+	76	+	+
3	0	0	±	6	+	+	16	+	+	84	+	+
4	0	0	0	16	+	+	24	+	+	24	+	+
5	0	0	0	24	+	+	42	+	+	36	+	+
6	0	0	±	35	+	+	54	+	+	42	+	+
7	0	0	±	28	+	+	0	0	0	58	+	+
9	0	0	0	0	0	0	48	+	+	41	+	+
10	0	0	±	19	+	+	2	+	+	0	0	0

ED: Number of eggs deposited
FS: Presence of sperm in female's spermatheca
MS: Presence of sperm in male's vasa deferentia.

Table 5.15: Effect of relative humidity on mating (eggs deposited and presence of sperm)

Insects no.	31%			43%			76%			80%			>90%		
	ED	FS	MS	ED	FS	MS	ED	FS	MS	ED	FS	MS	ED	FS	MS
1	25	+	+	0	0	0	27	+	+	2	±	±	0	0	0
2	41	+	+	69	+	+	0	0	0	2	±	±	0	0	0
3	17	+	+	26	+	+	6	+	+	0	0	0	1	±	±
4	20	+	+	1	±	+	41	+	+	18	+	+	6	±	±
5	2	±	±	10	+	+	36	+	+	35	+	+	0	0	±
6	34	+	+	6	±	±	5	±	±	22	+	+	0	0	±
7	37	+	+	30	+	+	2	±	±	4	±	±	0	0	±
8	8	+	+	32	+	+	51	+	+	16	+	+	0	0	±
9	42	+	+	24	+	+	49	+	+	6	±	±	0	0	0
10	68	+	+	18	+	+	32	+	+	2	±	±	0	0	0

ED: Number of eggs deposited
FS: Presence of sperm in the female's spermatheca
MS: Presence of sperm in the male's vasa deferentia.

males showed very little sperm in vasa deferentia (±) or even 0. This indicates that at low temperature sperm production decreases or even stops. These results suggest that in U. cupressiana mating success could not occur at low temperature or in winter. These results correspond to the field conditions where the beetles mostly emerged, mated and oviposited in late spring and summer when the temperature is going up from average 18 to 25°C (see App. 2). Similar observations on Dysdercus fasciatus were made by Clarke & Sardesai (1959) where copulation and oviposition occurred in adults maintained at any temperature except 15 and 40°C.

It has been argued that temperature is one of the most important of the environmental factors influencing various physiological processes of insects. LeCato & Pienkowski (1972b) pointed out that temperature alters the sperm structure and activity, reducing oviposition and eggs hatchability in alfalfa weevil. Low and high temperatures adversely affected the fecundity. They further suggested that low or high temperatures tested can be used to achieve economic control by sterilization or desemination in alfalfa weevil.

In U. cupressiana, low temperature could perhaps be used for desemination since successful reproduction could not occur at low temperature.

Experiment 2. Mating and relative humidity

The experiment was carried out at 25°C constant temperature (14 hours daily photoperiod). 50 females were used. One group of 10 females was kept at each relative humidity. Each female was continuously paired with a male in the same age-group in an oviposition chamber (cylindrical plastic container with tight cover). Saturated salt solution was put in the bottom of the container to maintain the following relative humidities: Group 1, 31%, LiCl solution; Group 2, 43.5%, MgCl solution; Group 3, 75%, NaCl solution; Group 4, 80%, KCl solution; and Group 5, >90%, Distilled water. Six fresh cut twigs of C. sempervirens were put in. The twigs and the beetles were kept out of the solution with wire gauze. Eggs and sperm were recorded as in experiment 1.

The results are presented in Table 5.15. Data showed that in high relative humidity the average number of eggs deposited decreased to 10.7 at 80% RH even almost zero at 90% RH. Also the amount of sperm present in the female's spermatheca was very low (±) at 80% and almost 0 at 90% RH. Sperm in the male's vasa deferentia also very low (± or even

zero) in high RH (80 & >90%). This indicates that sperm production decreased or stopped altogether at high RH. The results suggest that high RH is unfavourable for mating activity in U. cupressiana, low to moderate RH being favourable conditions for mating. These results correspond to the field conditions in that, as mentioned before, most beetles emerged and actively mated and oviposited in late spring and summer when the RH is moderate in spring to low during summer (see App. 3).

Experiment 3. Mating and individual factor ?

The experiment was carried out in conditions suitable for oviposition (25°C constant temperature, 48-54% RH, 14 hours daily photoperiod). 30 newly emerged females were used. Each was kept continuously with a male of the same age-group and size of body, in an oviposition chamber with 6 fresh cut twigs of C. sempervirens for oviposition. After one week or when the beetles died, the number of eggs deposited and the presence of sperm in female's spermatheca and male's vasa deferentia were recorded using the same procedure as in experiment 1. The male's testes were removed and the size was measured.

The results are presented in Table 5.16. Data showed 27% or 8 females did not deposit eggs and had no sperm in their spermatheca. Five of the males who were paired with those females did not have sperm in their vasa deferentia or in the vas efferens (zero), 3 of the males had only little sperm (±). These results suggest that some males of U. cupressiana are unable to produce sperm, i.e., are infertile. The males that produced little sperm can copulate but cannot ejaculate or transfer sperm to female's genitalia (see section 5.2.5). Presumably this is due to some individual (genetic) factors in the males.

Numerous observations have been made on female fecundity by previous workers but scant attention has been given to male potency. However, it has been argued that nutrition plays little part in male reproductive activity. Johanssen (1961) states that starvation does not produce infertile males in Oncopeltus though the testes and seminal vesicles are somewhat smaller than those of fed males of the same age. Similar results had been demonstrated in Cimex by Cragg & Titschack and in Rhodnius by Buxton (Johansson, 1961). Starvation has also been known to lower the activity of the male accessory glands in Rhodnius (Khalifa in Johansson, 1961) and in Tribolium (Palm in Johansson, 1961).

Table 5.16: Effect of individual factor of male on mating (eggs deposited and the presence of sperm) and testes size

Pairs no.	No.eggs	Female Sperm	Male Sperm	Testes Size	
				L	W
1	12	+	+	34	16
2	24	+	+	26	12
3	94	+	+	32	16
4	87	+	+	30	16
5	72	+	+	22	12
6	10	+	+	24	12
7	0	0	±	22	12
8	0	0	0	26	14
9	0	0	±	25	13
10	78	+	+	22	12
11	2	+	+	24	12
12	64	+	+	22	14
13	0	0	0	26	14
14	0	0	±	24	12
15	2	+	+	22	12
16	52	+	+	28	14
17	49	+	+	30	16
18	0	0	±	26	14
19	19	+	+	22	12
20	68	+	+	26	14
21	72	+	+	32	16
22	0	0	0	24	14
23	49	+	+	22	12
24	24	+	+	16	10
25	16	+	+	20	12
26	0	0	0	24	12
27	25	+	+	22	12
28	30	+	+	26	14
29	16	+	+	22	12
30	52	+	+	30	16

L: Length of testes
W: Width of testes
Female Sperm: sperm within female's spermatheca.

There were no differences between infertile and fertile males in the size of the testes in U. cupressiana (see Table 5.16). The beetles that were used in these studies, emerged from field infested twigs. When they were collected they were already mature larvae, prepupae, pupae or teneral adults. So starvation probably did not occur.

Inbreeding may affect the reproductive activity in U. cupressiana. As mentioned before (see Chapter 4), U. cupressiana like other longicorns, has brood trees. Once a tree have been encountered by beetles, the population builds up within that tree. Beetles emerging from the tree mate and deposit eggs in the same tree. This cycle could be repeated several times depending on the size of the tree (see Chapter 6). In the field I found in such tree more than 4 generations (as far as I can tell). Thus, the probability of inbreeding in such a tree is high. In addition, almost specimens or infested twigs that were collected in the field were taken from severely attacked trees or brood trees. Perhaps the unsuccessful mating or incapability of males of U. cupressiana in transfering sperm to female's genitalia might be due to reduced vigor or fitness of males, which, in turn may be due to inbreeding in nature.

The possibility that inbreeding and crossbreeding may affect the number of insects in nature has been demonstrated by Turner (1960) in Oncopeltus fasciatus Dal. He found that inbreeding resulted in loss in vigour and a reduction in number of eggs and in survival of progeny. A similar case had also been observed by Dobzhanzky (Turner, 1960) in Drosophila. However, their observations only looked at female fecundity and did not study male potency.

In this present study both female and male were considered in order to find out the causes of unsuccessful mating or incapability of male in mating success of U. cupressiana population. Unfortunately there was too little time to test these aspects thoroughly. Nevertheless, it is worthwhile to suggest that inbreeding may be involved in fluctuation of U. cupressiana population and other longicorns and seems to be worth testing further.

5.3 OVIPOSITION/ HOST SELECTION

Oviposition behaviour of U. cupressiana has been discussed in a previous Chapter (Section 4.2.5.5). In the present section, studies on host preference or selection strategy and some factors which may affect the oviposition pattern are emphasized.

5.3.1 Host selection

Host selection is an important aspect of the life cycle of insects whose offspring posess only a limited ability to disperse during their feeding stage (Leather, 1985; Tabashnik, 1985). For phytophagous insects, the selection of a host plant for oviposition has significant implications for both insects and plants (Zimmerman et al., 1984).

Insect perspective -

Particularly for those with sedentary larvae it is essential for their eggs to be deposited on plants with acceptable secondary chemistry and enough resources to ensure complete larval development. For some insects, i.e., Panolis flammea, oviposition preferences reflect the trade-off between growth rate and survival (Leather, 1985). It is thus important that the mother selects a host that is of more than marginal acceptability to offspring. Given a choice of hosts, the mother must select the host which will provides the best chance of survival to her offspring, i.e. a high growth rate, a low mortality level etc. For other lepidopterans, adults are able to select host plants that are nutritionally most acceptable to their offspring (Wiklund, 1974; Chew, 1977; Myer et al., 1981; Williams, 1983 ; Daglish et al., 1986 etc). Observations on Tenebrio monitor by Gerber and Sabourin (1984), indicate that females attempted to avoid poor quality food when selecting oviposition sites and also to avoid ovipositing when eggs and larvae were present. In pine sawfly (D. similus) the oviposition rate and the number of survivals are positively correlated (Huber & Hain, 1984), and in Rabdophaga terminalis there was an agreement between plant species selected by females and larvae survival (Ahman, 1984). In another case, phytophagous insects are restricted to a narrow range of acceptable food plants (Courtney, 1981). Even among suitable hosts, the larval fitness may vary and ovipositing females have often (Singer, 1971; Tabashnik et al., 1981) but not always (Courtney, 1981) been found to prefer the species yielding the highest fitness. Jaenike (1978) proposed that the host selection maximises individual fitness although there is no reason to assume that all

females in a population make use of their optimum strategy (Daglish *et al.*, 1986).

Plant perspective -

Plants are often under a strong selective pressure to minimize the amount of damage done by phytophagous insects (Zimmerman *et al.*, 1984). It is very common for plants to respond to herbivores by developing the ability to produce distasteful or poisonous chemicals (Rhoades, 1983; Feeny in Zimmerman *et al.*, 1984; Rudinsky, 1966) or secondary oleoresin (Berryman, 1969; Berryman and Ashraf, 1970). The diversity of herbivore deterrents used by plants makes it exceedingly unlikely that individual insects will be able to detoxify many of the compounds they encounter.

Classically, the phases of the host selection process in insects have been delineated as follows: host habitat finding, host recognition and acceptance, and host suitability (Kogan, 1977). It can be noted that host suitability has nothing to do with the process which consists of actions by the herbivore but is just one of the conditions for success. Furthermore, Kogan has postulated some models of resource selection strategies, most of which involve at least some degree of interplay between chemical and visual stimuli. Numerous examples exist where both chemical and visual stimuli, operating sequentially or simultaneously, play a role in host plant location by a variety of insects (Procop y & Owens, 1983; Courtney, 1981; Yamamoto *et al.*, 1969), etc.

Accordingly, insects are very selective when choosing oviposition sites within these habitats. During the selection of oviposition sites, a large number of physical, chemical, and biological factors are assessed (Gerber & Sabourin, 1984).

Host selection in Cerambycids is still poorly understood. As mentioned previously, cerambycids are characterized by having brood trees, i.e. trees from which the beetles emerge, then mate and deposit eggs without moving away. Consequently, the population builds up in such trees. This is apparently the case in *U. cupressiana* in the field.

In this present study a series of experiments was carried out to elucidate host plant selection and/or oviposition preferences by *U. cupressiana*, particularly host acceptance and host suitability, and some factors determining the oviposition pattern. Almost all the experiments were conducted at 25°C constant temperature, 54% RH, 14 hours photoperiod. The beetles were kept in oviposition chambers (section 5.2).

5.3.1.1 Physical factors of host and oviposition

1. Moisture content of twig

Experiment 1

Ten pairs of newly emerged beetles were used. Each pair was given 5 twigs of C. sempervirens of different moisture content. The differences in moisture content were produced by cutting the twigs at different times before the experiment, and allowing them to dry out for 0, 2, 4, 6 or 8 days. The relative moisture content (RMC) of twigs was determined as mentioned in Chapter 2. At the end of the experiment the number of eggs deposited was recorded.

The results are presented in Table 5.17. A two-way Anova revealed no significant differences between the mean number of eggs deposited on twigs of different RMCs, and between individual females, suggesting that females deposit their eggs on twigs at random with respect to twig moisture.

Experiment 2

Six pairs of newly emerged beetles were used. Each pair was given six twigs of C. sempervirens of different moisture content. The twigs were cut and allowed to dry for 0, 1, 2, 3, 4 or 5 days before using. The RMC of twigs was determined as mentioned before. At the end of the experiment the number of eggs deposited was recorded.

The results are presented in Table 5.18. A two-way Anova again revealed no significant differences in the mean number of eggs deposited on twigs of different RMCs, and between individual females. Females randomly deposited their eggs on twigs. In other words, there is no discrimination of different RMC of twigs by ovipositing females.

Experiment 3

12 pairs of newly emerged beetles were used. Each pair was given six twigs of C. sempervirens of different moisture content. The twigs were cut and allowed to dry for 0, 14 or 28 days before using. The RMC of twigs was determined. At the end of the experiment the number of eggs deposited was recorded.

Table 5.17: Mean number of eggs deposited by females of U. cupressiana on 2, 4, 6, and 8 day cut twigs of C. sempervirens

Treatment (day cut)	RMC (mean ± SE)	Mean no. eggs deposited	F	P
0	83.25 ± 0.63	2.5	2.164	>0.05
2	73.07 ± 0.60	2.8		
4	71.09 ± 0.76	5.8		
6	69.25 ± 0.57	2.4		
8	66.92 ± 1.30	6.8		
Females:			2.231	>0.05
1		5.6		
2		2		
3		1.2		
4		1.2		
5		1.6		
6		2		
7		6		
8		6.4		
9		4.4		
10		10.2		

A 2-way Anova
RMC: Relative Moisture Content

Table 5.18: Mean number of eggs deposited by females of U. cupressiana on 0, 1, 2, 3, 4, and 5 day cut twigs of C. sempervirens

Treatment (day cut)	RMC (Mean ± SE)	Mean no.eggs deposited	F	P
0	80 ± 0.03	7.50	0.732	> 0.05
1	75 ± 0.03	11.67		
2	69 ± 0.01	13.50		
3	40 ± 0.01	9.67		
4	36 ± 0.04	3.83		
5	30 ± 0.01	4.50		
Females:			1.348	>0.05
1		9.67		
2		7.67		
3		12.67		
4		5.33		
5		0.33		
6		15.0		

A 2-way Anova
RMC: Relative moisture content (%).

The results are presented in Table 5.19. A two-way Anova showed significant differences in the mean number of eggs deposited on twigs of different RMC ($P<0.001$). Tukey's test revealed that females deposited significantly more eggs on fresh-cut twigs (0 day) than on 14 day or 28 day twigs. But there is no difference in the mean number of eggs deposited by individual females.

Females could discriminate between fresh twigs and drying ones. This might be due to a chemical cue which in drying twigs was decreasing. Similar observations were made on Osphranteria coerulescens (Sharifi et al., 1970) which were provided with fresh and dry shoots and showed their preference by choosing fresh twigs for ovipositing.

General discussion

In choosing the oviposition sites ovipositing females of U. cupressianna could not discriminate between different RMC of twigs. This was indicated by there being no difference in the mean number of eggs deposited. But they could discriminate between fresh and dry twigs. As mentioned above, the apparently volatile chemicals in dry twigs have decreased. These conditions are more likely to hinder the ovipositing females in depositing their eggs on dry twigs. The effects of the volatile chemical of the host plants on oviposition will be discussed in a succeeding section.

2. Substrate characteristics

Experiment 4. Distance between the tip of twigs and oviposition

Ten pairs of newly emerged beetles were used. Each pair was given 2 twigs of 25cm length of C. sempervirens. At the end of the experiment or soon after the death of the female, the number of eggs deposited was recorded.

The results are presented in Table 5.21 and Fig. 5.5. A two-way Anova showed significant differences in the mean number of eggs deposited ($P<0.01$). Tukey's test revealed that females deposited significantly more eggs between 5 and 10cm from the tip. Also, more eggs were deposited between 5 to 10 and 10 to 15cm from the tip than were deposited over 15cm from tip. Ovipositing females preferred to deposit their eggs in a certain position on the twig. These results are

Table 5.19: Mean number of eggs deposited by females of *U. cupressiana* on 0, 14, and 28 day cut twigs of *C. sempervirens*

Treatment (day cut)	RMC (mean ± SE)	Mean no.eggs deposited	F	P
0	79.9 ± 2.64	16.50	47.001	<0.001
14	22.5 ± 1.07	5.08		
28	16.8 ± 1.25	1.92		
Females:			2.338	>0.05
1		2		
2		15		
3		6.33		
4		8.67		
5		9.33		
6		9.33		
7		9		
8		8		
9		7.67		
10		3.33		
11		10.33		
12		5		

A 2-two Anova
RMC: Relative moisture content (%).

Table 5.20: Mean number of eggs deposited by females of *U. cupressiana* on different age of twigs

Twig age group	Mean no.eggs	F	P
1	12.92a	6.896	< 0.001
2	12.17ab		
3	3.33bc		
4	0.33c		
5	0.17c		
Females:		1.904	> 0.05
1	1.8		
2	0.2		
3	15		
4	14.6		
5	6.4		
6	4.6		
7	11.4		
8	0.6		
9	3.6		
10	4.6		
11	4		
12	2.6		

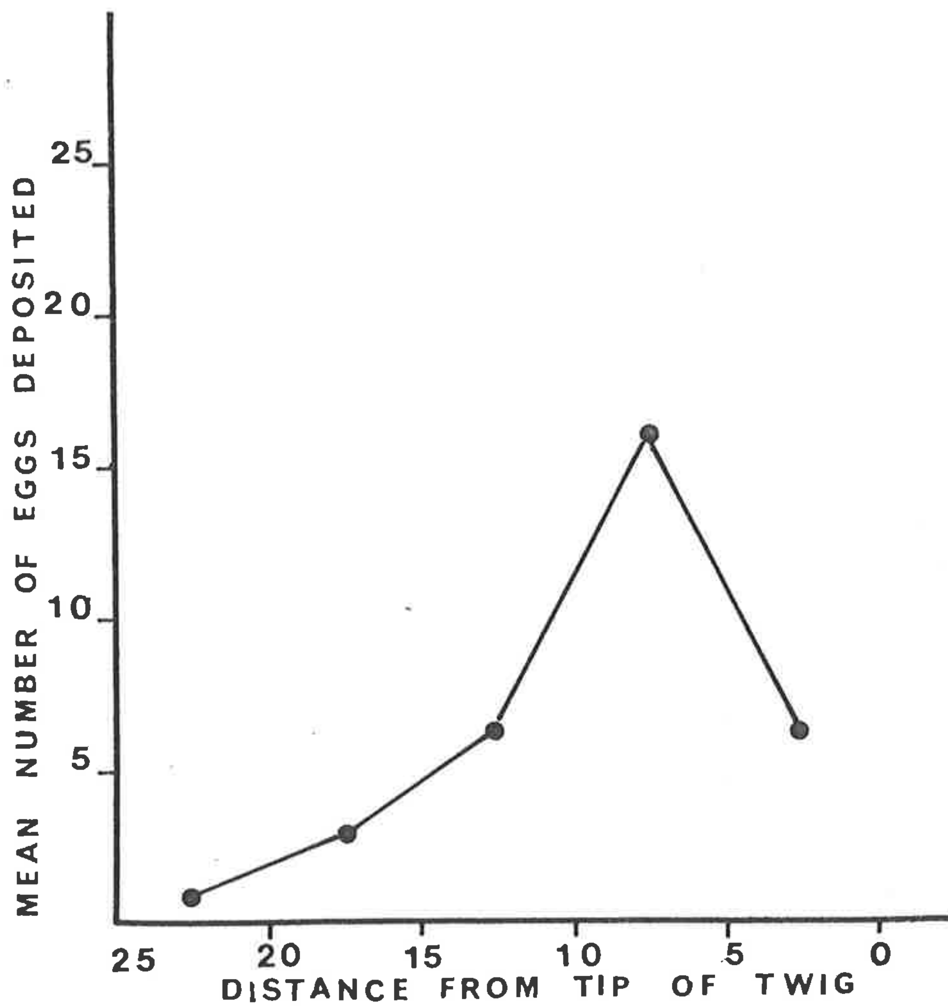
A 2-way Anova
Means followed by the same letters are not significantly different (Tukey test).

Table 5.21: Mean number of eggs deposited on twigs some distance below the tip of twig

Site on twig (position from the tip)	Mean no.eggs	F	P
5 cm	6 bc	5.810	< 0.005
5 to 10 cm	15.1ab		
10 to 15 cm	6.2b		
15 to 20 cm	2.8c		
> 20 cm	1.6c		
Females:		2.234	> 0.05
1	1.8		
2	4.6		
3	4.2		
4	3.8		
5	5.6		
6	11		
7	3		
8	2.2		
9	14.8		
10	12.4		

A 2-way Anova
Means followed by the same letters are not significantly different (Tukey test).

Fig. 5.5: Mean number of eggs deposited and oviposition sites on twigs.



MEAN NUMBER OF EGGS DEPOSITED
25
20
15
10
5
25
20
15
10
5
0
DISTANCE FROM TIP OF TWIG

consistent with those found in potted tree experiments (see section 4.2.5.5).

Experiment 5. Twig age and oviposition

12 pairs of newly emerged beetles were used. Each pair was given 5 fresh-cut twigs of C. sempervirens. Each of these pieces of twigs was taken from a 60cm twig which was cut into 5 pieces of ca. 10cm in length and labelled 1 to 5, starting at the tip. At the end of the experiment the number of eggs deposited was recorded.

The results are presented in Table 5.20. A two-way Anova showed significant differences in the mean number of eggs deposited ($P<0.001$). Tukey's test revealed that females deposited more eggs on twig sections 1 & 2 than on sections 3, 4 and 5. This result suggests that the female deposits more eggs on the younger parts of twigs. This implies, of course, that the ovipositing female can discriminate between the young and old parts of twigs.

Experiment 6. Twig size and oviposition

12 pairs of newly emerged beetles were used. Each pair was given six fresh-cut twigs of C. sempervirens, 15cm in length. Twigs were grouped into 3 sizes, i.e. (1) 2.80-3.85mm, (2) 3.95-5.50mm and (3) 6.40-8.22mm in diameter. The twigs were taken from about the same distance with respect to the tip of the twig (the same age). At the end of the experiment, or after the death of the female, the number of eggs deposited was recorded.

The results are presented in Table 5.22. A two-way Anova showed significant differences in the mean number of eggs deposited ($P<0.005$). Tukey's test indicated that females deposited significantly more eggs on the smallest twigs (2.8-3.85mm). The results suggest that ovipositing females could discriminate between different sizes of twigs, and that they tend to choose small rather than bigger sized twigs for ovipositing.

Experiment 7. Simulated twigs and oviposition

Eight pairs of beetles were used. Each pair was given 5 pieces of glass tube (20cm in length) in different sizes (diameter), i.e. 2, 4, 6, 8 and 10mm. Before tubes were placed in the container they were treated as follows: each tube was spirally covered with filter paper (2mm

Table 5.22: Mean number of eggs deposited on different sizes of twigs

Twig diameter (mm)	Mean no. eggs deposited	F	P
2.80 to 3.85	14.33a	10.265	< 0.001
3.95 to 5.50	3.83b		
6.40 to 8.22	0.17b		
Females:		1.349	> 0.05
1	9.67		
2	13.67		
3	0		
4	16.33		
5	6.33		
6	10.33		
7	4.67		
8	0		
9	5		
10	1.33		
11	3.33		
12	2.67		

A 2-way Anova
Means followed by the same letters are not significantly different (Tukey test).

Table 5.23: Mean number of eggs deposited on various sizes of simulated twigs

Simulated twig size (mm)	Mean no.eggs	F	P
2	9.875	4.9284	< 0.01
4	11.25		
6	.25		
8	.375		
10	0		

Means followed by the same letters are not significantly different (Tukey test).

in width) from one end to the other end, and brushed with host homogenate. The homogenate was made by blending 10g of twig with 100ml distilled water. The number of eggs deposited was recorded daily. The eggs were removed and placed in a petridish with moist filter paper. Tubes were brushed daily with homogenate after the eggs had been removed.

The results are given in Table 5.23. The data show that females deposited almost all their eggs on the small tubes (2 and 4mm), very few on 6 and 8mm, and none on 10mm. This indicates that ovipositing females are discriminating on the basis of size itself and not on some other factors.

Experiment 8. Test of preference

The experiment was carried out in the laboratory (20 to 25°C, 48% RH, fluorescent light (Philips 36/33 White). Five mated females were tested for their preference on 3 sizes of glass tube (2, 4, and 8mm). Each female was alternately placed in a plastic container, and was then offered a tube which had been treated as in experiment 7, for a maximum of 5 minutes or until the beetles had moved away (timed from when the beetles alighted on the tube until they moved away). The tube was replaced with an other tube as in following seguences:
2-4-8-4-2-8-8-4-2-4-8-2-8-2-4-2-4-8-4-8-2-8-2-4-2-8-4-4-2-8. After finishing these sequences, the female was replaced with another female and treated as the first one, etc, till the fifth one. The time spent sitting or alighting on each tube was measured by using a stop watch. The number of probings, and the number of eggs deposited, were recorded.

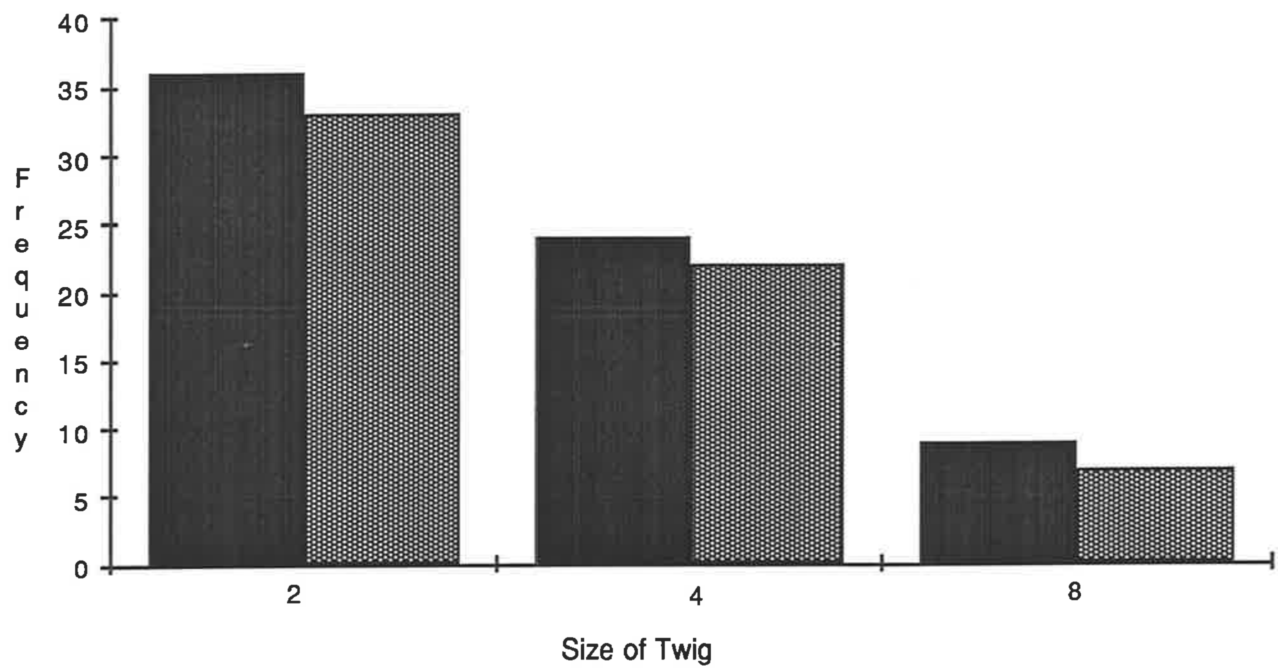
The results are exhibited in Table 5.24, Fig. 5.6 & App. 20. The data show that there was a strong relationship between size of tubes, time spent, and number of eggs deposited. On small size (2 and 4mm) tubes females spent almost all the time offered (300 seconds), sitting and bending their abdomens. As a result there was a high frequency of eggs (one or 2 eggs) deposited on the small tubes. In other words, frequency of the longest time (300 seconds) or frequency of successful time (time when eggs were deposited) was high on small (2 and 4mm) tubes and low on large tubes (8mm). This suggests that on a suitable substrate, ovipositing females used almost all their time for ovipositing. As mentioned previously (see section 4.2.5.5) once the female has alighted on a tree, she deposits almost all her eggs on that tree. So in the field it might happen that a gravid female deposits almost all her eggs on the tree

Table 5.24: Frequencies of successful time (eggs deposited), number of eggs deposited per one turn offered, and time spent alighting by five females and twig size

Twig size (mm)	No.eggs	Frequency of egg number per spent time						
		1	2	3	4	5	6	7
2	0	9	1	0	0	0	0	7
	1	0	0	0	0	0	0	13
	2	2	1	0	1	0	0	16
4	0	17	5	2	0	0	0	1
	1	0	0	1	0	0	0	8
	2	0	0	0	0	0	0	14
8	0	27	7	2	1	2	0	1
	1	0	0	0	0	0	0	8
	2	0	0	0	0	0	0	0

Time spent:
(1) 0 to 49 seconds, (2) 50 to 99 seconds
(3) 100 to 149 seconds, (4) 150 to 199 seconds
(5) 200 to 249 seconds, (6) 250 to 299 second
(7) 300 seconds.

Fig. 5.6: Relation between oviposition and twig diameter (size). Solid bars are frequency of the number of trials of which beetles spent the whole 5 minutes offered on twigs, dotted bars are frequency of the number of trials of which beetles deposit eggs.


40
35
30
25
20
15
10
5
0
Frequency
2
4
8
Size of Twig

from which she emerged, and then flies on to an adjacent tree with the few eggs that are left within her abdomen. This suggestion is supported by the observations that in the field a newly attacked tree could commonly have only one or 2 dry twigs as the result of establishment of first instar larvae (L1).

General discussion

In selecting oviposition sites, the female of U. cupressiana can discriminate between twigs with respect to both age and size. Small size and young twigs are chosen for oviposition. As mentioned in Chapter 4, ovipositing females mostly deposited their eggs on small twigs (2mm in diameter), 7 to 30cm from the tip of the twig on potted trees. These observations corresponded to the field observations, where most eggs were deposited on small twigs, indicated by small dry twigs on the crown of trees after the establishment of young larvae. Oviposition is also indicated by the presence of chorion which remains attached to twigs for several months after the first instar larvae have penetrated the twig. Apparently, areas more than 15cm below the tip of twigs for an old tree or 30cm for a young potted tree, and larger in diameter than 6mm, are difficult for young larvae to bore into. In addition, because larvae usually tunnel the twig distally (upward) 4 to 13cm (section 4.2.5.5), after penetrating, eggs are very seldom deposited at the tip of twigs. Similar results were obtained for Osphranteria coerulescens by Sharifi et al., 1970), for Oberes schaumii (Nord et al.; 1972a, 1972b), for Pissodes strobi (Sullivan, 1960, 1961), for Arrhenodes minutus (Buchanan, 1960), and for Hexamithodera semivelutina (Rondonuwu et al.,1979), where ovipositing females are able to discriminate between the sizes of trees, branches, or twigs, and to choose those suitable for oviposition.

5.3.1.2 Chemical factors of host- and non-host plant and oviposition

1. Host- and non-host plant

Experiment 1. Non-host plant

Eight pairs of newly-emerged beetles were each given fresh-cut twigs of 4 species of Australian native trees, i.e., Callitris collumelaris, Eucalyptus steedmanii, Acacia longifolia, and Melaleuca stypheliodes. Two twigs were taken from each species and inserted through

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a hole in the lid of a small plastic vial filled with water. After 7 days, the number of eggs deposited was recorded. The females were then transferred to containers with twigs of C. sempervirens for one night.

The results are given in Table 5.25. Most females did not deposit eggs except for 2 females which deposited 1 egg each on Callitris twigs. This indicates that the female of U. cupressiana retains her eggs in conditions without host plants. However, on transfer to the containers with host twigs, all females deposited eggs on the first night.

Experiment 2. Host and various non-host plants

Eight pairs of newly-emerged beetles were given 2 twigs of the host plant (C. sempervirens) and non-host plants (Callitris, Acacia, Eucalyptus, and Melaleuca) in vials of water. After 7 days, the number of eggs deposited was recorded.

The results are presented in Table 5.26. Observations revealed that all females deposited eggs either on Cupressus or Callitris, and none on other species of non-host plants. This suggests that the presence of the host plant triggers oviposition, on one other species, at least. In other words, the chemical cue of the host plant stimulates egg deposition. The mean number of eggs deposited per female, however, was very low (range, 2-8; mean±SE, 3.8±0.86). This implies that there was an interference of non-host volatile chemical that deterred oviposition.

Regardless of other non-host species, the T-test showed no significant differences between the mean number of eggs deposited on Cupressus and Callitris ($P>0.05$). To test the preference of female beetles between both species of tree the next experiment was carried out.

Experiment 3. Host and non-host plant

Eight pairs of newly emerged-beetles were given freshly cut twigs of Cupressus and Callitris in vials of water. After 7 days, the number of eggs was recorded.

The results are given in Table 5.27. A T-test shows no significant difference in the mean number of eggs deposited between tree species ($P>0.05$). This result is consistent with the result above. The test implies that there is no discrimination by ovipositing females between Cupressus and Callitris. This might be due to similar chemical stimuli being found in both species of plants, since Cupressus and Callitris are coniferous.

Table 5.25: Number of eggs deposited on non-host plant

Non-host plant	Total number of eggs deposited
Callitris collumelaris	2
Eucalyptus steedmanii	0
Acacia longifolia	0
Melaleuca stypheliodea	0

Table 5.26: Mean number of eggs deposited on host and non-host plants

Host and non-host plants	Mean number of eggs deposited	Remarks
Cupressus	2.3 ± 0.59	host
Callitris	1.5 ± 0.50	non-host
Acacia	0	non-host
Eucalyptus	0	non-host
Melaleuca	0	non-host

Table 5.27: Mean number of eggs deposited on *Cupressus* and *Callitris*

Host and non-host plants	Mean number of eggs deposited	Remarks
Cupressus	5.13 ± 1.08	host
Callitris	4.00 ± 1.31	non-host

Experiment 4. Oviposition on *Callitris*

The experiment was carried out in a plant growth room (25°C, 14 hours daily photoperiod). Eight pairs of newly-emerged beetles were used. Two pairs were released in each of 4 cages (75x75x100cm) with 2 potted plants of *Callitris collumelaris* in each cage. After 7 days, the number of eggs was recorded.

Females deposited their eggs normally on *Callitris* in the absence of the host plant. The usual number of eggs was deposited (range 6-21 eggs per tree). This result suggests that the chemical cue is more likely to play an important role in stimulating oviposition, since both genera of tree are known to be genetically isolated (Lord, 1974; Harrison, 1975; Boland *et al*. 1985). Apparently, in both *Callitris* and *Cupressus*, there exist volatile chemical compounds that can stimulate egg deposition.

Discussion

Since the ovipositing female can retain her eggs on a non-host plant, and immediately lays them in the presence of a host plant, it is obvious that she makes certain demands on the environment which must be met before she will deposit eggs. Under unfavourable environmental conditions such as lack of suitable places to oviposit, many species of insects reabsorb their eggs (Raabe, 1986; Hinton, 1981). Others retain their eggs for a certain time but, as they grow older searching for suitable oviposition sites, they also become less particular and in time may deposit almost anywhere, e.g., *Macroglossum stellatarum* and *Catacala* (Hinton, 1981). In *U. cupressiana*, the mated female retains her eggs until death if the host plant is not present. Her willingness to oviposit on *Callitris* might be due to the presence, in both *Cupressus* and *Callitris*, of the same volatile chemical or secondary compounds that can trigger egg deposition.

Females deposited very few eggs on *Callitris* which was placed together with other non-host twigs, and they deposited less than normal if they were provided with host and non host twigs. This might be due to the interference of non-host volatile chemical that deterred the oviposition. The female beetles deposited their eggs normally, however, if they were provided with host twigs only. This implies that increasing the concentration or amount of host volatile chemical may trigger egg deposition. Similar observations were shown for *Amrasca devastans* by

Saxena and Basit (1982a, 1982b) where the number of eggs deposited by ovipositng females reduced in the presence of the non-host plant.

There appears to be no preference between Cupressus and Callitris, irrespective of the original host. Dutty (1953) and Craighead (1923) in applying Hopkin's host selection principle or theory of larval memory, (female insects prefer to oviposit on plant species where they themselves fed as larvae) to Cerambycid beetles, argued that the condition of the host is the most important factor in oviposition, and a species will select a new host in the optimum condition, rather than an old host in unfavourable conditions.

On the other hand, Knull (in Saliba,1974) and Saliba (1974) describe the Cerambycid female as selective primarily as to host and secondarily as to condition. The latter view was found to apply to U. cupressiana. It was obvious that in conditions without host plants oviposition did not occur. The female's readiness to deposit eggs on Callitris indicates that the factor is chemical rather than physical in nature. It might suggest that both oviposition preferences and detailed behaviour patterns involved in oviposition are inherited characteristics of the species.

This finding indicates that the earlier host of U. cupressiana was Callitris spp, later extended to Cupressus spp. It is possible that isolation has produced host specificity to the Cupressus spp. According to Morgan (peronal comm.), this species was found attacking Callitris spp. in the field. However, during the course of this study the author did not find such a case, since Callitris spp. are very rarely found in the Adelaide plains, where U. cupressiana are abundant on Cupressus spp. In addition, Cupressus spp. are introduced plants, while Uracanthus spp. are indigenous in Australia. It is clear that oviposition preferences and behaviour are important factors in the ecology of phytophagous insects and especially U. cupressiana. Hence, further studies are required in the field behaviour of U. cupressiana.

2. Host species

Experiment 1. Laboratory studies

Ten pairs of newly-emerged beetles were used. Each pair was maintained in an oviposition chamber with fresh-cut twigs of 7 species and varieties of Cupressus, i.e. C. sempervirens, C. tolurosa, C. glabra,

C. macrocarpa horizontalis Aurea (golden cypress), C. m. horizontalis (green cypress), C. m. bruniana and C. cashmeriana. Each species or variety was represented by one twig. All 7 twigs were put in a small vial with water and a perforated lid. After 7 days, or following the death of the female, the number of eggs deposited was recorded.

The results are presented in Table 5.28. A 2-way Anova shows no significant differences in the mean number of eggs deposited ($P>0.05$). Females deposited their eggs on all species and varieties of Cupressus which were tested. This suggests that there are no preferences among species of Cupressus by ovipositing females. Between female beetles, however, there was a significant difference ($P<0.01$). Data showed that 2 females did not deposit eggs at all. This might be due to individual factors of beetles (see section 5.2.5).

Experiment 2. Field cage studies

The experiment was carried out at the Waite Agricultural Research Institute orchard in Nov.1984. Seven species and varieties of Cupressus potted plants (ca. 3 years old) were used. Seven potted plants of 7 species were randomly placed in circle within a cage (2x2x2.5m, with aluminium frame and plastic mosquito-net covers. Seven cages were used as replicates. Two weeks before the experiment, all plants were trimmed to present a similar surface area on each tree. In each cage 6 pairs of newly-emerged beetles were released. After 7 days the number of eggs deposited was recorded and labelled with aluminium tags. There was somtimes an error in counting the number of eggs directly within the trees, i.e. a few eggs were not counted. To reduce the error, 6 weeks after the eggs deposited, and the first instar larvae had established, the number of dry twigs and freshly labelled twigs were counted.

The results are presented in Table 5.29. A 2-way Anova shows no significant difference in the mean number of eggs deposited ($P>0.05$). Females deposited their eggs on all species and varieties of Cupressus which were tested. This suggests no preference among Cupressus spp. by ovipositing females. These results agree with the laboratory experiment (see experiment 1).

It was obvious that U. cupressiana could attack all species and varieties of Cupressus tested, and there were no preferences among those species, even though some species such as C. cashmeriana and C. glabra were rarely found in the field. The remaining species are very

Table 5.28: Mean number of eggs deposited on twigs of *Cupressus* spp.

Host species	Mean number of eggs deposited	F	P
C. sempervirens	2.1	1.53	>0.05
C. glabra	1		
C. tolurosa	1.9		
C. macrocarpa horizontalis Aurea	1		
C. macrocarpa horizontalis	1.9		
C. macrocarpa bruniana	2.2		
C. cashmeriana	1.7		
Females:		4.05	<0.01
1	1.7		
2	0		
3	2.6		
4	1.9		
5	0		
6	2.6		
7	2.6		
8	2.1		
9	1.9		
10	1.6		

A 2-way Anova.

Table 5.29: Mean number of eggs deposited on potted trees of *Cupressus* spp.

Host species	Mean number of eggs deposited	F	P
C. sempervirens	5	1.31	>0.05
C. glabra	3.14		
C. tolurosa	4.57		
C. macrocarpa horizontalis Aurea	5.29		
C. macrocarpa horizontalis	2.71		
C. macrocarpa bruniana	1.57		
C. cashmeriana	4.57		
Females:		1.24	>0.05
1	2.7		
2	3.6		
3	3.6		
4	3.6		
5	6.6		
6	2.6		
7	4.3		

A Two-way Anova

Table 5.30: Mean number of eggs deposited and host plant chemical

Treatment	Mean number of eggs deposited	F	P
dry + homogenate	50.25a	33.53	<0.001
wet + homogenate	8.38b		
dry no homogenate	0 b		
wet no homogenate	0 b		

Means followed by the same letters are not significantly different.

common. The results of these 2 experiments are consistent with the fact that in the field almost all common species were seriously attacked by U. cupressiana, particularly at certain locations in the Adelaide Plain, and in other parts of South Australia, Victoria, and New South Wales.

3. Crude twig homogenate

Experiment 1. Oviposition and host crude homogenate

32 pairs of newly-emerged beetles were used, each pair being kept in an oviposition chamber with 4 simulated twigs. There were 4 treatments with 8 replicates.

Simulated twigs were made from 24cm diameter filter papers. One paper was cut in half and each half was tightly rolled until it become ca. 2.5mm in diameter and was glued on the inside surface away from the edges. Crude twig homogenate was made by blending 10g of young twigs of C. sempervirens with 100ml distilled water. The simulated twigs were treated as follows: (1) Twigs were soaked in crude homogenate until they were saturated. They were then removed, and put on a piece of paper towel for 15 minutes to allow them to dry. (2) Twigs were treated the same as in (1) but after they were dry, were put again in a small vial with water in it about one third from the bottom of vial. (3) Twigs were treated the same as in (1) but homogenate was replaced with distilled water. (4) Twigs were treated the same as in (2) but homogenate was replaced with distilled water.

The number of eggs was recorded daily until the end of the oviposition period. The twigs were replaced with new ones daily. Eggs were taken off the old twigs and put in a petridish with moist filter paper.

The results are presented in Table 5.30. A one-way Anova shows significant differences in the mean number of eggs deposited ($P<0.001$). Tukey's test revealed that females oviposited eggs in an amount which is significantly high on simulated dry homogenate twigs. No eggs were deposited on simulated twigs without homogenate. On wet homogenate twigs the number of eggs deposited was low. Perhaps the high humidity within the chamber affects egg deposition (see section 5.3.1.3) or the twig surface is too wet and unsuitable for ovipositing. As previously mentioned, under unfavorable environmental conditions such as lack of

suitable oviposition site, the female retains her eggs or deposits very few.

Experiment 2. Oviposition and host- and non-host crude homogenate

24 pairs of newly-emerged beetles were used. Each pair was given simulated twigs. Crude twig homogenates were made from host twigs of 3 species of native trees, i.e., Eucalyptus sp, Melaleuca sp, and Acacia sp. Three treatments were used with 8 replicates as follows: (1) twigs were soaked in host homogenate until saturated, removed, allowed to dry on a piece of paper towel, and placed in the chamber with a pair of beetles. In each chamber 4 twigs were placed. (2) 8 twigs were soaked in host homogenate and 24 twigs in non-host homogenate (8 twigs in each species of tree homogenate). They were then removed, dried on a piece of paper towel, and put in the chamber. Four twigs were put in each chamber, one for each species of tree homogenate. (3) Twigs were treated the same as in (1) but homogenate was replaced with distilled water as a control. The number of eggs deposited was recorded daily. The eggs were removed and placed in petri dishes with moist filter paper. The twigs were replaced with new ones daily.

The results are presented in Table 5.31. A one-way Anova shows significant differences in the mean number of eggs deposited ($P<0.001$). Females deposited significantly more eggs on twigs with host homogenate only (Tukey's test). No eggs were deposited on twigs with non-host homogenate. The mean number of eggs deposited on twigs with host homogenate in treatment 2 was low, indicating that the presence of a non-host chemical reduces the number of eggs laid on the host. These results are consistent with the findings in experiment 2 in Section 1.

Experiment 3. Oviposition and alpha-pinene

Six pairs of newly-emerged beetles were used. Each pair was kept in an oviposition chamber with simulated twigs soaked in aqueous emulsions at 0.25% concentration (100ml of distilled water + 0.25ml alpha-pinene). For a control, twigs were soaked in distilled water. The number of eggs deposited was recorded, and twigs were replaced with new ones daily.

The data showed no significant difference between control and treatment. Two females deposited a few eggs (2 and 5 respectively) and the others none. This indicates that alpha-pinene does

Table 5.31: Mean number of eggs deposited and host + non-host plant chemical

Treatment	Mean number of eggs deposited	F	P
Host chemical	45a	14.64	<0.001
Host + non-host chemical	33.25a		
Non-host chemical	0b		

Means followed the same letters are not significantly different.

Table 5.32: Oviposition response of females of <u>U.cupressiana</u> at 8 constant temperatures

T (°C)	OP (day)	Mean no.eggs per female		HU	SP
		Total	Per day		
15	6	1c	0.17	4.56	+-
20	5	10bc	2.0	28.80	+
25	4	18.67bc	4.67	43.04	+
27.5	4	21.67bc	5.29	53.04	+
30	3	26.17ab	8.72	47.28	+
32.5	2	24.67ab	12.33	36.52	+
35	2	31.00ab	15.5	41.52	+
37.5	2	11.17bc	5.59	46.59	+-

Means followed by the same letters are not significantly different (P = 0.02, Tukey test)
T: temperature, OP: oviposition period
HU: heat unit, SP: sperm presence.

not have enough power to stimulate egg deposition. Perhaps alpha-pinene should be combined with other volatile compounds of the host plant such as beta-pinene, camphane, etc. so as to be strong enough to stimulate oviposition. Unfortunately, at the time of the experiment, other compounds were not available.

Discussion

It is obvious that a chemical factor or volatile chemical substances produced by the host play an important role in the egg deposition of *U. cupressiana*. Where there is no host, the ovipositing female retains her eggs. She does so until the end of her life, if a host is not available. Hinton (1981) stated that there is little doubt that the odour and/or taste of the plant are usually of much greater significance in triggering oviposition behaviour than any other factors. Furthermore, it was noted that volatile terpenes attract scolitid beetles to the tree for oviposition.

Ovipositing female beetles vary in their response to secondary plant substances such as volatile terpenes. In *U. cupressiana*, alpha-pinene is not an attractant, and might even be repellent. It is also repellent for *Myclopphilus* (Kangas *et al*., in Hinton, 1981) though it is an attractant for *Hylastes nigrinus* and *Dendroctonus pseudotsugae*. The latter are also attracted to Limonene and Camphane (Rudinsky, 1966; Hinton, 1981). It is also obvious that the presence of volatiles of a non-host plant reduces the total number of eggs deposited by the female of *U. cupressiana* on the host plant. Apparently, non-host plant volatiles deterred oviposition by *U. cupressiana* in the laboratory as well as in the field.

Saxena & Basit (1982a) have demonstrated that the reduction in the number of eggs deposited by leafhoppers on its host leaves is caused by one of the following:
"- A reduction in the proportion of insects colonising the host leaves as by the non-host sponge gourd the volatiles of which enhance the insect's ovipositional response. - A reduction in egg deposition by the insects after their arrival on host leaves by the volatiles of the non-host castor leaves which do not affect the arrival/stay of the insects on host leaves."

In *U. cupressiana*, either in the field or in the laboratory, the latter might be working, since in the laboratory both host- and

non-host twigs and simulated twigs with host and non-host homogenates were visited but eggs were deposited only on host twigs or simulated twigs with host homogenate.

The interference with the establishment of the phytophagous insect on its host plants by certain non-host plants has been demonstrated for leafhopper (Amrasca devastans) (Saxena & Basit, 1982a; 1982b); Phyllotreta cruciferae (Tahvanainen & Root in Perrin & Phillips, 1978); Plutella xylostella by Buranday & Raros in Perrin & Phillips, 1978; P. xylostella, Aleyrodes brassicae, and Empoasca kraemeri (Perrin & Phillips, 1978).

It has been argued that mixed- or intercropping of plant or cultivars is a common cultural practice in many countries and among its potential advantages are effects on the population dynamics of pests which may minimize crop damage (Way, 1977 in Perrin and Phillips, 1978).

The findings of this study, as well as the examples above, suggest that it might be worthwile to use a mixed cropping practice such as a combination Cupressus sp. and native trees as one of the ways of controlling the U. cupressiana population.

5.3.1.3 Physical factors and oviposition

1. Temperature

Experiment 1. Various constant temperatures and oviposition

The 48 pairs of beetles used were newly-emerged from twigs which had been collected from the field. Each pair was maintained in a jar (12x7cm) with a mosquito-net cover. They were allowed to copulate for ca. 2 hours. In each jar was then placed 5 freshly cut twigs of C. sempervirens for oviposition. A group of 6 jars was placed in each of 7 controlled temperature chambers (15, 20, 25, 27.5, 30, 32.5, and 37.5°C). The number of eggs deposited was recorded daily. The eggs were then removed and put into a petridish with moist filter paper. Twigs were replaced daily with new ones. The observations were made until the termination of the oviposition period (7 days). Both male and female were dissected and observed for the presence of sperm. Data were analyzed using Anova, with Tukey's test used to compare the means at various temperatures. Linear regression analysis was also done, with total egg production per female regressed against temperature (15, 20, 25, and 30°C).

The intercept method was used to estimate the threshold temperature for oviposition.

The results are given in Table 5.32, Figs. 5.7, 5.8, and 5.9. Analysis of variance shows significant differences in the mean number of eggs deposited ($P<0.002$). The mean number of eggs deposited per female changed with temperature in a non-linear relationship (see Fig 5.7). The fecundity increased linearly with temperatures from 15 to 35°C, peaked at 35°C, then decreased sharply. At 32.5°C the number of eggs per female diverged from the linear line. This was possibly due to the variability of insects and also to the number of replications being only 6. The oviposition rate increased linearly with temperature from 15 to 35°C, peaked at 35°C, and then decreased sharply at 37.5°C (see Fig. 5.8). When the oviposition period was plotted against temperature, however, a significant negative relationship resulted (Fig 5.8). The oviposition period ranged from 2 to 6 days. At high temperatures most eggs were produced within 2 days after the emergence of adults. The mean fecundity ranged from 1 to 31 eggs per female. In the lowest (15°C) and highest temperatures (37.5°C) the number of eggs produced was reduced. This indicates that low and high temperature can affect the oviposition activities. When the insects were dissected, a few sperm (±) were found in the spermatheca of females subjected to 15 and 37.5°C, while a greater number (+) was found in the spermatheca of the remaining females. This might suggest that at temperatures of 15 and 37.5°C no repeated matings occurred, or that there was no transfer of sperm during the trial. In most dissected males, no sperm were seen except in one male from the group subjected to 15°C which had a bundle of sperm in his vasa deferentia. The sperm had probably been produced before the trial started. As mentioned before, insects had been allowed to copulate before the trial. This indicates that in low or high temperatures the transfer of sperm did not occur.

These results are consistent with the findings in section 5.2.6. According to Henneberry & Leal (1979), high temperature either kills functional sperm or interferes with sperm transfer or both. Furthermore, Le Cato & Pienkowski (1972a, 1972b) have demonstrated that in alfalfa weevil low and high temperatures possibly caused damage to both eggs and stored sperm. In *U. cupressiana*, it is obvious that low and high temperatures may affect the sperm production or transfer but not affect the eggs since within the abdomen of females mature eggs are found. In 15°C

Fig. 5.7: Various constant temperatures and the number of eggs deposited.

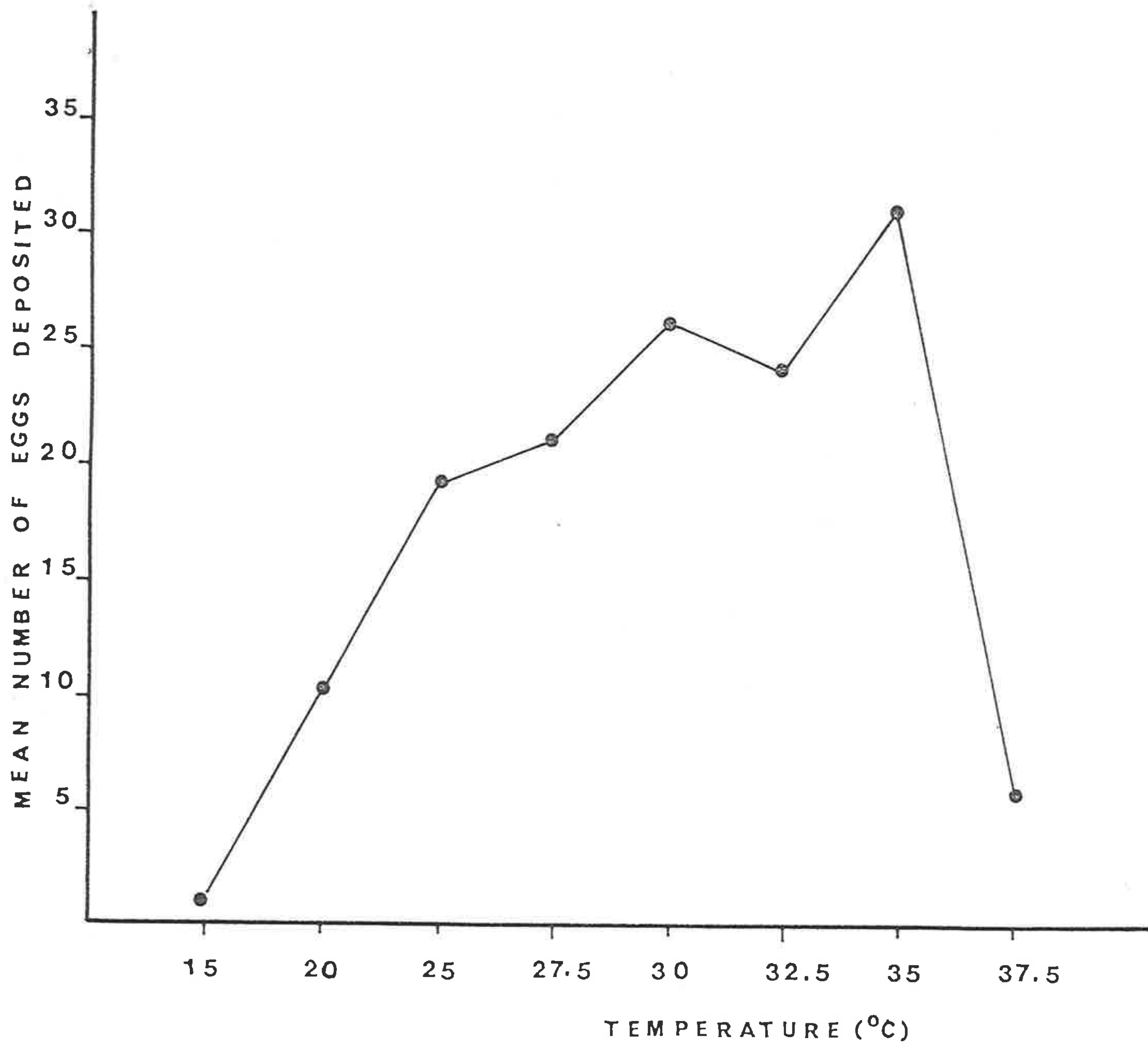

MEAN NUMBER OF EGGS DEPOSITED
35
30
25
20
15
10
5
15
20
25
27.5
30
32.5
35
37.5
TEMPERATURE (°C)

Fig. 5.8: Various constant temperatures and oviposition rate.

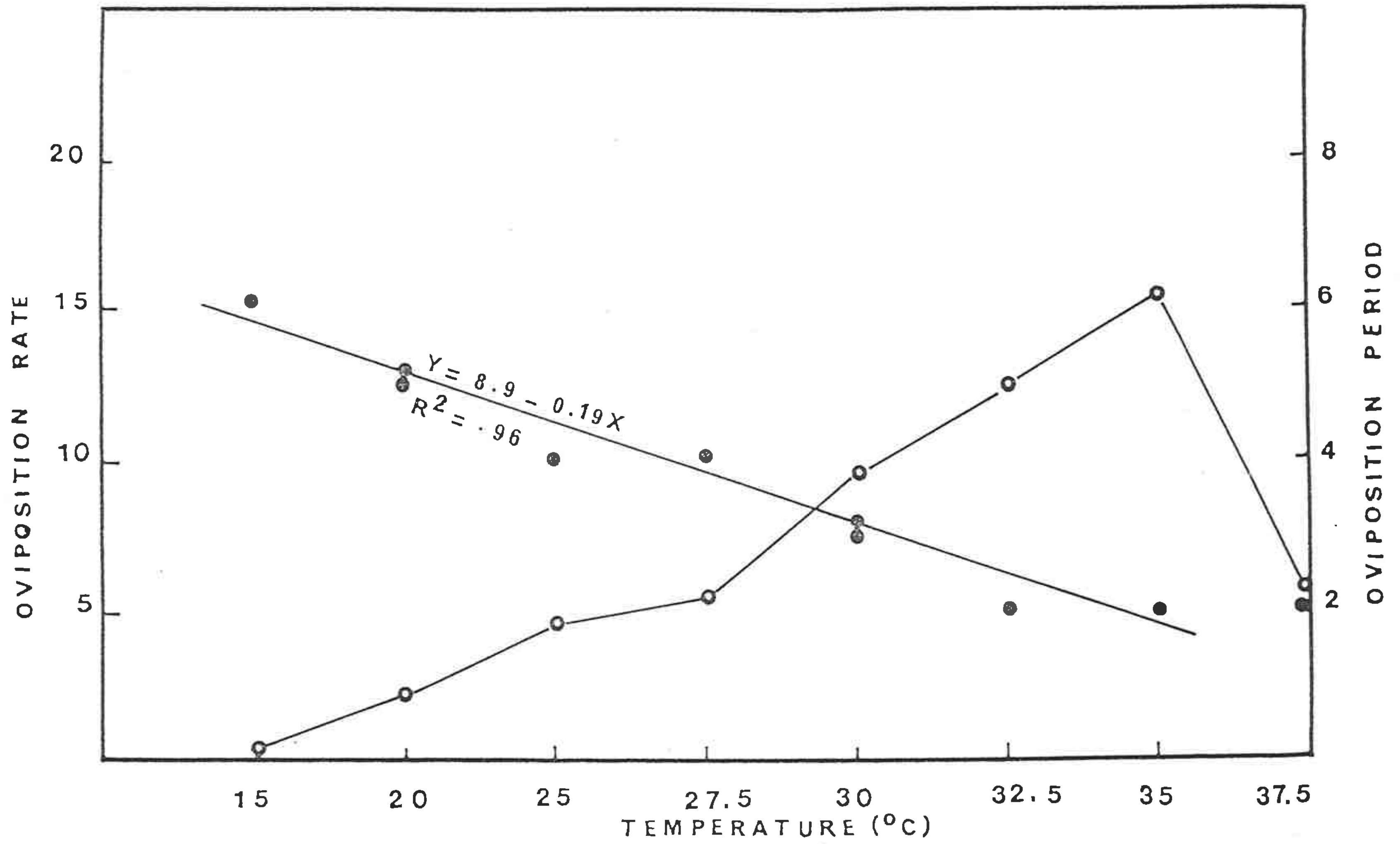
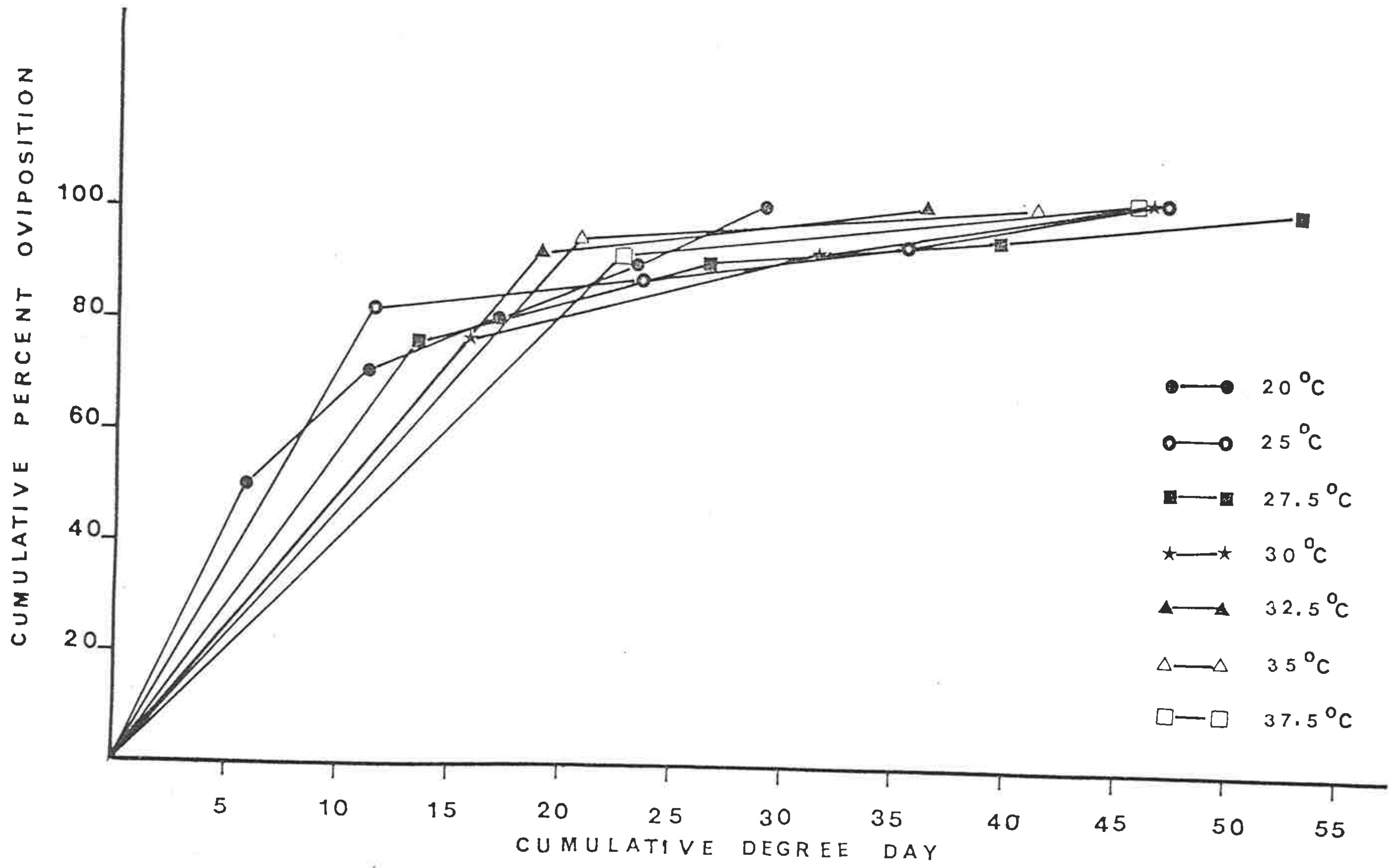

20
15
10
5
OVIPOSITION RATE
8
6
4
2
OVIPOSITION PERIOD
Y = 8.9 - 0.19X
R2 = ·96
15
20
25
27.5
30
32.5
35
37.5
TEMPERATURE (°C)

Fig. 5.9: Cumulative degree day and cumulative percent oviposition


CUMULATIVE PERCENT OVIPOSITION
100
80
60
40
20
5
10
15
20
25
30
35
40
45
50
55
CUMULATIVE DEGREE DAY
20 °C
25 °C
27.5 °C
30 °C
32.5 °C
35 °C
37.5 °C

only 4 females deposited a few eggs and 2 others did not. This indicates that low temperature is not suitable for oviposition. As mentioned previously (see section 5.2.6), low temperatures are not suitable for mating. In this experiment all females had already been allowed to copulate for 2 hours before the experiment commenced. Thus, low temperature is unfavorable for U. cupressiana reproduction. Certainly, no beetles emerge during cold winter temperatures in the field.

In high temperatures (30 and 35°C) females deposited a high number of eggs. Since the female U. cupressiana deposits eggs only at night (see Chapter 4), high nocturnal temperatures may primarily affect oviposition. Thus, in high nocturnal temperatures, a large U. cupressiana egg population should be produced. Similar observations in Elasmopalpus lignosellus are found by Mack & Backman (1984) and in Liriomyza trifolii (Parella, 1984).

As mentioned previously (see section 4.2.5.1), the number of beetles emerging increases with temperature. Thus there is no doubt that some outbreaks of cypress twig borer in South Australia during summer can be associated with high temperatures. Only a few eggs were deposited when females were held at a constant 15°C, a temperature probably approaching the threshold temperature of oviposition. The relationship between mean number of eggs deposited per female and temperature (20, 25, and 30°C) was expressed by the regression equation $Y = -22.14+1.16X$ ($T=24.01$, $P<0.05$, D.F=1, $R2=0.99$). The high R2 value demonstrates the small amount of variability in oviposition at the temperatures tested. Solving X with $Y = 0$ yields 14.28°C, which is the theoretical threshold temperature for oviposition. Day-degrees (Heat Unit) were calculated using the base temperature (14.28°C).

When the cumulative relative distribution of oviposition was plotted against cumulative degree-days, it displayed a strong relationship. About 90% of all oviposition occurs within 30 to 35 degree-day of oviposition period (see Fig 5.9). This value coresponds with the estimated mean degree-days of the female oviposition period (see Table 5.32). This finding may be useful in predicting when a female will oviposit, and hence in predicting potential damage or infestation in the field.

Experiment 2. Fluctuating temperatures and oviposition

The experiment was carried out under laboratory conditions. Eight pairs of newly emerged beetles were used. They were allowed to copulate for ca. 2 hours before the trial. Each pair was maintained in a plastic container with 6 fresh cuts of twig of C. sempervirens for ovipositing. The number of eggs deposited and the temperature were recorded daily. The experiment was terminated after 7 days.

The results are given in Table 5.33. The data show that only 2 females deposited a few eggs (2 and 4 eggs) and most were infertile. The temperature recorded during the trial ranged from 9 to 17°C. This indicates that at low nocturnal temperatures, oviposition does not occur. When the same beetles were moved to 25°C constant temperature, they deposited eggs soon after. Such a case may happen in the field since in summer the temperatures fluctuate widely, particularly nocturnal temperatures. Hence, it can be predicted that low nocturnal temperatures in spring and summer prevent female U. cupressiana from depositing eggs.

2. Humidity

Experiment 1. Humidity and oviposition

The experiment was carried out at 25°C, 54-10% RH and 14 hours daily photoperiod. Six groups of 8 pairs of newly emerged beetles and 6 selected relative humidities (31, 43.5, 53, 76, 85, and >90%) were used. The beetles were maintained as follows: each pair was kept in a cylindrical plastic container (25x7cm) with a tight plastic cover. The container was one third filled with a saturated salt solution. Six freshly cut twigs of C. sempervirens were supported on wire gauze. For each level of relative humidity, 8 females were used. At the end of the trial (after 7 days) the number of eggs was recorded.

The results are given in Table 5.34 and Fig. 5.10. Analysis of variance shows a significant difference in the mean number of eggs deposited ($P<0.005$). Females deposited a high number of eggs at low relative humidity. When the number of eggs per female was plotted against relative humidity, a non-linear relationship resulted (see Fig 5.10). The number of eggs deposited per female apparently remains constant from low to moderate RH, then it decreases at high relative humidity. The mean number of eggs deposited per female diverged from the curve line at 53% RH, however. This is possibly due to the variability of insects. The

Table 5.33: Oviposition and fluctuating temperatures (9 to 17°C)

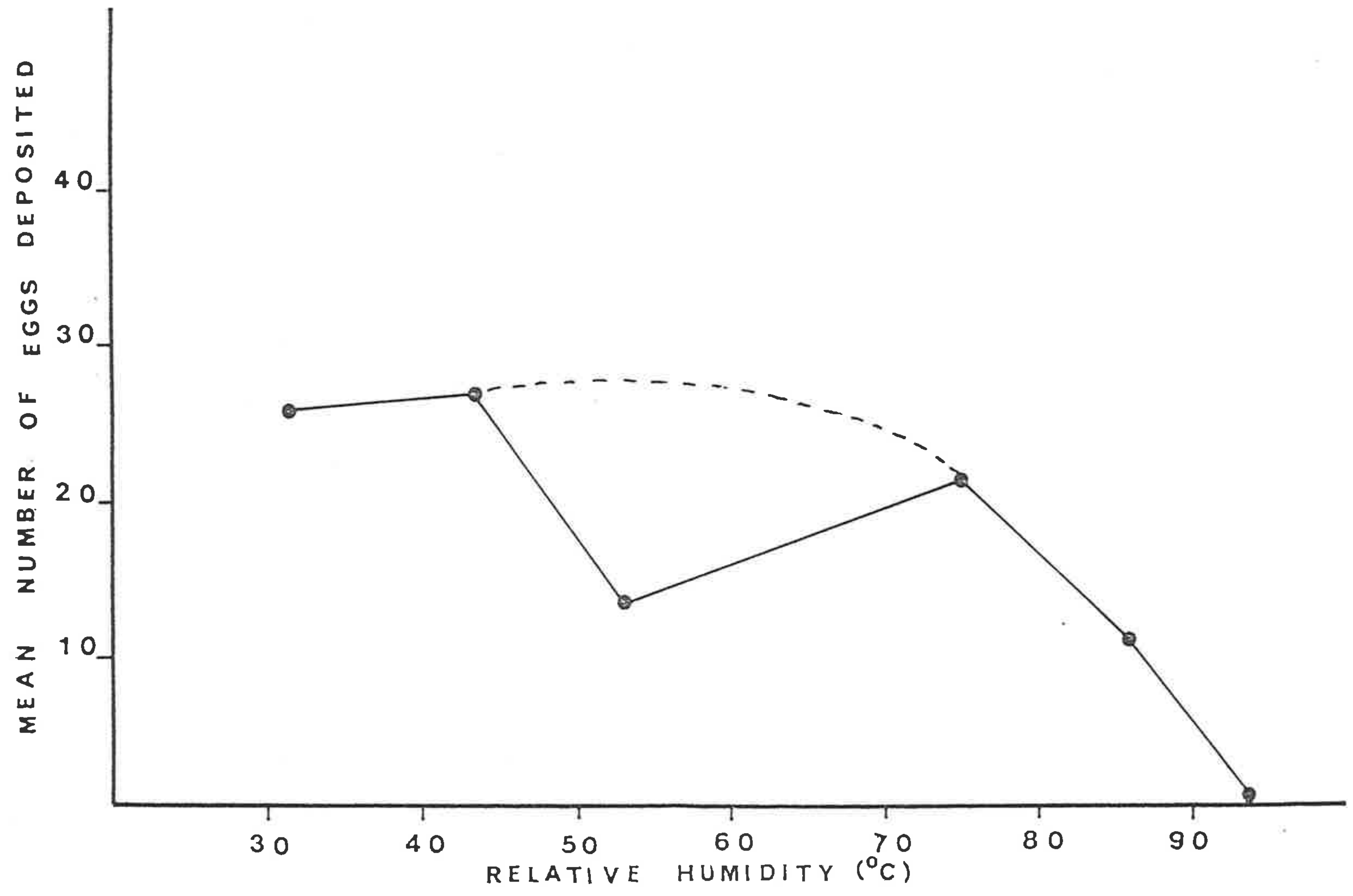
Beetles number	Number of eggs deposited
1	0
2	0
3	2
4	0
5	0
6	4
7	0
8	0

Table 5.34: Mean number of eggs deposited and various relative humidities

Relative humidity (%)	Mean no.eggs per female	F	P
31	25.5 a	3.735	< 0.005
43.5	26.38a		
53	13.00ab		
76	21.00ab		
85	10.50ab		
>90	0.88b		

Means followed by the same letters are not significantly different (Tukey test).

Fig. 5.10: Various humidities and oviposition


MEAN NUMBER OF EGGS DEPOSITED
40
30
20
10
30
40
50
60
70
80
90
RELATIVE HUMIDITY (°C)

results suggest that low to moderate relative humidity levels favour the oviposition of U. cupressiana. High relative humidity, conversely, is an unfavorable condition for oviposition. Most beetles that were subjected to a >90% RH died after 2 or 3 days. This indicates that beetles could not withstand such a high RH.

This finding contradicts those in bruchid beetles (Zabrotes subfasciatus, Callosobruchus analis F, and C. maculatus F) by Howe & Currie, 1964 (in Hinton, 1981), found to deposit fewer eggs as the RH falls. In some species, such as Acanthoscelides obtectus Say, however, the oviposition did not seem to be affected by variations of RH at the temperature considered (Hinton, 1981). In U. cupressiana, the oviposition behaviour does seem to be affected by changes of RH. Apparently, in high temperatures (25°C) and in a fairly restricted range of RH (30-76%) most eggs will be deposited. These results correspond to the field condition where the beetles undertake the reproductive activities in late spring and summer, usually dry or low in RH in South Australia.

3. Photoperiod

Experiment 1. Various photoperiods and oviposition

The experiment was carried out in constant temperature cabinets (25°C). Three groups of 8 pairs of newly emerged beetles were used. Each group was maintained in the following way: (1) each pair of group 1 was placed in a cylindrical plastic container with 6 fresh cuts of twig of C. sempervirens for oviposition. The containers were then maintained in a cabinet with zero hour daily photoperiod (no light at all) during the trial; (2) each pair of group 2 was treated in the same way as (1) but kept in a cabinet with a 14 hour daily photoperiod; and (3) each pair of group 3 was treated in the same way as (1) but kept in a cabinet with a 24 hour daily photoperiod. Light used was 5 Watt, fluorescent, White light. The number of eggs deposited was recorded after 7 days of the trial.

The results are given in Table 5.35. Analysis of variance shows a significant difference in the number of eggs deposited per female ($P<0.01$). Tukey's test revealed that females deposited a significantly high number of eggs at zero and 14 hour daily photoperiods, while at a 24 hour daily photoperiod the number of eggs deposited per female was low. This suggests that under continuous light conditions the oviposition

Table 5.35: Mean number of eggs deposited and various photoperiods

Photoperiod (hour)	Mean no.eggs per female	F	P
0	46.625a	6.92	< 0.01
14	46.50a		
24	15.25b		

Means followed by the same letters are not significantly different (Tukey test).

behaviour of female U. cupressiana changes. She retains some of her eggs if subjected to continuous light conditions. Dark conditions, however, favour oviposition. Evidence is thus gained that adult U. cupressiana has a nocturnal reproductive strategy.

5.3.1.4 Conclusion

The findings indicate that the reproductive strategy of U. cupressiana is a function of mating and oviposition. Successful reproduction depends greatly on mating and oviposition success. Mating success is found to be a product of individual factors of the male (size and fitness) and physical factors of the environment (temperature in particular). Oviposition success is a function of mating success, host plant, and physical factors of environment (temperature, RH, and photoperiod). In this case, the individual factors of the female were neglected.

It might be said that success in mating, presence of host plant, and high nocturnal temperature and low relative air humidity during late spring and summer favour reproductive activities. The success in reproductive strategy will lead to the outbreak of population of U.cupressiana.

CHAPTER VI

CHAPTER 6

DISTRIBUTION AND POPULATION GROWTH OF CYPRESS TWIG BORER ON THE ADELAIDE PLAIN

6.1 INTRODUCTION

Spatial distribution is one of the most characteristic ecological properties of species, unlike growth and reproduction which often vary more between generations within a species than they do between species (Taylor, 1984). Furthermore, Taylor states that information on spatial distribution is vital for pest sampling programs in agriculture and medicine and for any animal survey or forecasting methodology, as well as for the basic understanding of wildlife conservation and human demography. No field sampling is valid without understanding the underlying spatial distribution.

Population dynamics has traditionally sought to explain spatial distribution as the by-product of environmental heterogeneity and reproductive population growth acting on random processes of movement and mortality (Bartlett, 1949, 1975 in Taylor, 1984).

Some factors that may play an important role in determining insect distribution have been proposed by previous workers such as: interplant and intraplant variation in nutritional quality (Dixon, 1967; Edmunds & Alstad, 1978; Jounet, 1980; Gilbert, 1982; Haack *et al.*, 1987) and/or defense against herbivores (Miles, 1972; Feeny, 1976); host plant vigour, as represented by size and growth form (Service, 1984); predation (Sanders and Knight, 1968; Addicott, 1978); insect activities, feeding and oviposition (Malavasi *et al.*, 1983; Hori, 1982): habitat features, (Sawyer & Haynes, 1985; Hori, 1982): altitude (Karasawa, 1966 & Masukawa, 1967 in Hori,1982); weather or climate (Andrewartha & Birch, 1954, 1960; Halparin, 1980); host age and density and soil (Halparin, 1980); temperature (Cohet *et al.*, 1980 in Schnebel & Grossfield, 1984); etc.

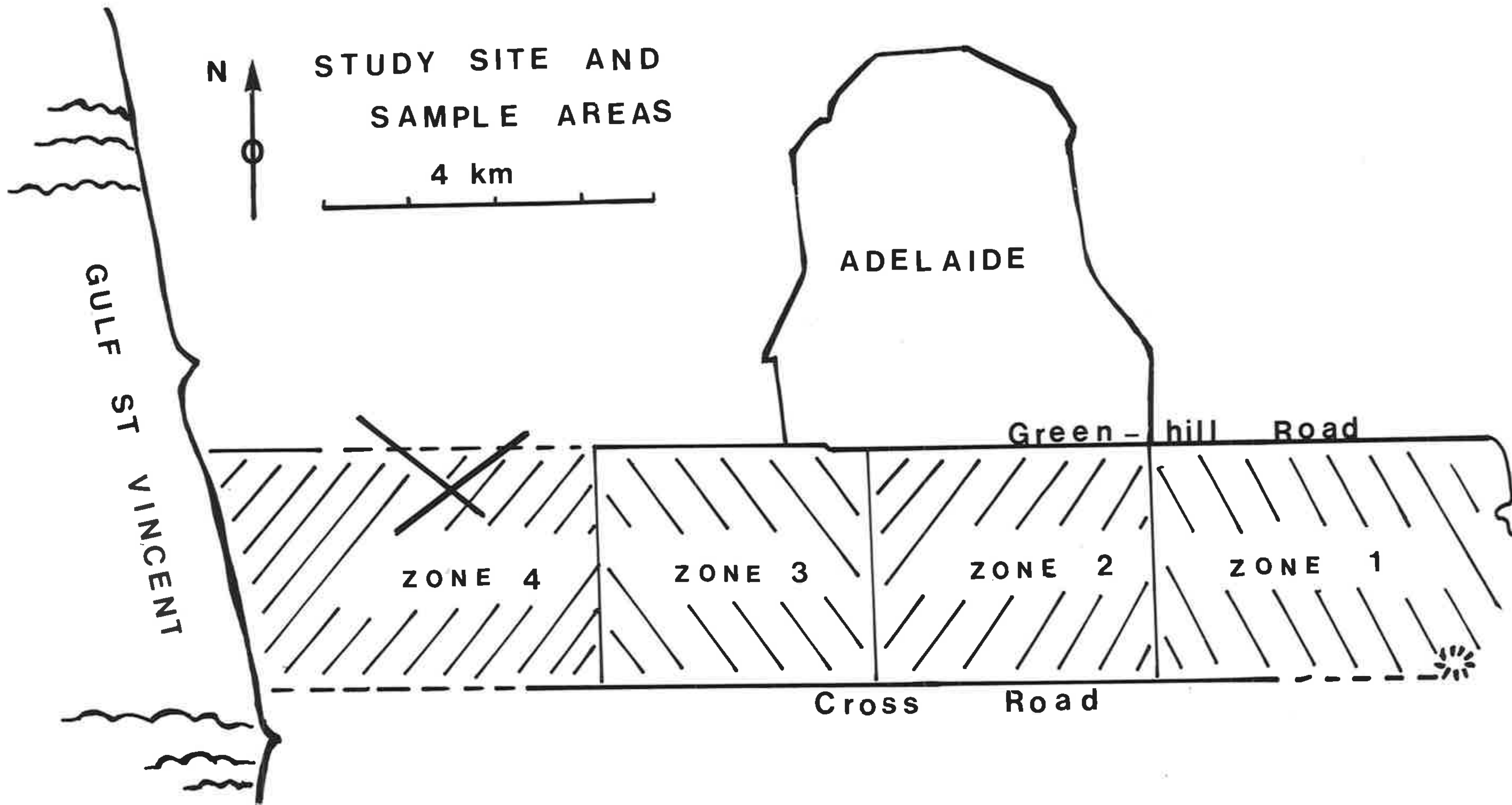
The field study of the distribution and the population growth of cypress twig borer (CTB) was carried out on the Adelaide Plain, S.A. in 1985 and 1986. Within the sample area (study site), about 70% of pencil cypress (*Cupressus sempervirens*) trees have been attacked. The first objective of this study was to describe the differences in population densities vertically on trees and horizontally across the study site. The second was to determine the factors that may affect the population

densities, and the third was to describe the relationship between the population densities of generations and to determine the growth of the population of the species.

6.2 SITE AND METHODS

The site of study chosen was an East-West strip of Adelaide suburbs, from the foothills of the Mount Lofty Ranges to the sea, bounded on the North by Greenhill Road and on the South by Cross Road (Fig. 6.1). All *Cupressus sempervirens* within the study site were mapped and categorized into unattacked and attacked trees. The area was about 450 ha, and was divided into 884 quadrats each of which was about 0.5 ha. The quadrats were grouped into 4 zones (sample areas) going East to West. Ten quadrats were selected at random (using a computer program) from each zone, and within each quadrat 2 infested trees were drawn at random for sampling. Each individual tree was divided into 3 crown strata (levels): top, middle, and bottom parts. All dried twigs and branches (each one revealing the presence of an individual insect) were counted, and placed into one of 4 categories depending on the generation of borers that had caused the damage: Current growth ("N0"), consisting of dried twigs or branches that were caused by larvae hatched in the current year - i.e. generation N0; Currently attacked twigs ("N1"), consisting of dried twigs or branches that were caused by larvae hatched in the previous year - i.e. generation N1; Previous generation ("N2"), consisting of dried twigs or branches that were just attacked 2 years previously; Old attacked twigs ("N3"), consisting of dried twigs or branches that were just attacked 3 years ago; and Very old attacked twigs ("N4"), consisting of those that were caused more than 3 years ago by generation >N3. Additional variables that were measured and described were the height and the maximum width of trees, and tree shape. The height of the trees was measured using a 2-metre wooden stick that was placed upright against the bottom of the tree. Moving about 10 steps away from the tree, I calibrated my extended thumb against the stick and then used the thumb to measure height and maximum width of the tree. Tree shapes were catagorized into 3 main shapes: conical, cylindrical, and ellipsoidal. Two ways of analysis of variance was used to examine the differences in vertical and horizontal population densities. The relationship between area of trees and population densities, and the relationship between 2 generation population densities were tested by using regression analysis.

Fig. 6.1: Study site and sample areas.


STUDY SITE AND
SAMPLE AREAS
N
4 km
ADELAIDE
GULF ST VINCENT
Green - hill Road
ZONE 4
ZONE 3
ZONE 2
ZONE 1
Cross Road

6.3 RESULTS AND DISCUSSION

6.3.1 Vertical and horizontal distribution

The analysis showed that there was no significant difference in vertical distribution of population densities, but there were horizontal differences between zones (see Table 6.1).

Further using the LSD for P=0.05, the population density in zone 3 was significantly higher than in the other zones; the density in zone 4 was also higher than that in zones 2 and 1; zone 2 was intermediate between 4 and 1; and the lowest density was in zone 1 (Fig. 6.2). The reason for this is still not clear but might be due to heterogeneity of environment, such as rainfall, humidity, soil, natural enemy activity, host age and density, etc.

On the basis of my field observations I concluded that the differences in the population distribution of cypress twig borer (U. cupressiana) were more likely to be the result of:

- Differences in host plant density and abundance
- Differences in host plant age
- Differences in host plant habitat

These 3 hypotheses were tested and discussed below in relation to problems that still require elucidation.

6.3.1.1 Population density and host tree distribution

Regression analysis of the relation between the number of trees within quadrats and attacked twig densities showed no significant difference within any zones (see Table 6.3). This indicates that the number of trees within quadrats does not significantly affect the distribution of cypress twig borer populations. As mentioned previously, the cypress twig borer, like other cerambycids, appears to produce 'brood trees', i.e. the trees from which the beetles emerge or on which they feed as larvae and on which they deposit their eggs. For further discussion, see section 6.3.1.3.

6.3.1.2 Population density and host tree age

The age of host trees (C. sempervirens) varies within zones. According to their owners, almost all the sample trees were about 25 to 35 years old. When the number of generations was recorded, 4 or 5 generations were often found on either 25 or 35 year old trees. Sometimes

Table 6.1: Density of attacked twigs for N0 to N4 within strata on trees and within zones

Site	N0	N1	N2	N3	N4
Zone 1	1.56a	0.94a	0.39a	0.23a	0.02a
Zone 2	3.45ab	1.55ab	0.76ab	0.23a	0.07ab
Zone 3	5.91b	2.45b	1.72b	1.02b	0.38b
Zone 4	3.98ab	1.45ab	1.10ab	0.67ab	0.25ab
P value(%)	<0.1***	<0.1***	<0.1***	<0.1***	<0.1***
Top	4.24	1.74	1.09	0.67	0.23
Middle	3.69	1.70	1.03	0.53	0.20
Bottom	3.25	1.36	0.87	0.42	0.11
P value(%)	>50	>50	>50	>50	>20

No: current growth generation; N1: current generation;
N2: previous generation; N3: three years ago generation;
N4: more than three years ago generation;
*= <5%; **= <1%; ***= <0.1%.

Table 6.2: The regression of number of attacked twigs per square metre on the surface area of the trees, for three different shapes of trees, and for each of four generations of *U. cupressiana*

Generation	NO	N1	N2	N3
Conical trees:				
Mean number of attacked twigs	88.04	41.55	25.53	13.77
P value (%)	<0.1***	<0.1***	<0.1***	>50
Cylindrical trees:				
Mean number of attacked twigs	73.42	30.42	20.11	11.84
P value (%)	>50	>5	>5	<5*
Ellipsoidal trees:				
Mean number of attacked twigs	144.2	65.07	35.43	19.71
P value (%)	>50	>50	>50	>50
All sample trees:				
Mean number of attacked twigs	94.40	43.03	25.98	14.35
P value (%)	<0.1***	<0.1***	<0.1***	<1**

NO, N1, N2, and N3: as defined in Table 6.1
*= <5 %
**= <1 %
***= <0.1 %

Table 6.3: The regression of number of attacked twigs and number of trees within four zones

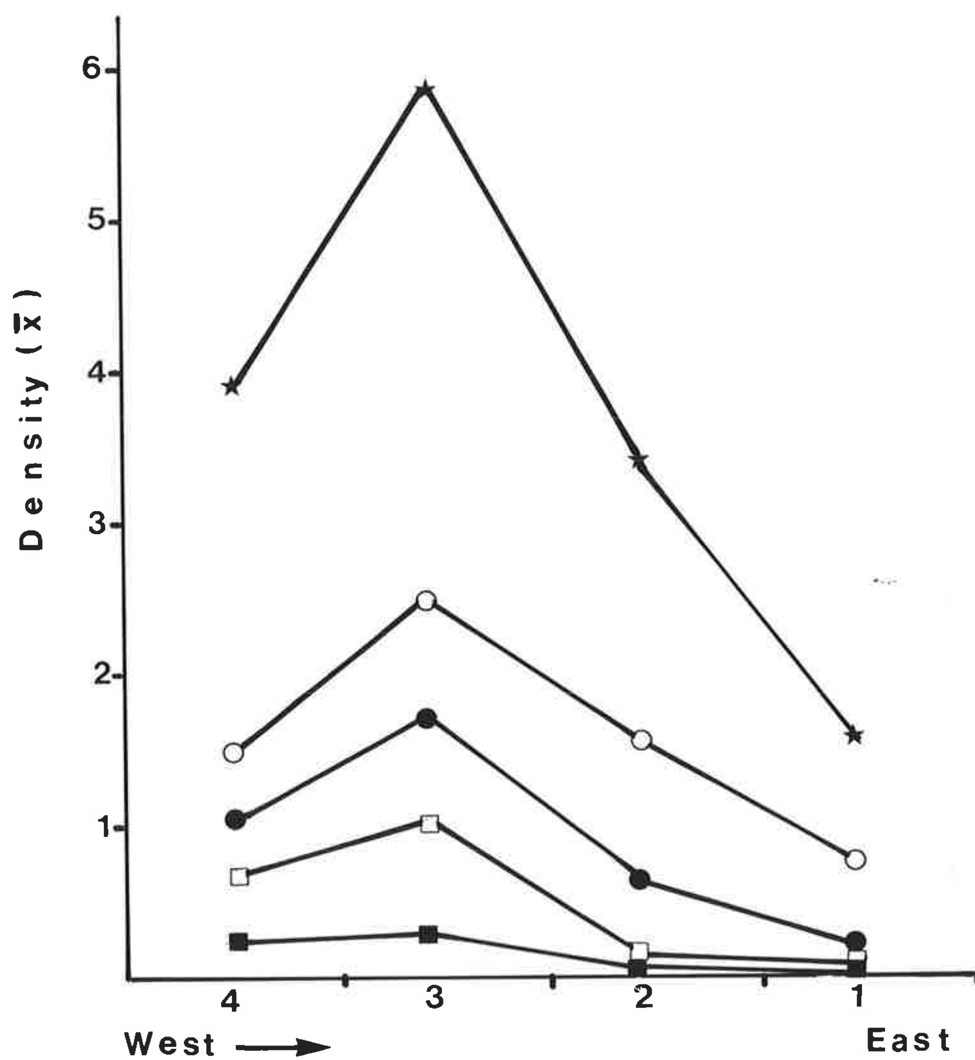
Zone	Mean number of trees	Mean number of attacked twigs	P value (%)
1	5.65 ± 0.80	85.45 ± 11.30	>50
2	5.20 ± 0.22	206.65 ± 55.65	>20
3	4.30 ± 0.52	287.10 ± 70.74	>50
4	5.80 ± 0.69	141.05 ± 18.75	>5

Table 6.4: The regression of number of attacked twigs and number of generations within four zones

Zone	Mean number of generation	Mean number of attacked twigs	P value (%)
1	3.9 ± 0.14	85.45 ± 11.30	<0.5**
2	3.85 ± 0.47	206.65 ± 55.65	<0.1***
3	4.40 ± 0.18	287.10 ± 70.74	<5*
4	4.35 ± 0.20	141.05 ± 18.75	<0.1***

* = <5%
**= <1%
***= <0.1%

Fig. 6.2: Horizontal distribution of CTB (*U. cupressiana*).



Horizontal distribution of CTB

(★—★ N0 ○—○ N1 ●—● N2 □—□ N3 ■—■ N4)

only one or 2 generations were found. This indicates that the age of the host tree is unlikely to affect the distribution of the cypress twig borer population. It is more likely that the length of time the tree has been attacked by the species may affect its population density.

A regression of the number of attacked twigs against number of generations resulted in a significant difference within the 4 zones (see Table 6.4). This implies that the greater the number of generations within trees the higher the population. In other words, the longer the tree has been attacked by cypress twig borer (U. cupressiana), the higher the population.

6.3.1.3 Population density and surface area of trees

Examination of the growth habit of individual trees showed that the density of twigs per square metre 'surface area' of the crown was not significantly different in trees of different shape, i.e. conical, cylindrical, and ellipsoidal (see App. 58). Furthermore, the occurrence of dried twigs resulting from the establishment of young larvae indicated that female beetles apparently deposited their eggs only on the twigs that were located on the outer surface of the tree crown. Thus it was a valid test of relative intensity of attack for different trees to count the number of twigs attacked per square metre surface area of the tree.

When a regression analysis was used to test the relation between surface area of the trees and attacked twig densities, regressions were significant for the generations N0 (current growth generation), N1 (current generation), N2 (previous generation) in conical trees, and for generation N3 (the 3 years ago generation) in cylindrical trees. But the regressions were not significant for any generation in ellipsoidal trees (see Table 6.2). This might be due to the number of sample trees that were almost conical. Over all the sample trees, however, regressions for all generations were highly significant, indicating that there was a significant relation between attacked twig density and the surface area of the trees (Fig. 6.3). The larger the surface area of a tree, the greater the intensity attack or the density of attacked twigs by each generation.

Like other cerambycids, beetles of the cypress twig borer emerge from the tree where they fed as larvae, and deposit their eggs on the same tree. Some of them probably deposit almost all their eggs on that tree and migrate to adjacent trees with only a few eggs remaining to be deposited on them. This is consistent with findings in experiments

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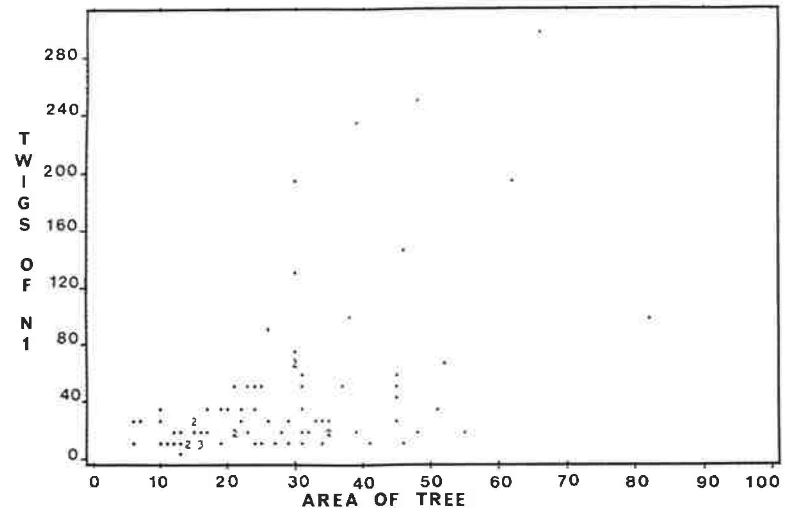
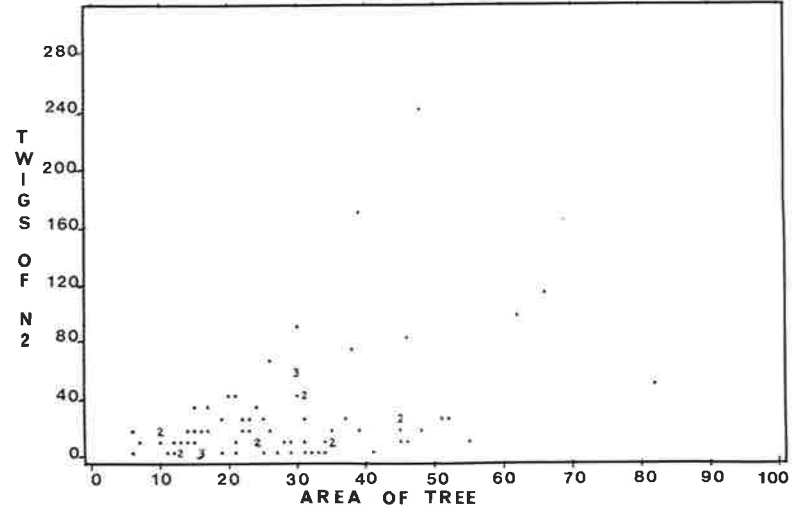
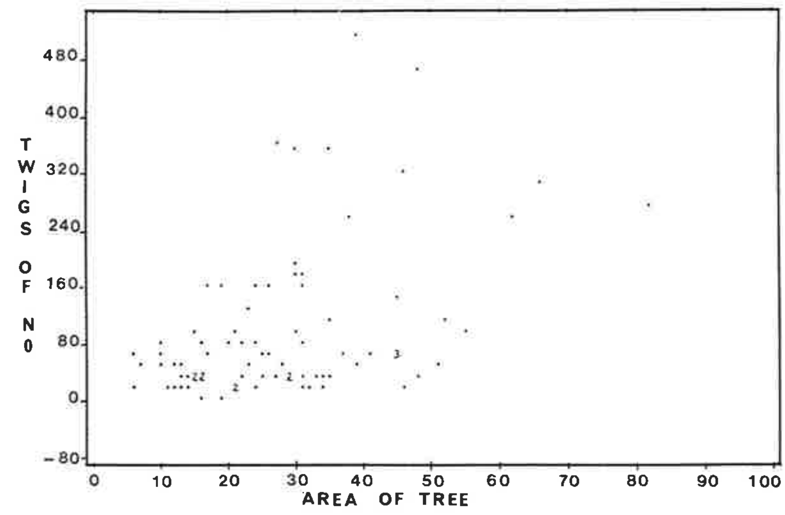
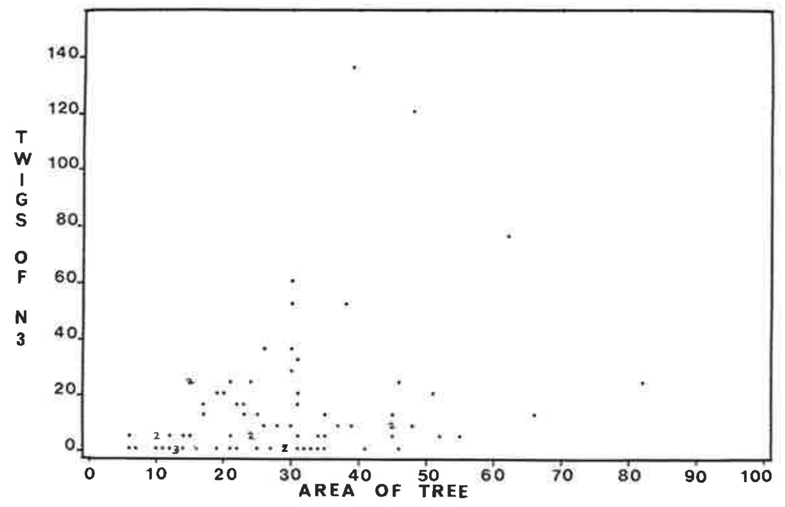
Fig. 6.3: Density of attacked twigs and surface area of trees.


TWIGS OF N1
280
240
200
160
120
80
40
0
0 10 20 30 40 50 60 70 80 90 100
AREA OF TREE


TWIGS OF N2
280
240
200
160
120
80
40
0
0 10 20 30 40 50 60 70 80 90 100
AREA OF TREE


TWIGS OF N0
480
400
320
240
160
80
0
-80
0 10 20 30 40 50 60 70 80 90 100
AREA OF TREE


TWIGS OF N3
140
120
100
80
60
40
20
0
0 10 20 30 40 50 60 70 80 90 100
AREA OF TREE

with potted trees. Once the mated female alights on a tree that is suitable for oviposition, she spends most of her time crawling and depositing her eggs. As stated before, females of U. cupressiana deposit almost all their eggs on the first night after copulation by a male and the few remaining on the second and third days.

It is often found in the field that trees which have been severely attacked by this species produce a great number of new shoots after twigs or branches have been girdled by larvae. Although, as indicated above, there was no apparent overall difference in 'surface' density of twigs in trees of different shape, nevertheless, when trees (of any shape) had been attacked the compensatory growth of the tree may favour the reproductive strategy of the insect by providing more oviposition sites for the next generation.

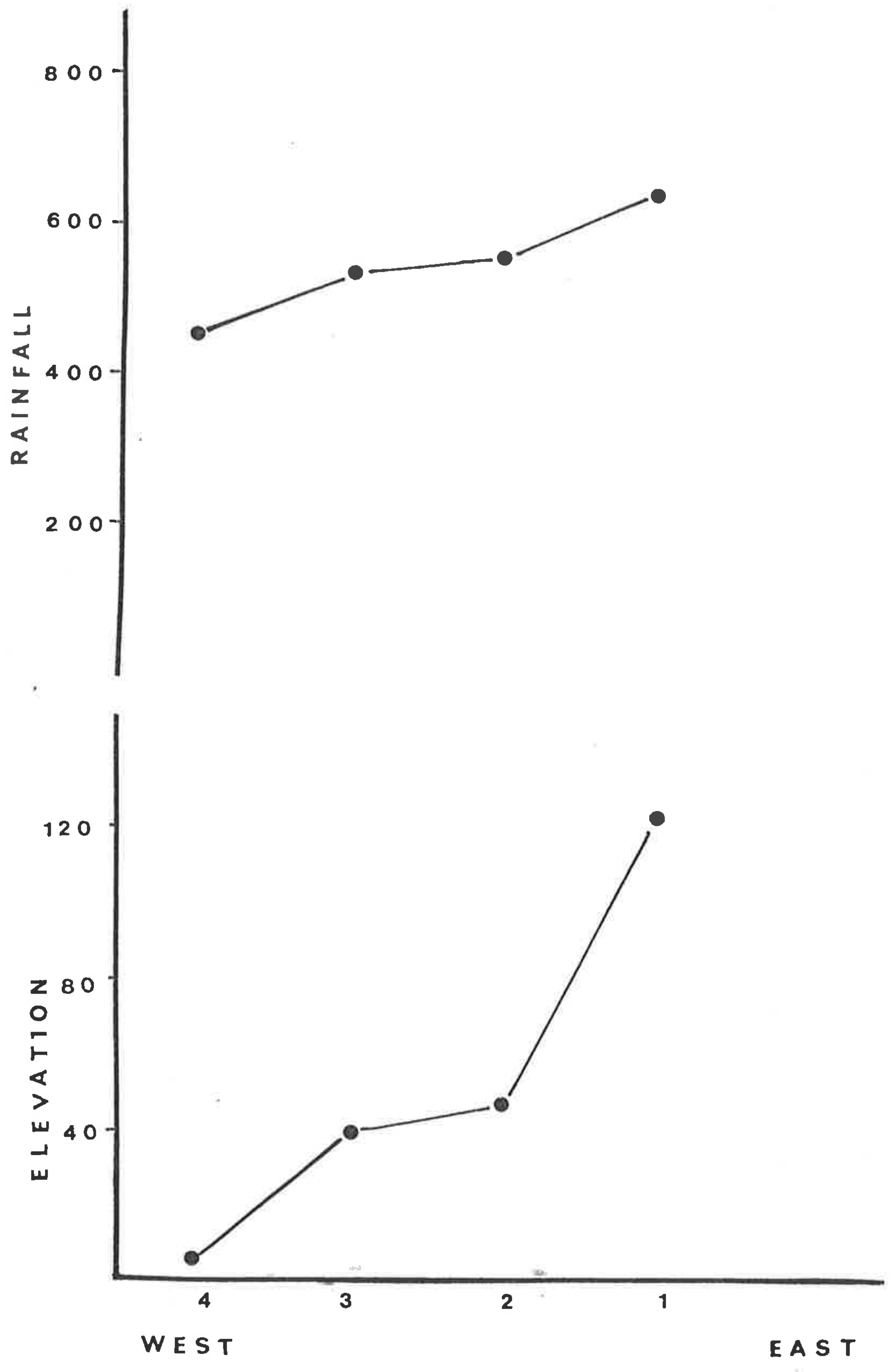
6.3.1.4 Population density and host tree habitat

This section is concerned with the effect on quality of the host tree habitat or climatic factors (rainfall and temperature) and type of soil. Examination of meteorological data indicated that there were differences between the study zones. Meteorological data from 4 meteorological stations in the vicinity of the 4 zones showed there were differences in rainfall. The highest rainfall was in zone 1 (close to station 4) and the lowest rainfall was in zone 4 (in which station 1 was located). In zone 2 and 3 the rainfall was intermediate (see Fig. 6.4). With respect to temperature, however, there was no difference between zones.

In zone 1, with high rainfall, the population density was significantly lower than in the others. Whereas in zones 3 and 4 with low rainfall, the population was relatively high. This suggests that rainfall may play an important role in insect population. According to Schwerdfeger (1976) the spatial distribution of rainfall in the Adelaide region is strongly correlated with altitute. It is lowest in the coastal area and increases towards the slopes of the Mt. Lofty Ranges.

Trees grown in areas with high rainfall might be more resistant than those grown in low rainfall areas. It has been proposed that susceptibility of conifers to bark beetle attack may be associated with water balance (Rudinsky, 1962; Bushing and Wood, 1964); or water relations (Vite and Rudinsky, 1962). Furthermore, Vite and Rudinsky (1962) have argued that water relations were also reflected in the

Fig. 6.4: Mean daily rainfall in four zones within study site.



800
600
400
200
RAINFALL
120
80
40
ELEVATION
4
3
2
1
WEST
EAST

oleoresin pressure of individual trees and that rainfall causes fluctuation in oleoresin pressure.

Thus it is believed that trees grown in an area with high rainfall are more likely to be resistant to U. cupressiana attack, due to high oleoresin exudation pressure, than those grown in a low rainfall area.

There were also differences in soil type between zones. According to Northcote (1976), the soil in the coastal area is sandy and highly permeable, and towards the foothills there are heavy loams and clay soils which are less permeable (Fig. 1.2). It might be suggested therefore that the type of soil could also have an effect on the distribution of U. cupressiana. It is believed that when trees are grown on sandy soil under long periods of drought during summer, the type of soil may have a major effect. Kramer and Kozlowski (1960) have pointed out that the water content of trees decreases during summer down to a minimum as a result of heavy loss in transpiration, then increases again during autumn and winter. This might suggest that trees grown on sandy soil have a lower water content and oleoresin exudation pressure during the dry summer than trees grown on clay soil. The trees that have a low oleoresin exudation pressure are more susceptible to attack of U. cupressiana; thus sandy soil as well as low rainfall may favour the insect's survival and abundance.

As previously mentioned, the reproductive activity of cypress twig borer occurred mostly during late spring and summer. Young larvae mostly became established during the dry summer. At that time the physiological condition of the trees favours larval establishment. It is obvious that climate, particularly rainfall, and soil type affect the spatial distribution of cypress twig borer on the Adelaide plain. According to Andrewartha and Birch (1960), the climate of Adelaide is broadly like that of the region near the Mediterranean Sea. The winter is mild, and the mean minimum and maximum temperatures for July (the coldest month) are 7.5 and 15°C., respectively. The summer is hot and rather severely dry and the mean minimum and maximum temperatures for January (the hottest month) are 16.3 and 30°C., respectively. Temporal distribution of rainfall is strongly correlated with season. Most rainfall is experienced between May and September, i.e. from late autumn to early spring. Rainfall during the rest of the year is generally light.

6.3.2 Generation relationship between current growth generation (NO) and other generations

When the relation between the number of attacked twigs of NO and other generations was tested by regression analysis, each regression was significant at P<0.1% (Fig. 6.5).

The slopes indicate that there was an increase in population from each of the N3, N2, N1 generations to NO. The slopes of the regression were greater for the relation between NO and N2,and NO and N3, because, of course, the increases in population were measured over 2 and 3 generations respectively (see Fig. 6.5).

These results suggest that since the last 4 years the population of U. cupressiana has been increasing. One thing can be explained that there might be favourable conditions for reproductive activity and the establishment of young instar larvae.

High nocturnal temperatures during summer favour reproductive activities, while severe summer drought favours larval establishment. These produce high survival and abundance of the species within generations. Data show that there is a syncronisation of life history of the species and field condition. Laboratory experiments revealed that the larvae or prepupae of U. cupressiana tend to diapause under unfavourable conditions particularly in low temperatures. Adult beetles stay longer in their mines if conditions are not favourable for reproductive activity. They tend to emerge during bright, sunny and warm days. All such cases much favour the increase of U. cupressiana populations.

6.3.3 Population growth

If we asssume that there was no emigration and immigration, and that the twigs that fell off can be ignored, the ratio between the number of attacked twigs of 2 successive generations can be used to predict the crude rate of increase of the population in the field. The formula :

$$I = Nn + 1 / N \quad \text{or} \quad I = NO / N1 \text{ etc.}$$

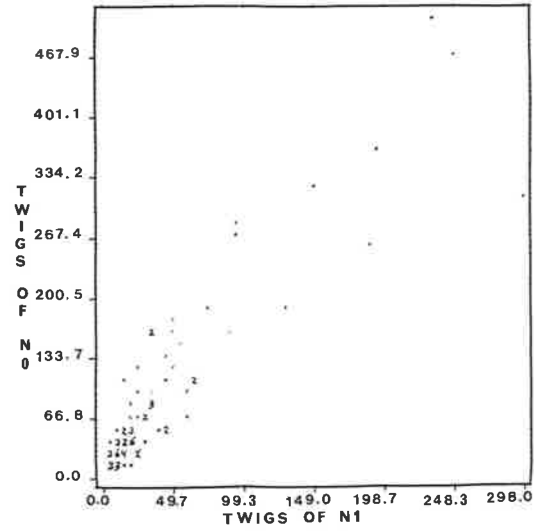
(counting backwards)

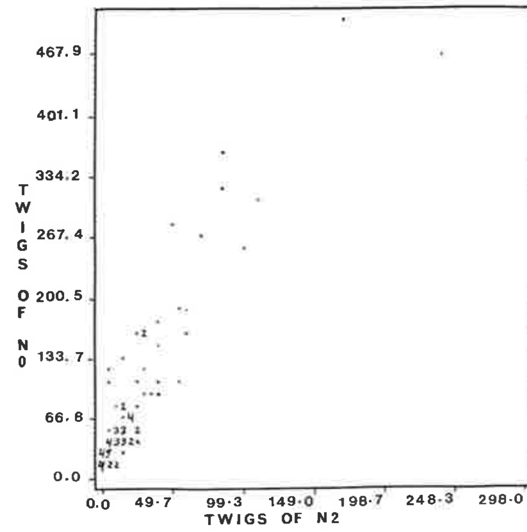
I: Crude rate of increase

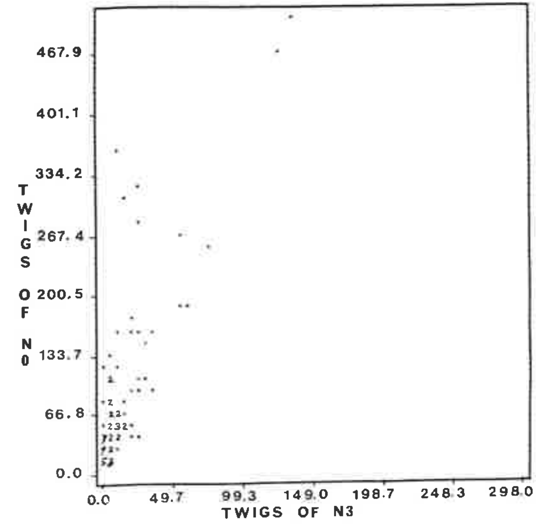
N: Generation at a given year

Nn+1: Successive generation of a given year generation

Fig. 6.5: Relationship between generations of *U. cupressiana*.


467.9
401.1
334.2
267.4
200.5
133.7
66.8
0.0
TWIGS OF N0
0.0
49.7
99.3
149.0
198.7
248.3
298.0
TWIGS OF N1


467.9
401.1
334.2
267.4
200.5
133.7
66.8
0.0
TWIGS OF N0
0.0
49.7
99.3
149.0
198.7
248.3
298.0
TWIGS OF N2


467.9
401.1
334.2
267.4
200.5
133.7
66.8
0.0
TWIGS OF N0
0.0
49.7
99.3
149.0
198.7
248.3
298.0
TWIGS OF N3

NO: Current growth generation -i.e. larvae hatched in the current year
N1: Current generation - i.e. larvae hatched in the previous year

The crude rates of increase (I) were calculated for each shape of tree, for each generation, and for each of the 4 zones.

- Rate of increase on 3 tree shapes

Table 6.5 showed that there were no significant differences between shapes of trees within any generation. So the rates of increase in zones can be more readily compared.

- Rate of increase in 4 zones

As shown in Table 6.6, there were differences in the rates of increase between generations and between zones. In zone 4, the rate of increase from current generation (N1) to current growth generation (NO) was significantly different from that between N2 and N1. But in zones 1, 2, and 3 , there was no significant difference in rate of increase between any generation.

Comparing zones, the rate of increase from N1 to NO was significantly different in zone 4 from that in zone 1; and the rate of increase from N3 to N2 in zone 2 was significantly different from that in zone 3 and 4.

Within zone 4, the rates of increase suggest there was a slower rate of increase in generation N2, but a higher rate of increase from N1 to the current growth generation (NO). This might be due to annual heterogeneities of season, particularly in temporal distribution of rainfall which varies from year to year. Population trends within the other zones were not clear. Possibly survival within zone 4 was particularly high in relation to the other areas. Differences in larval survival were most likely due to the differences in the physiological condition of the trees which the larvae were attacking. This in turn is likely to be the result of differences in the habitat of the trees being attacked. However, within the total area, there was no significant difference in the rate of increase per generation.

Table 6.5: Rate of increase of three generations of U. cupressiana in three different shapes of trees

Tree shape	N0	N1	N2	N3
Conical	2.14 ± 0.31a	1.85 ± 0.28	2.30 ± 0.56	-
Cylindrical	2.51 ± 0.40	1.57 ± 0.10	1.76 ± 0.13	-
Ellipsoidal	2.25 ± 0.06	1.78 ± 0.22	2.57 ± 1.17	-

Values are means ± standard error

Table 6.6: Rate of increase of three generations of U. cupressiana in four zones

Zone	N0	N1	N2	N3
1	1.69 ± 0.16a	2.3 ± 0.30	2.70 ± 0.49	-
2	2.17 ± 0.26	1.99 ± 0.10	3.63 ± 0.81/*	-
3	2.36 ± 0.13	1.45 ± 0.32	1.53 ± 0.16	-
4	2.79 ± 0.29*/*	1.35 ± 0.09	1.54 ± 0.19	-
Total area	2.12 ± 0.23	1.77 ± 0.24	2.03 ± 0.39	-

Values are means ± standard error
N*P < 5% for generation within a zone
N/*P < 5% for zones within one generation.

6.4 CONCLUSION

- The distribution of the cypress twig borer was not different vertically within trees, but it was significantly different between zones.
- The larger the area of trees, the greater the population.
- The longer the trees had been attacked, the higher the population, and the more severe the infestation.
- Climate, rainfall in particular, and/or physiological conditions of the host might have a major role in the distribution pattern and population growth of cypress twig borer.

CHAPTER VII

CHAPTER 7

HOST-PLANT AND INSECT INTERACTION

7.1 INTRODUCTION

The extent and importance of insect host-plant interactions are subjects of much current interest. The various plant characteristics and environmental factors affecting suitability for growth and survival of immature insects have been reviewed recently (Scriber, 1984; Krischick and Denno, 1983; and Rhoades, 1983). An increase in the rate of survival of immature insects may lead to 'outbreak' of insects.

The causes of fluctuations in insect populations have been the subject of much argument between entomologists. Five categories of explanation have been proposed. First, physical factors, particularly variation in weather, that are themselves independent of animal numbers, i.e. density-independent factors, have been proposed as the main determinants of animal abundance (Andrewartha and Birch, 1954). Second, biotic factors, such as competition for food, predation, parasitism and disease, effects of which were presumed to vary with population density (density-dependent factors), have instead been considered to be the most important causes of changes in animal abundance (Nicholson, 1954; Wellington, 1957, 1960; Chitty, 1960; and Klomp, 1964 in Rhoades, 1983). Third, the effect of physical stress on the nutritional quality of plants have been thought to initiate outbreaks of herbivores (White, 1969, 1974, 1976, 1978, and 1984). Fourth, active defensive responses of trees have been said to be largely responsible for population cycles (Haukioja and Hakala, 1970; Benz, 1974, 1977 in Rhoades, 1983). Fifth, the relation between nutritional quality on the one hand and the defensive properties and responses of plants to attack by herbivores on the other, were considered to be the main determinant (Miles, 1972; Sen Gupta and Miles, 1975; Miles _et al_. 1982a; Rhoades, 1983).

In this study, some aspects of insect host-plant relationship of _U. cupressiana_ were investigated and discussed particularly in conjunction with insect survival, behaviour and host tree response. The main aim of this study was to determine the key factor determining mortality of young instar larvae. For this reason, a series of experiments was carried out.

7.2 EFFECT OF WATERING REGIMES

7.2.1 Attack behaviour and larval survival in relation to host composition

An experiment was carried out in a plant growth room with fluctuating temperature and 14 hours daily fluorescent light (Rockpile, WARI). 32 potted trees of Cupressus sempervirens (2-3 year old, ca. 150cm height) were used. Two months before the start of the experiment, the trees were treated and maintained as follows.
Pots with trees were soaked until the soil in the pot became saturated. Each was then drained for 30 minutes and weighed. The trees were divided into 4 groups. In group 1, the trees were weighed immediately after draining and kept at almost the same weight during the trial by adding a small amount of water (approx. 200ml) every other day; weights were checked twice a week. In group 2, the trees were weighed after 4 days further draining and kept at almost the same weight thereafter as indicated for group 1. In group 3, the trees were weighed after a total of 8 days draining and thereafter kept at almost the same weight as described above. In group 4, the trees were weighed after a total of 12 days draining and similarly kept at almost the same weight.

After 2 months, 4 potted trees (one from each group) were randomly placed in a cage of 1x1x1.5m (wooden frame and nylon cover). Eight cages were used as replicates. Three pairs of newly emerged beetles were released in each cage. They were allowed to copulate before releasing. At the start of the experiment, 3 twigs were taken, one each from the upper, mid and lower parts of the tree respectively, and the relative moisture content (RMC) of twigs (relative turgidity) was determined by using Weatherly's method (Kramer and Kozlowski, 1960) (see Chapter 2).

The water potential particularly of dry stems of saplings after they had been girdled by the older stage larvae was determined using a 'Protimeter Surveymaster', moisture meter which is designed for obtaining a direct reading of percentage moisture content in wood below the surface (it can be also used on concrete, plaster or brick).

Four weeks after the beetles were released, at the time when the first instar larvae start to penetrate the twigs, 3 twigs were taken from each site (lower, middle, and upper parts) of the trees. The needles of cut-twigs were removed and the remaining parts were chopped and put immediately into liquid Nitrogen, freeze dried and stored at -10°C until

the analysis was carried out. The analysis of twig tissue was as follows.

Total free amino-nitrogen

Amino-nitrogen determination was modified from the method that was employed by Miles et al. (1982a). Samples of 2.0g. freeze dried powder were homogenised for 1 min. in 30ml pre-chilled, oxygen free 'MCW' (methanol, chloroform, water: 20, 10, 8) and centrifuged at +1°C for 15 min. at 1500 r.p.m. The supernatant was placed at +1°C and the 'pellet' extracted twice more in MCW. To the combined supernatants, sufficient chloroform and water were added to make the solvent ratio 2:2:1.8 and the mixture left to separate at +1°C. The upper (aqueous) phase was reduced to less than 5ml in a rotary evaporator at 30°C and made up to 10ml with 80% ethanol. The aqueous extract contains mostly amino acids and sugars. Estimation was by the method of Rosen (1957), using ninhydrin; results were read on a spectrophotometer at 570nm. A standard curve was prepared using leucine.

Total carbohydrates.

Carbohydrate determination was by the method of Yemm and Willis, (1954). Samples of 0.1ml of 'aqueous extract' were made up to 1.0ml with water and layered carefully onto 5ml 0.2% anthrone in 26N sulphuric acid in a 150x25mm test tube in ice, left for 5 min., placed in a boiling water bath for exactly 10 min., and allowed to cool. Blanks and samples, were diluted similarly, and read against water on a spectrophotometer at 630nm. A standard curve was prepared using glucose.

Total crude lipids

Extraction of total crude lipids was modified from the method of Maudinas et al. (1982): 2.0g freeze-dried leaf powder was homogenised in 20ml acetone for 1 min., filtered, the pellet extracted 3 times in 20ml choroform : methanol (2:1). The bulked filtrates were washed with 40ml 1% NaCL, allowed to separate and the lower phase evaporated to dryness in a pre-weighed flask, and weighed to yield total lipids.

Seven days after the beetles were released, the number of eggs deposited was recorded and twigs on which the eggs deposited were labelled with aluminium tags. Two months later the survival of first

instar larvae was recorded by counting the number of dry twigs which have been girdled by larvae (survival itself was measured directly in a later experiment to avoid mechanical damage to the tree, hence further observations will be made in this experiment). Infertile eggs, parasitism and other factors which may be involved in the establishment of first instar larvae were recorded. The experiment lasted for 8 months after the beetles were released. At that time the growth and development of larvae, survival, larval weight, and some factors that may have caused larvae mortality were recorded.

Analysis of data - The proportion of mortality and survival were transformed to arcsin square root, and were analyzed by using one-way ANOVA. The remaining data (i.e. number of eggs deposited, larval weight, length of mine, total amino nitrogen, carbohydrate, lipids, and RMC of twigs) were analysed using linear regression without transformation. Individual means were separated using Tukey's honestly significant differences (HSD) at the 5% level.

The results are presented in Tables 7.1-7.5. The RMC of twigs varied between groups of trees; it was significantly higher (74%) in group 1 trees which were well watered than in those growing with the least water (42%) ($P<0.001$). Total free amino-nitrogen content was also significantly higher in high RMC trees (30 mg/g dried material) than in the lowest RMC trees (16 mg/g dried material) ($P<0.002$). The reason for this was unclear but might be due to interference of physiological processes within trees which were growing under conditions of water shortage.

According to Kramer (1962), water deficits considerably affect the physiological and biochemical processes of the trees. Schnider and Childers (1941) (in Kramer, 1962) found that respiration often increased while photosynthesis decreased in apple trees growing in drying soil. The hydrolysis of starch to sugar has been observed in apple trees with high water deficit by Magness _et al_. (1933) (in Kramer, 1962). Nitrogen metabolism also is materially affected by water deficits (Kramer, 1962). The breakdown of ribonuleic acid (RNA) is hastened by leaf water deficits (Gates and Bonner, 1959, in Kramer, 1962). Kessler (1959) (Kramer, 1962) found an inverse relationship between water stress and nucleic acid content in sunflower. It has been concluded by Gates (1955, 1957) (Kramer, 1962) that even small reductions in water content have significant effects on metabolism.

Table 7.1: Number of eggs deposited, survival of L1, and nutritional composition of trees maintained at constant pot weight, 0, 4, 8, and 12 days after cessation of watering (see text).

Trial (day)	RMC (%)	MED	ML1S (%)	Amino-N (mg/g)	CH2O (mg/g)	Lipid (mg/g)
0	74.87±2.14a	12.78±2.14	41.22±3.24c	29.99±3.38a	40.06±2.31	49.52±5.79
4	69.45±0.48b	8.50±2.81	59.69±1.93bc	20.98±0.44b	37.43±1.34	46.86±4.18
8	57.96±2.07c	9.13±2.17	68.26±2.61b	20.21±0.30b	46.71±5.47	62.72±7.50
12	41.66±1.41d	8.13±2.91	82.25±3.94a	16.28±1.43b	39.70±3.54	47.04±2.50
P	< 0.001		< 0.001	< 0.002		

Means followed by the same letters are not significantly different
RMC: Relative Moisture Content
MED: Mean number of eggs deposited per tree
ML1S: Mean proportion of L1 survivals per tree (%)
CH2O: Carbohydrate.

Table 7.2: Larval survival, growth and development, and the length of mines on trees maintained at constant pot weight, 0, 4, 8, and 12 days after an initial cessation of watering (see text)

Trial (day)	PNS (%)	Growth and Development	Mean Weight of larvae(L6&L7)	Mean Length of Mine (L6&L7)
0	13.69	L4 - L7	41.55±7.22	406.82±35.50b
4	22.06	L5 - L7	44.56±6.48	422.22±28.13b
8	15.06	L5 - L7	67.43±13.90	456.25±54.05ab
12	17.75	L4 - L7	38.23±5.59	603.75±33.24a
P				< 0.05

Means followed by the same letters are not significantly different
PNS: Percentage survival per tree

Under the conditions of the experiment described here, it is possible that the low RMC treatments interfered with photosynthesis to the extent that less nitrogen was fixed.

Total carbohydrates and total lipids did not differ significantly, however, between group of trees. It is unclear why carbohydrate should remain constant; perhaps reduced production of photosynthate was compensated by changes in metabolism and transport.

There was no significant difference in mean number of eggs deposited in the 4 groups of trees (see Table 7.1). There was thus no evidence of discrimination by ovipositing females between trees growing under different watering regimes. Nevertheless, there was a significant difference in proportional survival of larvae between groups of trees ($P<0.001$). The Tukey test revealed that a high proportion of larvae survived on group 4 trees which were maintained in a condition of water shortage and which had a low relative moisture content (RMC) and a low level of total free amino-nitrogen in consequence. Conversely there was a high mortality on trees which had a high RMC and high levels of total free amino-nitrogen.

Surprisingly, survival was the lowest (41.2%) in trees with high total free amino-nitrogen and almost double (82.3%) that in the low nitrogen content trees, as shown in Table 7.1; whereas the data show that survival did not correlate with total carbohydrate nor total lipid content of trees. If amino-nitrogen is assumed to be nutritionally advantageously (White, 1969), these findings may indicate that the survival of first instar larvae was not affected by changes in the nutritional composition of the plant but that some other influence was critical. Certainly the significant decrease in survival of young instar larvae of *U. cupressiana* on high nitrogen content trees does not conform with the findings of White (1969, 1974, 1978, and 1984) or those of Miles *et al*. (1982a) working on cabbage aphids. The finding in this experiment is, however, consistent with those for the cabbage white butterfly by Slansky and Feeny (1977), for *Paropsis atomaria* by Miles *et al*. (1982b), for *Costelytra zealandica* by Prestidge and East (1984), and for peach aphids (*Myzus persicae*) by Jansson and Smilowits (1986), where nitrogen level of plant did not seem to affect the insect survival or growth.

One possible explanation for the cause of mortality of young instar larvae of *U. cupressiana* was an active defensive response of the trees to attack by the larvae. Survival was significantly correlated with

RMC - i.e water status of the trees. There was high survival on trees with a low water status. This implies that tree vigour may play an important role in young instar larvae mortality. In addition, no parasitism was encountered and also few infertile eggs were encountered (ca. 1-2%).

In older larvae (L3 to L7) the mortality factors most often encountered were cannibalism (10-30%), twig-fall and desiccation (8-12%) and excessive oleoresin flow (2-7%) (see Table 7.3). The experiment with small potted trees (ca. 175cm height after 8 months) showed that an average of 2 larvae could survive while the remainder were killed by other larvae. This was probably due to the fact that larval mines tended to become connected with each other, since some parts of dead larval bodies such as the head could be found in the larval mines of survivors. Such a case is rarely encountered in the field, since females deposit their eggs individually on twigs. The mortality caused by twig-fall could have been due in part to careless handling during the trial although infested twigs were liable to fall naturally in the field. The mortality of older larvae (L3 and L4) was caused mainly by excessive oleoresin flow, related to RMC ($P<0.05$, $R=0.98$). The higher the RMC of twigs the higher the mortality. This indicates that for trees having enough water, high RMC and hence a high level of oleoresin flow may affect the number of larvae surviving. Some dead larvae were found near hardened resin blocking larval mines in twigs, just a few cm from the stem. Apparently the death of larvae was caused by starvation, since they were not able to penetrate the hardening oleoresin blocking their mines. The excessive resin flow was produced by trees after the larvae girdled the trunk. It was often observed that larval mines from twigs to the trunk were connected with each other. Dead larvae were sometimes found within larval mines in the upper parts of trees, their deaths having also been caused by hardened oleoresin blocking their mines.

In the field it was frequently observed that a larva had partly girdled a big twig or branch but had then gone back to the small twig which it had first penetrated and in which it had developed. Presumably the larva thereby avoided excessive oleoresin flow produced by the tree as a response to its girdling attempt. Sometimes, however, such larvae were found to have died, presumably from starvation when they could not penetrate the sticky hardening resin blocking their mines. Often, larvae could be discovered still alive just behind a recently formed resin

Table 7.3: Mortality of L3 - L7 and its causative factors in trees featuring in Tables 7.1 and 7.

Trial (days)	TNED	TLM (%)	Proportion of Mortality (%)		
			Oleoresin	Cannibalism	Twig-fall
0	102	88	6.86	10.44	12.74
4	68	53	5.82	30.85	11.76
8	73	62	4.10	23.18	8.22
12	65	51	1.53	21.19	9.23

TNED: Total number of eggs deposited
TLM: Larval Mortality (%)

Table 7.4: Mean numbers of eggs deposited, L1 survivals, R.M.C, total free amino-nitrogen, total carbohydrate, and total lipid at strata within a group of trees (see text)

Strata	PML1 (%)	RMC	Amino-N (mg/gr DM)	CH2O (mg/gr DM)	Lipid (mg/gr DM)	Mean Eggs per tree
Upper	38.46	72.47±1.49	30.95±5.11	43.63±2.91	67.08±3.40	1.19±0.15
Middle	36.73	66.80±2.70	23.01±2.39	46.71±5.47	58.78±4.47	4.59±0.37
Lower	32.32	65.33±2.45	18.53±2.91	42.91±3.97	56.64±3.71	3.09±0.19

PML1 : Mortality of L1
RMC : Relative moisture content
CH2O : Carbohydrate
DM : dried material

plug but they did not appear keen to penetrate the hardening resin.

Data also showed no differences in the growth and the development of larvae between groups of trees. In both high and low levels of total free amino-nitrogen, larval instars had already reached L4 to L7 after 8 months. There is also no significant correlation between mean weight of instars L6 and L7 and total amino-nitrogen ($P>0.05$). In mean length of larval mine, however, there was a highly significant correlation ($P<0.01$, $R2=0.97$) between groups of trees (see Table 7.2). There was a negative linear relationship between length of larval mine and the total free amino-nitrogen. This suggests that the lower the nutrition quality of plant, the longer the larval mine. Apparently, larvae of U. cupressiana adjust their intake of food to maintain the same rate of growth and weight on trees with different nutritional value. These results are consistent with field observations on larval mines of twigs (see Chapter 4).

A widespread response amongst chewing insects to lower available nitrogen levels in food is to increase the rate of food ingestion (Hesjedal, 1984). This conformed with the observations of Slansky and Feeny (1977), quoted above, in which chewing insects showed an ability to compensate by increasing rate of consumption, thereby maintaining a satisfactory growth rate.

Within single potted trees, RMC, total free amino-nitrogen and total crude lipids vary from high in upper parts of trees to low in the lower parts. Total carbohydrate, however, is not significantly different between different parts of the tree.

The number of eggs deposited also varied within trees. It was high on middle and lower parts of the tree (see Table 7.4). In other words, the number of eggs deposited did not correlate with nutritional factors at any particular part of the trees and it would appear that nutritional levels do not influence the ovipositional behaviour of females of U. cupressiana. As mentioned in Chapter 4, ovipositing females usually go down to the lower part of the tree before depositing their eggs and then starts depositing eggs while crawling up onto successive twigs of the tree.

The proportional mortality of L1 at different strata (sites) on trees was not significantly different (see table 7.5). For older instars (L3 to L7), survival at different strata on the trees again was not significantly different. Mean length of mine and larval weight were significantly different ($P<0.001$), however, between strata on the tree (see

Table 7.5: Proportion of L3-L7 larvae surviving, mean length of mine, and weight of mature larvae at strata within a group of trees (see text)

Site	L3 - L7 survival (%)	Mean length of mine (mm)	Mean weight of larva (mg)
Top	17.94	272.50±60.19(4)b	21.92±3.96 b
Middle	18.36	334.58±29.10(12)ab	29.48±3.90 ab
Lower	20.20	478.60±22.17(26)a	57.91±5.50 a
P		< 0.001	< 0.002

Values in brackets are actual numbers of surviving larvae
Means followed by the same letters are not significantly different

Table 7.6: Number of eggs deposited, mortality (caused by resin flow) and water potential following various watering regimes and different soil types

Trial (day)	Mean no. of eggs deposited	Mortality (%)	Mean reading of water potential(bars)
0	23.75±1.93	32.53±1.70a	5.28±0.29a
4	10.75±2.44	26.86±1.55ab	9.48±0.79b
8	13.58±2.77	10.75±1.69bc	20.80±0.53c
12	12.83±1.39	0.0 c	39.50±0.15d
P		< 0.005	< 0.001
Soil	17.71±1.78	18.78±2.59	17.88±3.54
Soil+sand	12.67±1.57	16.28±2.66	19.65±3.34

Means followed by the same letters are not significantly different

Table 7.5). The Tukey test showed that at the lower parts of the trees, larval mines were longer than those at upper part. This might be due simply to the length of available twigs, however. As mentioned previously, once a larva has girdled a twig, or a branch or a trunk, it usually tunnels distally, parallel to the axis of the branch or trunk. At the lower part of the tree, the larvae have more chance to extend their mines distally, while at the upper part they are more limited.

There were also significant differences ($P<0.02$) in mean weight of larvae (L6 & L7) at different strata within trees (see Table 7.5). The Tukey test showed that larvae at the lower parts of trees were heavier than those at the upper parts. This might be influenced by the moisture status of the wood after it has been girdled by the larvae. As mentioned previously (Chapter 4), older stage larvae (L3-L4), after they had girdled the twigs or branches or even the trunk of young trees, then tunnelled and developed in the distal part of the branches or twigs which became dry as a result of the girdling.

As discussed below, high moisture content because it is related to oleoresin pressure could be lethal to young larvae if they tunnelled and girdled the twigs, but once the twigs were girdled, they become considerably dry and excessive dryness could also be lethal. Observations on the moisture status of these dry regions were was recorded as the 'water potential' measured directly with a moisture meter. This instrument indicated a higher moisture status (>15%) in girdled twigs in the lower parts of a tree, presumably because they remained attached to the fresh proximal part of the trunk and a lower moisture status (<15%) in girdled twigs at the top part. Some larvae that were found dead at the upper part of the tree appeared to have died through desiccation. These observations imply that low moisture status of the wood may have affected insect fecundity and survival. Such a case is often found in the field if the trees are in very bad attack conditions. One or 2 mature larvae could be found in a dry branch. Those at the top part are usually smaller in size or die before emerging as an adult.

Conclusion.

In U. cupressiana, the oviposition behaviour is not affected by different nutritional status of tree or stratum (site) on the trees. The feeding behaviour of the larvae, however, varies with the nutritional status of the part of the tree. The larval mine is longer where

nutritional value is low, presumably as a result of increased feeding which compensates for poorer nutrition. There is no correlation between insect survival and total free amino-nitrogen. Larval mortality is more likely as a result of active defence of host trees. This case will be discussed in detail below.

7.2.2 Attack behaviour and larval survival in relation to host-defence response.

48 trees of C. sempervirens (2-3 years old, 1.5 meter high) were separated into 2 groups. The first group of 24 trees was potted in soil (recycled) and treated throughout the trial as follows:

(1) 6 trees (saplings) were watered daily;

(2) 6 trees were watered every 4th day;

(3) 6 trees were watered every 8th day;

(4) 6 trees were watered every 12th day.

All the trees were kept in the glasshouse with natural light and a fluctuating ambient temperature. The second group was potted in a mixture of sand and soil (2:1) but otherwise given the same 4 watering treatments as in first group. Cessation of watering for treatment (4) was begun first, for treatment (3) 4 days later, for treatment (2) 8 days later; treatment 1 consisted of trees watered daily from the start. On day 12 (counting from the sessation of watering for treatment 4) beetles were released on all trees simultaneously as follows: From each treatment one tree was randomly placed in a cage (1x1x1.5m, nylon cover), and 4 pairs of newly emerged beetles were released. For each treatment, 6 replicates were applied. On the same day as the beetles were released, the water potential (measuring water deficit) was measured with a pressure bomb on a twig cut at the middle part of the tree. In this experiment the measurement of the water status of the trees was changed from water content (as measured either by RMC or by the direct reading moisture meter) to water deficit (measured by pressure bomb). Samples for the determination of water status were taken between 0500 to 0600h. Seven days after the beetles were released, the cages were removed and eggs deposited were counted and allowed to hatch. The twigs on which eggs were deposited were labelled with red woollen strings. Young larvae which survived for 3 months were recorded and all labelled twigs, dried or fresh, were cut and put in paper bags, dissected and examined under a light microscope.

Data were analysed by 2-way ANOVA, using within cell replicates and linear regression. Mortality and survival data were transformed into arcsin square root. Individual means were separated using Tukey's honestly significant differences (HSD) at 5% level.

The results are presented in Tables 7.6 and 7.7. Readings of average water potential (measuring water deficit) were significantly different between treated trees. For treated trees with a 12-day watering period, readings were significantly high (low moisture content) (39.5 bars in average), while for well-watered treatments they are low (high moisture content) (5.3 bars in average). This shows that water regimes can alter the water status of the trees. Trees grown under conditions of water shortage have a low water status, while those in well-watered conditions have high water status (see Table 7.6). Soil composition did not significantly affect the water status.

The analysis of variance revealed that there was no significant difference in mean number of eggs deposited within treated trees or within groups ($P>0.05$) (see Table 7.6). This indicates that ovipositing females did not discriminate between trees with different water status. These results are consistent with those in previous experiments.

The mortality factors encountered during the trial were high oleoresin flow, twig desiccation, infertile eggs and others (fallen twigs because of careless handling) (see Table 7.7). The percentage larval mortality caused by excessive oleoresin flow was significantly different between treated trees ($P<0.005$), but not between trees grown in the different soil types. The Tukey test revealed a significantly high larval mortality (29%) caused by oleoresin flow in well watered trees compared with poorly watered trees (0). It is obvious that mortality due to oleoresin flow must be a key factor in the survival of young instar larvae of _U. cupressiana_. Oleoresin flow is thus recognizable as a significant defence of a _Cupressus_ tree in response to the attack of _U. cupressiana_.

In the field, trees were found free from the attack by _U. cupressiana_ when grown on a hill with high rainfall, while those grown in the coastal areas with low rainfall were severely attacked. Bershing and Wood (1964) demonstrated that the susceptibility of conifers to bark beetle attack was associated with water balance. Oleoresin exudation pressure is believed, therefore, to be an indicator of water balance in the tree.

Table 7.7: Mortality of young instar larvae (L1 and L2) and mortality factors on trees grown on soil (recycled) and sandy soil (soil sand ratio, 1:2)

Trial	Total No. of eggs	Oleoresin flow (%)	Mortality factor Twig desic-cation (%)	Infertile (%)	Others* (%)
Soil	425	18.78	4.94	2.82	4.47
Soil+sand	328	16.28	5.79	2.13	1.82

* See text

It is well documented that resin (oleoresin) plays a significant role in the establishment of bark beetles (Scolytidae) within pine trees (Wood, 1962; Reid, 1963, Berryman and Ashraf, 1970, and Hodges et al. 1979).

Tree response

The response of trees to U. cupressiana attack varied within trees and between groups of trees. Within the experimental trees undergoing the 1st treatment (well watered trees) in which larvae died, 3 patterns of successful tree response were observed.

(1) When a first instar larva started to emerge from its chorion, it first chewed the chorion, then chewed the bark to which the chorion was attached then the phloem or sapwood. At that time, the tree produced a great amount of "secondary" oleoresin flowing to the part of the twig which had been chewed by the larva. At this time the larva could be killed if the oleoresin flowed out and covered the larva and chorion on the bark (see Fig. 7.1)

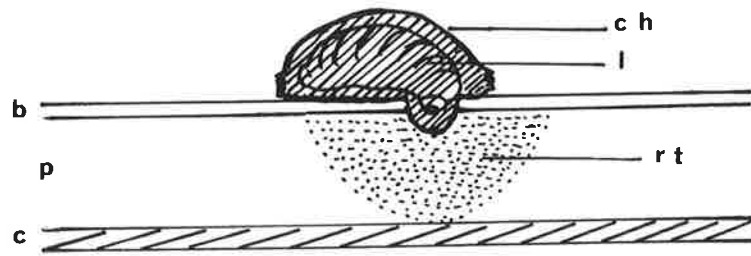
(2) If a first instar larva had successfully penetrated to the sapwood of a twig, it started a zigzag tunnel into the twig. At that time the tree produced a great amount of oleoresin that flooded the larval mine, and covered the larva (see Fig. 7.2). Some trees also produced a considerable amount of oleoresin in the tissue surrounding the larval mine. The content of phloem cells (sapwood cells) was thereby altered to a resinous condition and increased considerably in volume. The resinous cells eventually ruptured, forming a large oleoresin cavity in the sapwood of the twigs just beyond the larval mine. Larva died if the oleoresin then flowed into the larval mine, and covered the larva (see Fig. 7.3).

(3) Following successful establishment of a young larvae (L1 and L2) within a twig, the third or fourth instar larva (L3 or L4) tunneled downward via the proximal part of the twig to the trunk and girdles it. At that time, the tree produced a great amount of oleoresin that flowed up from the trunk into the larval mine within the twig and blocked further progress of the larva (see Fig. 7.4).

Within trees in groups which were watered only periodically, either every 4 or 8 days, the responses were confined to the last 2 patterns mentioned above. This is probably because between waterings,

Fig. 7.1 - 7.3: Two patterns of host tree response to the attack of larval *U. cupressiana*.

[b, bark; c, cambium; ch, chorion; l, larva; lm, larval mine; oc, oleoresin cavity; p, phloem; rt, resineous tissue].



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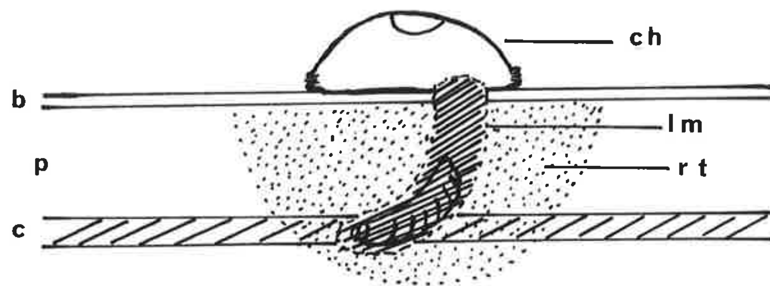

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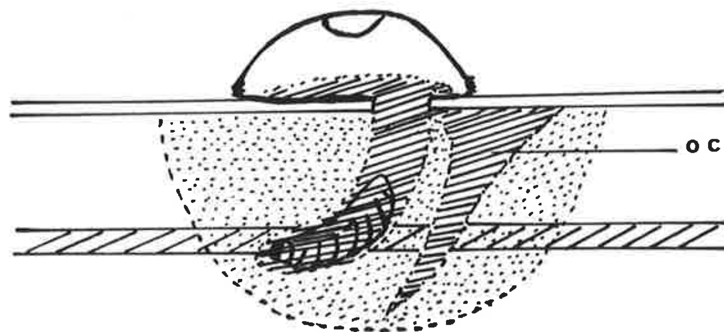
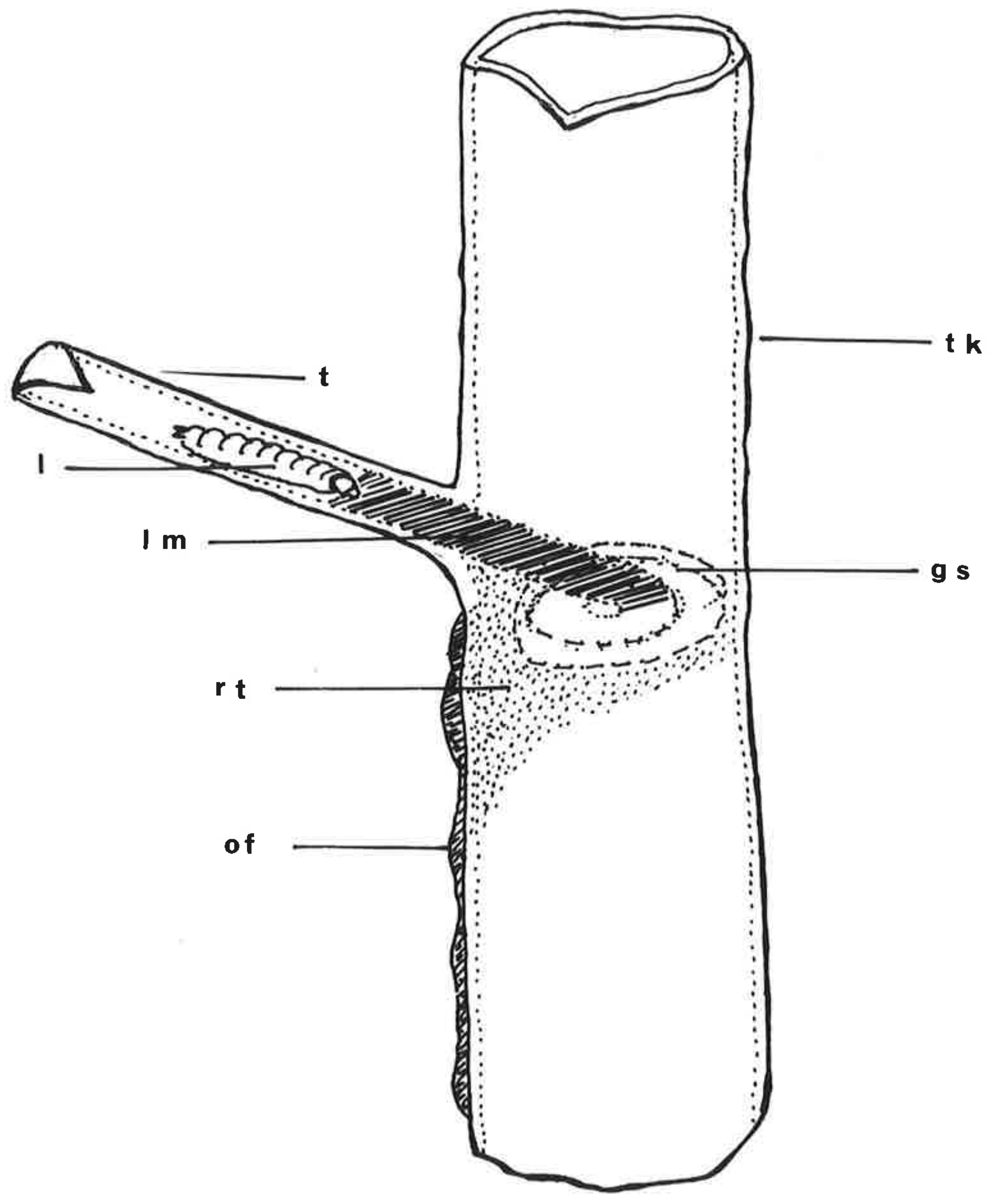


7 · 3

Fig. 7.4: The third tree response to the attack of larval *U. cupressiana* following the establishment of the young instar larvae (L1 & 2).

[gs, girdling site; l, larva; lm, larval mine; of, oleoresin flow out the surface of the bark; rt, resineous tissue; t, twig in which the L1 penetrated; tk, trunk that had girdled by the larva].



7.4

the larvae had a chance to tunnel longer before the next exudation of a high amount oleoresin by the tree.

According to Bourdeau and Schopmeyer (1957), the oleoresin exudation pressure in slash pine trees varies considerably with environmental conditions. It is high in the conditions of high humidity and low temperature. The pressure also varies with the time of the day. It usually reaches the highest value at dawn and the lowest in the afternoon during warm, clear summer days. Oleoresin is a viscous liquid secreted by epithelial cells, which separate to form resin canals or ducts which are especially active in the outer sapwood (Kramer and Kozlowski, 1960).

Mode of action

It seems likely that the mode of action of oleoresin in mortality, particularly in L1 (first instar larva) was suffocation. This was consistent with the discovery of larvae that had sunk into oleoresin and died covered by it. In a preliminary experiment, an attempt was made to determine whether the oleoresin had a purely physical effect on the respiration of the insects, or whether it had some intrinsic toxicity. To do this eggs were rolled in a thin layer of a solution of resin in methanol in the bottom of an excavated glass block. It had just been determined that rolling the eggs similarly in methanol alone had no effect on their viability. When treated with resin, either the entire chorion was covered or aproximately half of it, was found that no eggs hatched if they had been totally covered by resin but 70% hatched when only partially covered. When newly hatched larvae were rolled in a thin layer of resin, no difference was found in their longevity compared with untreated larvae, although larvae died when immersed in a thick layer of oleoresin. These results were consistent with the proposition above that interference with respiration alone caused death, not mere contact with the oleoresin.

In older larvae (L3 and L4), oleoresin apparently also acts as a mechanical barrier to feeding. As mentioned before, when the larva girdles the trunk or a big branch, oleoresin flows and blocks the larval mine. This causes the death of the larva due to the shortage of wood available as food. It is probably difficult for larvae to pass through the hardened and viscous oleoresin to find food.

Plate 8: Tree response: showing a dead hatching larva within chorion that had been covered by oleoresin after the larva had chewed the bark and phloem of the twig (top); a dead larva that had been covered by oleoresin after the larva had penetrated into the twig (middle); and hardened oleoresin blocking the larval mine within the twig just before the girdling site after the larva had girdled the trunk of a potted tree (bottom).

Is oleoresin a key factor?

Of the 3 causes of mortality of the first instar larvae (L1), secondary oleoresin - i.e. flow produced by trees as a response to attack by U. cupressiana - is probably the most important factor, and probably the key factor, in the population dynamics of U. cupressiana. Physical factors, particularly rainfall may also play an important role in increasing or decreasing the operation of this key factor.

Conclusion

The attack behaviour of U. cupressiana does not alter in trees with different water status. The host tree, Cupressus sempervirens produces secondary oleoresin as a response to U. cupressiana attack, and the oleoresin flow appears to be the key factor in the population dynamics of U. cupressiana. The operation of this factor will vary depending on physical factors such as the availability of water (by artificial watering or rainfall).

7.2.3 Larval behaviour and host plant vigour.

24 potted trees of C. sempervirens (2-3 years old, 1.5m high) were grown in an insectary chamber (fluctuating temperature, 14 hour photoperiod under fluorescent light) under well watered conditions. 3 months later, each group of 4 trees was placed in a cage and 3 newly emerged beetles were released. After 7 days the cages were removed and the eggs were allowed to hatched. Three months after the eggs were deposited and early instar larvae had become established, the trees were treated as follows:

(1) 6 trees were well watered daily throughout the experiment
(2) 6 trees were girdled at the bottom part of the tree (20cm from above ground) and well watered daily.
(3) 6 trees were kept short of water by watering every 12th day throughout experiment.
(4) 6 trees were girdled and similarly kept short of water.

Young larvae which had established within twigs located below the girdling site were removed by cutting off the twigs. Three months after the trees were treated, the oleoresin exudation was determined by punching (roundly cut a part of the bark, phloem and cambium) the trunk or stem about 1cm in diameter at about 25cm above the ground or 5cm above the girdling site. The oleoresin exudation was categorized by using

symbols: ++ (some large resin blisters surround the punching area and a few blisters had flowed down on the surface of the bark), + (some small blisters surround the punching area) and ± (almost no blister observed, the punching area was sticky only).

20 months after egg deposition, the larvae had stopped feeding as indicated by lack of frass production through the opening on the bark. The experiment was terminated.

At the end of the experiment, the trees were cut and dissected. The position of the larva, prepupa or pupa was recorded. Stage of development, weight, and length of mine were determined.

The results are presented in Table 7.8. A T-test shows a significant difference between length of mine within low water status trees and those in high water status trees ($P<0.1\%$). The larvae tunnelled longer (mean 63.67±3.60cm) within low water status trees than within high water status trees (mean 34.43±3.53cm). Within low water status trees, the larvae after finishing feeding and tunneling in the distal (upper) part of the stem or trunk then went down or tunnelled proximally, passing the larval girdling site and constructing a pupal chamber 10-50cm (average 34.43±3.53cm) below the larval girdling site. Of 12 larvae within the 12 low water status trees, 9 tunnelled proximally along the centre of the trunk to the base of the trees and constructed their pupal chambers at the base. This larval behaviour might cause the death of the tree (see Plate 11).

Those in high water status trees, however, after finishing feeding and tunnelling the upper part of the trunk also tunnel donwards but constructed a pupal chamber just beyond the larval girdling site or a few centimetres (4.64±2.27cm) within their mines in artificially girdled trees. Of the 6 larvae within the well-watered, artificially girdled trees, one larva constructed it's pupal chamber 10cm from the base of the tree and caused the death of the tree.

The data showed no significant difference in weight and development of larvae. 20 months after the eggs were deposited the larvae had already matured and stopped feeding (as indicated by lack of new frass extruded through the opening on the bark).

A T test revealed that the proportion of shreded wood in larval frass on poorly watered trees was significantly lower (75.5±1.23%) than that on well watered trees (80.5±0.72%) ($P<0.05$). This implies that larvae on poorly watered trees utilized the wood more efficiently than

Table 7.8: Pupation site, length of mine, and larval weight in relation to water status of host trees

	Well watered trees	Poorly watered trees
Pupation site (distance away from girdling site)	22.33±4.27	4.64±2.27
Larval weight	1229.27±171.67	1317.65±140.22
Length of mine	34.43±3.53	63.67±3.60
Oleoresin pressure:		
-girdled tree	+	±
-ungirdled tree	++	+
RMC (%)	78±1.31	41.66±1.41

RMC : relative moisture content

Plate 9: The attacked potted trees 20 months after the deposition of eggs: tree under shortage of water became completely dry, and well watered tree became partly dry (left). The attacked potted trees six months after egg deposition (right).

larvae on well watered trees, i.e. with high nutritional value. As a result, there was no significant difference in growth rate, development, and larval weight between both type of the trees.

It was obvious that larvae of U. cupressiana could compensate their feeding within different nutritional status trees to gain the same rate of growth.

Examination of oleoresin pressure of the trees shows a difference between treated trees (see Table 7.8). The oleoresin pressure was high (++) within well watered trees and low (+) within poorly watered trees. In both types of trees, girdling decreased the oleoresin pressure, it is low (+) and very low (±) respectively.

These results suggest that changes in water status of the trees may alter larval behaviour. Larvae within low water status trees, i.e. trees with low oleoresin flows - tunnel longer; this behaviour may be associated with a low suitability of sites available for the pupal chamber, rather than a need for additional nutrition. As mentioned previously, when larvae were placed within dowels of various RMC they prefered the dowels with high RMC for constructing their pupal chambers.

Such larval behaviour is often found in the field within severely attacked trees. On such trees, about 50 to 90% of larvae were found in tunnels proximal to branches or even the trunk; these caused serious damage or even death of young trees. The position of the pupal chamber in relation to the larvae girdling site varied within trees and between trees. Pupal chambers were very rarely found below the larval girdling site within trees grown on an area with high rainfall; here they were usually constructed just above the girdling site or somewhere within the distal, dry branches. Within trees grown on the low rainfall area, however, the larvae mostly tunnelled proximally into fresh parts of the branches or trunks and constructed their pupal chambers far from girdling sites.

It is obvious that the physiology of the trees affects larval behaviour.

Conclusion

Changes in water status of the trees may have altered larval behaviour. The larvae tunnel longer before establishing a pupation site and utilized the wood more efficiently within trees of low water status or with low oleoresin flows compared with trees of high status in either

Plate 10: Dissected shortage watered trees showing the pupal chambers at the base of the trees and larval mine along the centre of the trunk (left). Dissected well watered trees, showing the pupal chambers just a few cm from larval girdling site (right).

respect. U. cupressiana attacks were more severe on trees grown under conditions of water deficit than well watered trees.

7.3 ATTACK BEHAVIOUR AND LARVAL SURVIVAL IN RELATION TO HOST TREE FERTILIZER REGIMES

32 potted saplings of C. sempervirens (2-3 years old, 150cm high) were treated for 2 months before the start of the experiment as follows:

(1) 8 trees were kept well watered daily but without any fertilizer (as control)

(2) 8 trees were well watered daily. Once every 4 weeks they were watered with an aqueous solution containing 1.5 g/liter of salts Sulphate Ammonia, Potassium Nitrate, and Mono-ammonium Phosphate (60:11:9)

(3) 8 trees were similarly treated but with a salt solution of 3g/liter

(4) 8 trees were similarly treated but with a salt solution of 4.5g/liter.

The application of treatments was given throughout the experimental period of 12 months. After 2 months of treatment 4 trees (one from each treatment) were randomly placed in a cage (1x1x1.5m, nylon covers) and 3 pairs of newly emerged beetles were released. One week later, the cages were removed and the number of eggs deposited were counted with the aid of magnifying lenses and labelled. All trees were shifted to a big cage with a metal frame and plastic gauze cover. The eggs were allowed to hatch and the number of first instar larvae (L1) established was recorded 2 months after introduction of the beetles to the trees. Factors which may have affected establishment of L1 were recorded weekly. Established larvae were allowed to develop to maturity within the trees. At the end of the experiment, or 10 months after introduction of the beetles, all trees were cut and dissected. Larval survival was recorded and larval weight and length of larval mines were determined.

Nitrogen analysis.

At the time when the beetles were released, 3 twigs were taken from each tree (from the upper, middle and lower parts of the tree respectively) put into a paper bag and oven dried for 24 hours (85°C). The total nitrogen content (% dry weight) was determined using a micro-Kjeldahl method (McKenzie and Wallace, 1954).

Data analysis

Data were analyzed using one-way Anova. Mortality and survival data were transformed into arcsin square root. Individual means were separated using a Tukey's honestly significant difference (HSD) at the 5% level.

The results are presented in Tables 7.9, 7.10 and 7.11. Analysis of variance showed significant differences in nitrogen percentage (in dry weight) between treated trees and control trees. The nitrogen content of a twig was correlated with the amount of fertilizer solution given. The number of eggs deposited per tree, however, was not significantly different between low and high nitrogen content trees. This implies that there was no discrimination between trees with different levels of Nitrogen by ovipositing females U. cupressiana (see Table 7.9). These results are consistent with those in previous experiments. Also both, larval development and larval weight did not vary in relation to nitrogen level on treated and control trees. On the other hand, larval mines varied significantly in relation to nitrogen level of the trees. The length of mine was longest in trees with lowest nitrogen content (control) and decreased as the nitrogen content of the tree increased (see Table 7.11). This indicates that larvae which feed on low nitrogen resources may compensate their poor food quality by increased feeding. This finding supports those obtained in previous experiments.

Larval mortality either for young instars (L1 and L2) or older instars (L3-L7) was not significantly different between control trees and treated trees (see Tables 7.10 and 7.11). These indicate that changes in the nitrogen content of trees did not affect larval survival. This finding also supports those of the previous experiment.

NPK fertilizer applied on C. sempervirens saplings had a marked effect on nitrogen levels in the twigs and a negative effect on the consumption of larvae as indicated by a reduction in length of larval mines. This finding also supports those of the previous experiment. It was found that 3 larvae on trees of group 3 and one larva on group 4 with a high level of nitrogen, had ceased feeding and were ready to pupate earlier, as indicated by the existence of a pupal chamber and the occurrence of holes for adult emergence. This implies that larvae feeding within trees with a high level of nitrogen may develop either in one year or 2 years whereas those feeding in trees with a low level of nitrogen may develop in 2 years. As previously mentioned, U. cupressiana mostly has a

Table 7.9: Percent nitrogen (dry weight) of twig, number of eggs deposited, and larval survival at different nitrogen levels on <u>Cupressus sempervirens</u>

Fertilizer mixture (g/101)	% host nitrogen	Mean No.of eggs deposited per tree	Survival (%)
0 (control)	1.15±0.03c	10.00±1.26	29.08±3.59
15	2.09±0.06b	12.25±1.16	35.73±7.12
30	2.57±0.04a	14.63±2.36	28.03±3.08
45	2.79±0.14a	18.75±2.79	24.39±6.45
P	< 0.001		

Means followed by the same letters are not significantly different.

Table 7.10: Larval mortality and causative factors on trees featured in Table 7.9

Fertilizer mixture (g/101)	Oleoresin L1 (%)	Oleoresin L3&4 (%)	Cannibalism (%)	Others(twig-fall, desiccation and infertile eggs(%)
0	14.89	4.26	39.36	12.76
15	15.30	5.60	37.75	14.28
30	12.82	5.13	41.80	13.67
45	14.00	5.33	44.00	17.33

Table 7.11: Larval development, weight, and length of mine with different nitrogen levels on C. sempervirens*

Fertilizer mixture (g/101)	Larval instar	Larval weight (mg)	Larval mine (cm)
0 (control)	L6, L7	86.33± 9.48	628.33±23.72a
15	L6, L7	98.18± 9.26	430.00±37.99b
30	L6, L7	108.97±12.19	338.46±17.53bc
45	L6, L7	110.41±11.51	233.24±22.04c
P			< 0.001

* for details of trees, see Tables 7.9 and 7.10
Means followed by the same letters are not significantly different.

biennial life cycle, with a few individuals developing in one year. The insects may have either a biennial or annual life cycle depending on the time when the eggs were deposited (see Chapter 4). The findings in this experiment thus showed that host conditions (i.e. level of nitrogen) may affect the life cycle of the insects.

The mortality factors observed were cannibalism and excessive oleoresin flow (see Table 7.10). As mentioned previously within young potted saplings only 2 larvae on average survive on each sapling, because they kill each other after mines interconnect. In the field, such a case rarely occurs.

As previously mentioned, larvae dwelling in the upper part of a sapling (if 2 larvae were found within the same tree) had unsuitable conditions for development resulting in death of the larvae due to desiccation of the wood. If they survived, they were of small size.

The effect of excessive oleoresin flow on larval survival both for first instars (L1) and for older instars (L3 and L4) was not significantly different within treated and control trees. This implies that changing the nutritional level of the trees does not affect secondary oleoresin production when the trees are attacked by the insect. As mentioned earlier, however, changing the water status of trees markedly affected the oleoresin production.

Conclusion

Tree fertilization does not affect the female oviposition behaviour, larval survival or weight of U. cupressiana. However, it does affect larval feeding behaviour, and apparently the insect's life cycle.

7.4 LARVAL SURVIVAL AND HOST SPECIES

A total of 49 potted trees of 7 species and varieties of Cupressus (C. sempervirens, C. macrocarpa horizontalis, C. glabra, C. tolurosa, C. m. horizontalis Aurea, C. cashmeriana and C. m. bruniana) were tested for oviposition preferences and/or host selection of U. cupressiana adults. The procedure used was similar to that in previous experiments (see Section 5.2.7.1). Eggs deposited were allowed to hatch and the larvae to establish within the trees. Six weeks after the beetles had been released, the number of surviving first instar larvae was recorded by counting the number of dry twigs. Larvae were allowed to develop within the trees until they matured. The experiment was terminated 10 months

after the beetles had been introduced to the trees. At the end of the experiment, all trees were cut and dissected. Each larva was weighed and its instar determined. The survival rate was calculated.

The results are presented in Table 7.12. Analysis of variance showed that no significant difference (P>0.05%) in number of eggs deposited between different species of Cupressus. This indicates that U. cupressiana could attack all Cupressus spp. tested. Larval mortality in first instar larvae (L1) was high ranging from 20 to 32%. Within host species, however, there was no significant difference between larval mortalities. Survival rates for mature lavae (L6 and L7) were also not different between host species. ANOVA showed non-significant differences in the weight of larvae (P>0.05), and also in larval growth and development. Both L6 and L7 were found in all host species. These results suggest that all Cupressus spp. tested are suitable for growth and development of U. cupressiana. The beetles used had emerged from C. sempervirens twigs and branches which were collected from the field. Within the geographical area of study (Adelaide plain), C. sempervirens, C. m. horizontalis Aurea, C. m. horizontalis, C. m. bruniana, C. tolurosa, and C. glabra are commonly found in parks, private yards and cemeteries. C. horizontalis is commonly grown as a hedge in private yards. All these Cupressus spp. were badly attacked by U. cupressiana. From survey data in early 1986, it was found that about 70% of C. sempervirens trees had been attacked (see Chapter 6) regardless of the occurrence of other species of Cupressus. This indicates that U. cupressiana is a serious pest on Cupressus spp. in the Adelaide plain. It also was found in other parts of South Australia (Murray Bridge, Barrossa Valley, York Peninsula etc.) and in some parts of Victoria and New South Wales which are very dry areas). Although no survey was made for the specific answer of determining the occurrence of cypress twig borers in Australia, evidence of them has been seen by the author in dry parts of the South Eastern states of Australia, except for Tasmania where no symptom of cypress twig borer damage were seen during a brief tour, perhaps because of its higher rainfall and lower temperatures. Where cypress twig borer occurred, the damage was easily noticed since dead twigs or branches form brownish spots on the crown of the trees in late summer. The main cause appears to be lack of sufficient watering. Thus, it might be worthwhile to argue that the aesthetic value of ornamental trees could disappear because of lack of maintenance of the trees, particular during summer.

Table 7.12: Survival, weight, and development of larvae reared in various species of Cupressus for 10 months

Host species	Eggs Deposited	Survival (%)	% L1 Mortality	Weight (mg)	Instar (10 months)
sempervirens	5.00±1.11	14.28	24.29	110.34±15.21	L6 & L7
cashmeriana	4.57±1.09	11.76	26.47	93.63± 9.47	L6 & L7
glabra	3.14±1.44	11.36	31.82	147.80±25.64	L6 & L7
tolurosa	4.57±1.64	9.37	29.68	98.28± 5.94	L6 & L7
horizontalis	2.71±0.89	17.86	28.57	84.80±10.14	L6 & 17
bruniana	3.00±0.37	11.53	30.77	114.25±23.75	L6 & L7
h. Aurea	5.29±1.54	9.37	23.44	102.67±16.53	L6 & L7

Conclusion

U. cupressiana (cypress twig borer) appears able to attack almost all of the Cupressus spp. in South Australia, probably also in some parts of Australia where the rainfall is lower and unreliable; there is no evidence of discrimination by ovipositing females among Cupressus spp.

7.5 FIELD DATA

Within the study site (see Chapter 6) 2 zones were chosen – i.e. zone 1 and 4 – for study of the mortality of larvae due to oleoresin flow and larval behaviour. In each zone, as indicated in Chapter 6, 20 trees had been chosen as sample trees for population studies. Of these, 10 trees were randomly taken in zones 1 and 4, dry twigs or branches that had been girdled by larvae of U. cupressiana were taken from each tree and recorded; larval mortality due to oleoresin flow and larval behaviour were observed. Mortality of larvae due to oleoresin flow was indicated when twigs or branches had been girdled by larvae but no surviving larvae were found within them, or hardened oleoresin was found within part of a twig in which an L1 initially become established. Sometimes there were found dead larvae near hardened oleoresin. At the same time, 4 fresh twigs were taken, all just within reach of the ground (about 2m), from each direction (North, South, east and West) and at the bottom part of the tree for RMC determination. The twigs were cut and immediately put into a sealed plastic bag. Collections were made in summer (December and January), 1986/1987.

The data collected are presented in Tables 7.13 & 7.14, and Apps. 45 & 46. From these it can be seen that within twigs which were taken from zone 4 (coastal area with low rainfall), the mortality due to the oleoresin flow was very small (0.8%), particularly for older instar larvae (L4 or L5) after they had girdled the branches; a high proportion (85.5%) of the larvae had tunnelled downwards, passed their girdling site and had constructed their pupal chamber within big branches or trunks; the mean RMC of the twig was 58.8±2.4%. Within twigs which were taken from zone 1 (high rainfall), the mortality of L4-L5 due to oleoresin flow after the larvae had girdled the branch was high (8.7%); the proportion of larvae that had tunnelled past the girdling site was very low (0.2%); the mean RMC of twigs was 75.9±1.6%.

These findings indicate that within trees with a high RMC, the mortality of L4-L5 was high, whereas in low RMC trees it was low. The

Table 7.13: Data collected from ten trees in low rainfall area (towards coastal area) on the Adelaide plain in summer 1985/1986

Tree no.	Number of twigs observed	Mortality due to oleoresin flow (L3 to L5) (%)	Larvae tunnelled downwards into branch or trunk (%)
1	52	0 (0)	46 (88.5)
2	79	1 (1)	74 (93.7)
3	152	2 (1)	143 (94.0)
4	163	2 (0.6)	158 (96.9)
5	50	0 (0)	38 (65.5)
6	58	0 (0)	42 (72.4)
7	93	1 (1)	86 (92.5)
8	105	1 (0.9)	97 (92.4)
9	73	0 (0)	49 (67.1)
10	144	1 (0.6)	132 (91.6)

Averages:
Mortality, 0.8±0.25%;
Larvae tunnelled downwards, 85.5±3.83%;
RMC, 52.8±2.40%.

Table 7.14: Data collected from 10 trees in high rainfall area (towards foothills area) on the Adelaide plain in summer 1985/1986

Tree no.	Number of twigs observed	Mortality due to oleoresin flow (L3 to L5) (%)	Larvae tunnelled downwards past girdling site (%)
1	46	4 (8.6)	0
2	80	8 (10)	0
3	86	9 (10.5)	0
4	37	4 (10.8)	0
5	58	6 (10.3)	1 (1%)*
6	96	12 (12.5)	1 (1%)*
7	61	6 (9.9)	0
8	77	5 (7.1)	0
9	28	1 (3.6)	0
10	31	1 (3.2)	0

Averages:
Mortality, 8.7$\pm$0.98%;
Larvae tunnelled downwrds, 0.2%;
RMC, 75.9$\pm$1.60%.

*larvae tunnelled downwards about 10cm from girdling site.

proportion of the larvae that had tunnelled downwards past the larval girdling site was high within low RMC trees, but was low or almost nil within high RMC trees. These findings are consistent with the results of the potted tree experiments. Observations on the mortality of L1 in the field need intensive work and much time spent searching from one twig to another; such studies were more than could be encompassed within this study. It is suggested, that further investigations in this matter could be considered worthwhile to gain more precise estimates of the larval mortality due to oleoresin flow in the field.

Nevertheless, the findings from both the potted tree experiments and the field data are consistent with the concept that oleoresin is the key factor specifying the distribution of U. cupressiana populations in the field, particularly on the Adelaide plain.

7.6 CONCLUSION

- Artificial watering/rainfall may affect the composition of host trees.
- Changes in the composition of trees do not alter the reproductive behaviour of U. cupressiana, but do alter larval behaviour (feeding, construction of pupal chamber and damage to the tree).
- Survival of young larvae was not affected by changes in the nutritional composition of the host tree.
- Trees produce "secondary oleoresin", i.e. an induced oleoresin flow, as a response to attack by U. cupressiana.
- Oleoresin flow is most likely the key factor in the population dynamics of U. cupressiana.
- The operation of this key factor much depends on physical factors, rainfall and soil moisture in particular.

CHAPTER VIII

CHAPTER 8

GENERAL DISCUSSION

Cupressus sempervirens has been grown as an ornamental tree in South Australia for about 130 years. When the association of the indigenous CTB (*U. cupressiana*) with this introduced host began is still uncertain but information from tree growers suggests that it may be more than 20 years ago. In recent years there have been outbreaks, some quite prolonged and the insect has been recognized as a pest. However, its study was still neglected.

The original hosts of the insect were apparently certain native trees, such as the native cypress, *Callitris* spp. According to Morgan (personal communication) the insect has been found attacking *Callitris* in South Australia. Its establishment on a new host (*Cupressus* spp) is still poorly understood; it is possibly due to the rareness of the native host (*Callitris* spp), and the abundance and acceptibility of the introduced host. Experiments in the laboratory and with caged, potted trees have shown no discrimination by the ovipositing female between native hosts and introduced hosts (Chapter 5).

Both genera of trees are known to be genetically isolated (Lord, 1974; Harrisson, 1975; Boland *et al.* 1985). Possibly they nevertheless have sufficient chemical similarity with respect to primary attractants to the insect and nutritional quality that female beetles oviposit on both, and the larvae are able to survive, develop, and emerge.

Strong *et al.* (1984) proposed that 2 factors determine rates of colonization of new hosts by insects: (1) the area planted, and (2) the taxonomic, phenological, biochemical, and morphological match between introduced plants and the native flora. Moreover they argued that 3 categories of insect colonists move onto the new plant: (1) species that readily move into new crops, (2) species pre-adapted to the crop, and (3) species that seem to have shifted their host preferences (Turnipseed & Kogan, 1976 in Strong *et al.*, 1984). The establishment of *U. cupressiana* on *Cupressus* is probably due to colonizers of the second category. As mentioned previously, chemical cues might lead the female beetles to migrate and oviposit on *Cupressus* spp. Successful rearings from the first migrators would ensure that the species then became established on *Cupressus*.

The life history of U. cupressiana has some distinctive features. Sex ratio analysis showed that the ratio of males to females was significantly different at different times in the overall breeding season. There were more males early in the season (September to October) and more females later on (December to January) (see Chapter 4). This is because the developmental period of the male is shorter than that of the female. As previously mentioned, male larvae undergo 6 larval instars whereas almost all female larvae undergo 7 larval instars. Female beetles require a longer time to complete their sexual development than males. It was found under laboratory conditions that almost all males emerging early in the season did not find mates before the end of their life. A similar fate befell females which emerged late in the season. The most successful beetles were those that emerged during the peak of adult emergence (November) when the male to female sex ratio was 1. Very few females emerged in the early season. As a result, few offspring are produced early in the season, and this in turn allows very few beetles to emerge in the following year - i.e. those with an annual life cycle. Consequently most beetles emerge after 2 years (biennial life cycle) (see Chapter 4).

U. cupressiana synchronized its life history with field conditions by undergoing a diapause at the end of larval development. The insects depend on temperature to regulate their diapause processes (see Chapter 4). These processes show some variations in their seasonality. This results in a variable time of adult emergence. The periodicity of emergence of the beetles varied from 3 to 4 months. Insect activities, viz. adult emergence, mating and egg deposition are also temperature dependent. Warm sunny days favour the beetles' emergence, and high nocturnal temperatures favour reproductive activity (mating and egg deposition) (see Chapter 5). It is believed that bright sunny days and high nocturnal temperatures during late spring and summer may play an important role in the population trends of U. cupressiana in South Australia. However, in this study it was found that 10 to 20% male beetles are unsuccessful in their reproductive strategy. Such were all the beetles that emerged from twigs collected from severely attacked or densely populated trees. It was thought that within trees which have a dense population of insects (i.e., brood trees), inbreeding might occur. If such is the case then males of low vigour might arise.

It might be thought that poor nutrition or starvation may result in low vigour insects; for U. cupressiana, however, the data showed that nutrition was not the cause of low vigour, since larvae could compensate their growth by feeding faster and tunnelling longer within trees of low nutritional status compared with trees of high nutritional status (see Chapter 7).

Whatever the cause, unsuccessful reproduction of numbers of males might have an impact on population trends. At the zone 3 which had the highest density of population, the trend of population was unclear; at Zone 4, however, there was a slow rate of population increase from N3 to N2 and from N2 to N1, but a high rate of increase occurs at N1 to N0. This could well be due to an increase in reproductive potential and/or survival potential of the insects. Graham (1963) has proposed that inherent changes in reproduction and survival potentials may be a factor playing a substantial role in the increase or the decrease of population. He argued that the causes of insect increase should be sought in 2 main phenomena: the gain or regain in predominance of heritable factors of viability and fecundity that improve the capacities of a population to exploit the opportunities provided by the environment, and the gain of favourable environmental factors and/or the amelioration of restrictive conditions in the environment.

Study of the life table of CTB suggests that the key factors are those which: (1) operate on the first instar larvae, (2) operate on the third and 4th instar larvae, and (3) have a differential effect on the sexes. Of these factors, the one that is significantly and dominantly responsible for variable mortality is factor 1 above (Chapters 4 and 7).

Morris (1957) stated that "....... variation is the important attribute of mortality, and that low but variable mortalities may therefore have more influence on population trend than high but relatively constant mortalities". The influence of variable mortalities on population changes are considered to be important whether they are density dependent or density independent (LeRoux et al., 1963). Such mortalities are called "key factors" by Morris (1959) which according to him means "simply that changes in population from generation to generation are closely related to the degree of mortality caused by this factor, which therefore has predictive value".

The excessive oleoresin flow being produced by an attacked host tree may be considered to be a key factor in the population dynamics of U. cupressiana. The hypothetical relationships between oleoresins and U. cupressiana densities are as follows:

1. Insect density will be very low if the period of larval establishment coincides with the host tree condition that allows the tree to produce a great amount of oleoresin in response to larval attack.
2. Insect density will be low to medium when the period of larval establishment partially overlaps the period when the host tree is able to produce a great amount of oleoresin.
3. Insect density will be high when the peak of larval establishment coincides with the period when the host tree produces a very low flow of oleoresin.

The first relationship probably exists in an area with high rainfall or with a high moisture content of the soil, as in the foothills of the Mount Lofty Ranges. Adult emergence takes place in mid-spring, while egg hatching and larval establishment occur in late spring. At that time the host tree is still very vigorous. Hence high mortality occurs and most of the population fails to establish. Nevertheless, hatching and establishment also occur in late summer, resulting in the establishment of a part of population.

The second relationship probably exists in areas with intermediate rainfall, where the density of population is also intermediate. Apparently, the host tree retains sufficient vigour for a certain period in spring so that any larval establishment which occurs at that time has a high failure rate, whereas later, during summer, almost all larvae can establish.

The third relationship would be the cause of the highest population density which occurs in areas with lowest rainfalls, i.e. towards the coastal area on the Adelaide plain. Here, host tree vigour is apparently very low during the establishment of larvae, resulting in almost all young larvae being able to survive and establish. Data in Chapter 6 suggest that the population of CTB in this area or zone is rising. No doubt some factors may limit this rise, but tree vigour would not seem to be a key factor in this area.

The hypothesis that oleoresin flow is a key factor in the population dynamics of U. cupressiana would seem to provide an explanation

for both the distribution and abundance of insect in South Australia, the Adelaide plain in particular.

Field studies on the population showed that there is a significant difference in population distribution between sample areas (zones) (Chapter 6). The population density was lowest in the foothills of the Mount Lofty Ranges which had a high rainfall. The density of population increases toward the coastal areas which had a low rainfall. It is thought that the operation of the key factor much depends on climatic factors, rainfall in particular. The crude rate of increase of population varies either within zones or generations. It was shown that the rate of increase of the population was significantly high in the zone with lowest rainfall, and also the rate of increase in this zone was significantly high for the current growth population (NO). It was thought that the fluctuation in the rate of population increase in this zone from year to year coincided with fluctuations in seasonal rainfall that resulted in variability of mortality factors, oleoresin flow in particular. A prolonged period of rainfall might have a great effect either on the larval mortality or the reproductive activity of U. cupressiana. On the other hand, a drought year may favour the abundance of insect.

It has been stated by previous workers that rainfall or precipitation has a directly lethal effect on hemlock looper (Graham, 1963), spruce budworm (Greenbank, 1956) etc, and an indirect effect on bark beetle (Graham, 1963; Craighead, 1925; Hall, 1958; Vite, 1961 etc.); and sucking insects (Carpenter, 1940). Drought, however, may increase the frequency and severity of insect outbreaks, such as of bark beetles (Graham, 1963).

Study on the insect host-plant interactions showed that the host-plant produces secondary oleoresin as a response to larval attack. The amount of secondary oleoresin produced by the host tree was strongly correlated with the plant water status. High turgor trees could produce a great amount of oleoreresin, while low turgor trees produced a small amount of oleoresin or even almost none (Chapter 7). It is thought that the establishment of young instar larvae within high turgor trees depends also on intrinsic factors in the larva. It is believed that highly vigorous larvae, capable of tunnelling fast, might establish even within high vigour trees. It was found on well-watered potted trees that some larvae could establish and survive, even though part of their mines had been filled with oleoresin.

According to Krammer and Kozlowski (1960), the water status of a tree generally has a peak at dawn, decreases to a minimum level in the afternoon, then increases again during the night. It was believed that the cycle of oleoresin exudation pressure coincided with the diurnal cycle of the water status (turgor) of the trees. There was a regular diurnal cycle of oleoresin exudation pressure reaching a minimum at 1400 to 1600h and a maximum between midnight and dawn. The pressure varied depending on site, weather (light intensity and humidity etc.), soil moisture, and physiological condition of the tree. The pressure also varied between trees, tree strata, and even within radial parts of a tree (Vite, 1961). Moreover, Vite argued that the diurnal fluctuation of oleoresin exudation pressure was strongly correlated with water balance as a result of water absorption and transpiration of the tree. Thus, the distinctive diurnal fluctuation depends on weather and site. Consequently, there is also a seasonal diurnal fluctuation of oleoresin exudation pressure.

This might suggest that highly vigorous larvae could synchronize their feeding activities with the diurnal fluctuation of oleoresin exudation pressure. As mentioned in Chapter 4, after newly hatched larvae penetrated into the phloem and cambium of the twigs, they first made a zigzag tunnel with 2 or 3 bends, then they tunnelled straight up the distal part of the twig. Apparently, when the larvae successfully completed one zigzag, they had already avoided a hazardous oleoresin flow.

Prolonged rain (Rudinsky, 1966) or continuous sprinkling (Vite, 1961) raises the soil moisture to field capacity, resulting in an increased oleoresin exudation pressure.

Experiments with various watering regimes on potted trees showed that water supply could alter the water status of the tree as well as oleoresin exudation pressure. Field data revealed that trees grown in the zone with a low rainfall and low moisture content of soil had a low water status (RMC), and often also had a low oleoresin exudation pressure during summer. Whereas those grown in the zone with a high rainfall and high moisture content of soil had a high water status and often also had a high oleoresin pressure.

The findings here may suggest that watering regimes and/or rainfall, soil moisture in particular, have a strong effect on physiological conditions of the host trees and this results in differences in population distribution and the abundance of U. cupressiana on the Adelaide plain.

Natural enemies such as parasitic wasps and predatory clerids are found attacking older stages of *U. cupressiana* larvae. However, neither parasites nor predators were found attacking the early instars. It was believed that these biotic mortality factors did not affect the population trend of *U. cupressiana*. Cannibalism and excessive desiccation of wood had no effect on population trends in the field but had a strong effect in the laboratory and on potted plants.

Assuming that oleoresin flow is the key factor affecting *U. cupressiana*, several possibilities may be considered for its future control without the application of insecticides. It is widely accepted that using insecticide for wood borer control is far from being a successful strategy. Good maintenance of the trees is a way of controlling this species, i.e. by watering particular trees regularly, especially during the establishment period of young instar larvae (spring and summer). The implementation of this method does not raise any difficulties, particularly for *Cupressus* trees grown in private yards. However, control of *U. cupressiana* in trees grown in parks or cemeteries should take into account the aspect of floral diversity. It was found in this study that the fecundity of the *U. cupressiana* female decreased when the females were provided with both host and non-host trees (or twigs) for ovipositing.

It is widely accepted that ecologically complex plantations and forests with substantial floral and faunal diversity are less seriously affected by insect pests than those of more homogenous structure (Graham, 1963; Anderson, 1960; Strong *et al*., 1984).

Eradication of infested parts of trees is also important; i.e. removing or destroying all infested parts of the trees, such as twigs, branches or even bole or trunk, and burning them. For very severely attacked trees, it is suggested that the whole tree should be cut and burnt, and replaced with other species.

Note that the above recommendations were not made with the sole aim of controlling *U. cupressiana*. Other benefits that would accrue if these recommendations are implemented such as an improvement in the aesthetics of the ornamental trees in particular and the city in general.

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APPENDICES

Appendix 1. Key to Australian species of Uracanthus
(N.B. Figure numbers carry on from those in Chapter 3).

1. Apices of elytra either singularly pointed, asymetrically rounded or acutely rounded (e.g. Figs. 3.49, 3.60 & 3.85)................2
- Apices of elytra bispinose, truncate with a single tooth, or with some type of posterior notch or emargination (e.g. Figs. 3.61, 3.65 & 3.72)...11
2. Apices of elytra singularly pointed (e.g. Figs. 3.55, 3.64 & 3.76). 3
- Apices of elytra asymetrically rounded or acutely rounded (e.g. Figs. 3.85, 3.86 & 3.60)..9
3. Apices of elytra produced in middle and symetrical (e.g. Figs. 3.49 & 3.87)...4
- Apices of elytra produced proximally towards midline of body (e.g. Figs. 3.64 & 3.77)...5
4. Elytra with apices broadly pointed (Figs. 3.1A & 3.87), moderately punctate at base; pronotum strongly strigate across midline from base to apex but becoming irregular or curved about middle (Fig. 3.1A); male genitalia as in Figs. 3.3 & 3.4.......... ....cupressiana sp.n
- Elytra with apices acutely spinose and coarsely punctate towards base (Fig. 3.49); pronotum strigate at base (Fig. 3.126); male genitalia as in Fig. 3.19...............................acutus Lea
5. Elytral pilosity arranged in longitudinal lines..................6
- Elytral pilosity even and dense; elytra with 3 feeble elevated sculptural lines, apices with short, proximal spine (Fig. 3.64)
  [pronotum short and binodose (one node on each side of midline), sides rounded about middle and widened and depressed posteriorly; T7 with pointed corners (Fig. 3.103); clypeus semicircular and depressed; antennae thick, segments 5-10 produced on one side at apex, longer than body; male genitalia as in Fig. 3.31; length 40-42mm, width 9mm width; also see couplet 33]...gigas var. A Lea

6. Body (cuticle) reddish-brown to brown..............................7

\- Body black, pilosity white

[pronotum with pilosity uneven, strigate at base and binodose on each side of midline (Fig. 3.151); elytra moderately punctate with 3 elevated lines and 9 longitudinal lines of pubescence interspersed with almost hairless spaces, apices acutely spinose (Fig. 3.76); femur with dense pilosity; male genitalia as in Fig. 3.43]..suturalis Lea

7. Pronotum with pilosity even or uneven but without post lateral bands...8

\- Pronotal pilosity with longitudinal postlateral band of dense pubescence on each side, also with smooth, hairless space along middle (Fig. 3.132)

[elytra with 2 bands of dense pubescence (one along suture and one along margin), interspersed with sparsely pilose spaces, apices slightly toothed (Fig. 3.55); femur with dense pubescence; male genitalia as in Fig. 3.25].........................discicollis Lea

8. Pronotum with sides conspicously rounded at about middle, evenly and densely pilose (Fig. 3.152); antennae with segments 4-10 triangularly produced on the one side at apex; male abdomen with S 3 and S 4 (not S5) bearing a bundle of hairs; male genitalia as in Fig. 3.44.......................................ventralis Lea

\- Pronotum with sides angular about middle, unevenly pilose with some hairless patches (Fig. 3.156); antennae with segments 3-10 flat and obliquely produced on one side at apex; male abdomen with S3 - S5 bearing a bundle of hairs; male genitalia as in Fig. 3.47. ....multilineatus McKeown

9. Elytra with apices angulate proximally.........................10

\- Elytra with apices rounded (Fig. 3.85)

[elytra moderately punctate, basal half almost hairless but densely pilose posteriorly; pronotum irregularly strigate at base and apex, rugose and rugulose about middle, strongly tuberculate near base, sides weakly angulate, pilosity uneven (Fig. 3.160); antennae with segments 5-10 flat and produced on one side at apex; body yellowish brown, pilosity white]...............minatus Pascoe

10. Pronotum with sides angular about middle, with 2 longitudinal, postlateral bands of pubescence, remainder almost hairless, binodose across middle (Fig. 3.137); muzzle very short ('length about 1/4-1/3 of width); antennal segment 11 divided by feeble suture (i.e appearing 2-segmented); body reddish brown, pilosity

pale yellow...leai McKeown

- Pronotum with sides slightly rounded about middle, with one longitudinal postlateral band of irregularly dense pubescence on each side, remainder hairless (Fig. 3.161); muzzle short (length about 1/3-1/2 of width); body brown and pilosity white............ .... inermis Aurivillius

11. Apices of elytra bispinose..12

- Apices of elytra truncate with a single tooth, or other emargination...34

12. Elytral pilosity arranged in 2 or more longitudinal lines........13

- Elytral pilosity uniform or uneven but without longitudinal lines.. 18

13. Pronotum with 2 or 4 longitudinal post lateral bands of dense pubescence...14

- Pronotum with pilosity even or uneven but without longitudinal bands...17

14. Pronotum with 2 longitudinal postlateral bands which disappear before apex...15

- Pronotum with 4 longitudinal post lateral bands 2 on each side...16

15. Pronotum weakly depressed and tuberculate near base (Fig. 3.129); antennae with segment 11 divided by feeble suture (i.e. appearing 2-segmented); T7 and S7 truncate (Fig. 3.91); male genitalia as in Fig. 3.22...bivitta Newman

- Pronotum strongly depressed near base (Fig. 3.147); antennae with segment 11 undivided; T7 truncate, and S7 rounded and notched medially (Fig. 3.110); male genitalia as in Fig. 3.36 (also see couplet 39)......................................marginellus Hope

16. Elytra with almost hairless patch at shoulder, margined with dense ashen pubescence, remainder with dense pilosity that appears in numerous longitudinal fine lines, superimposed with very feebly elevated lines; pronotum with sides weakly angular about middle (Fig. 3.133); antennae with segments 5-10 flat, wide and produced on one side at apex, segment 11 divided by feeble suture (i.e. appearing 2-segmented); abdomen densely and evenly pilose, T7 rounded and notched posteriorly (Fig. 3.95); male genitalia as in Fig. 3.26; length 30-35mm, width 6-7mm....................... ....dubius Lea

- Elytra with 2 to 4 longitudinal lines of white pubescence from base to near apex, interspersed with almost hairless spaces; pronotum with sides strongly angular about middle (Fig. 3.149); antennae with segments 3-11 almost cylindrical or slightly producd on one side at apex, segment 11 undivided; male abdomen with first 3 segments (S3-S5) bearing a bundle of hairs, T7 truncate (Fig. 3.112); male genitalia as in Fig. 3.38; length 16mm, width 3mm..................................strigosus Pascoe

17. Head with very long muzzle (length about 1 1/2 times width), clypeus triangular; antennae with segments 3-11 cylindrical and thin; pronotum conspicuously strigate from base to apex across the midline, densely pilose with yellow pubescence on postlateral and lateral sides, hairless space along middle emarginated with white dense pilosity at base, sides rounded about middle and strongly depressed posteriorly (Fig. 3.138); elytra with apices widely emarginate and acutely spinose (Fig. 3.61), with elevated longitudinal sutural lines, minutely punctate, basal third of elytra unevenly pilose, sutural area hairless, marginated with narrow line of white pubescence, apices hairless and remainder evenly pilose; T7 of female abdomen rounded (Fig. 3.100); length 30mm, width 6mm......................................insignis Lea

- Head with short muzzle (length about 1/2 times width), clypeus semi-circular; antennal segments 4-10 dilated on one side at apex; pronotum strigate at basal third and apex, pilosity uneven or denser on both sides and remainder sparsely pilose, sides angular about middle (Fig. 3.139); elytra with apices narrowly emarginate, proximally more acutely spinose than outer side (Fig. 3.62), moderately punctate, with smooth patch at shoulder and 4 longitudinal lines of pubescence interspersed with almost hairless spaces; T7 of abdomen truncate (Fig. 3.101); length 14mm, width 5mm....................................glabrilineatus Lea

18. Elytra evenly pilose..19

- Elytra unevenly pilose..22

19. Pronotum with longitudinal bands of dense pubescence............20

- Pronotum with pilosity even and uneven but without longitudinal bands...21

20. Pronotum long (length about 1 1/2 times basal width), with one band of dense pubescence on each postlateral side, strigate across the midline at base and apex but not about middle, sides weakly angular about middle (Fig. 3.127); elytra with 3 longitudinal

elevated lines, apices strongly and narrowly emarginate, spines close together (Fig. 3.50); antennae with segments 4-10 flat, produced on one side of apex, segment 11 divided by feeble suture (i.e. appearing 2-segmented); clypeus almost triangular; first 3 segments of abdomen (S3-S5), each with a bundle of hairs; T7 truncate (Fig. 3.89); male genitalia as in Fig. 3.20; length 18-20mm, width 2-2,5mm.................................albatus Lea

- Pronotum short (length about same as basal width), with 2 bands of dense pubescence on each postlateral side, interspersed with hairless spaces, gently undulating and widely tuberculate on both sides of midline, sides rounded about middle (Fig. 3.143); elytra with 2 feeble longitudinal elevated lines, apices obliquely emarginate with the proximal corner more acutely spinose than outer side (Fig. 3.67); antennae with segments 4-10 acutely produced on one side at apex, segment 11 undivided; clypeus semicircular; abdomen densely pilose, T7 truncate (Fig. 3.106); male genitalia as in Fig. 3.34; length 26-32mm, width 5-6mm...... ....maleficus Lea

21. Pronotum binodose across middle, strongly strigate from base to apex across the midline and becoming irregular about middle, unevenly pilose, sides angular about middle (Fig. 3.136); elytra finely punctuate, densely and evenly pilose, with sutural and marginal lines of white pubescence, the remaining pilosity yellow, apices semi-circularly and narrowly emarginate (Fig. 3.59); antenna as long as body, with segments 4-10 flat, produced on one side at apex; clypeus semi-circular; abdomen densely pilose; male genitalia as in Fig. 3.29; length 25-30mm, width 4-5mm........... ....lateroalbus Lea

- Pronotum with 2 wide tubercles on each side of midline near base, weakly strigate at base, evenly pilose, sides widely rounded about middle and depressed posteriorly (Fig. 3.153); elytra moderately punctate towards base, evenly pilose with pale yellow pubescence; antennae shorter than body, segments 4-10 feebly produced on one side at apex; clypeus triangular; abdomen with fine moderate dense pilosity; male genitalia as in Fig. 3.45; length 16mm, width 1.5mm ....tropicus Lea

22. Antennae of male with a fringe of pubescence projecting ventrally on segments 3-10..23

- Antennae with uniform pilosity...................................25

23 Pronotum with pilosity even or uneven but without longitudinal bands...24

\- Pronotum with a longitudinal postlateral band of dense pubescence on each side of midline

[pronotum longer than basal width, strongly strigate from base to apex across the midline, sides weakly angular (Fig. 3.146); elytra unevenly pilose, with apices strongly and obliquely emarginate, acutely spinose (Fig. 3.70); antennae as long as body, thin, segments 5-10 triangularly produced on one side at apex; pilosity white; T7 truncate (Fig. 3.109)].............*pertenuis* Lea

24\. Elytra with narrow convex ridge from shoulder to about basal third, sparsely pilose, apices semicircularly emarginate and acutely spinose (Fig. 3.68); pronotum with sides weakly rounded about middle, sparsely pilose (Fig. 3.144); antennae longer than body, segment 11 divided by feeble suture (i.e. appearing 2-segmented); clypeus semicircular; T7 flat and truncate (Fig. 3.107); length 10mm, width 1.6mm.........................*parvus* Lea

\- Elytra with broad convex ridge from shoulder to external apical tooth, pilosity sligthly dense along the margin, apices obliquely and weakly emarginate, spines slightly acute (Fig. 3.83); pronotum with sides angular about middle, densely pilose (Fig. 3.158); antennae shorter than body; clypeus triangular; T7 rounded but notched (Fig. 3.122); length 19-20mm, width 2.8-3mm.... ....*dentiapicalis* McKeown

25\. Elytra with triangular hairless patch posterior to shoulder or with hairless patches at base, sometimes triangular region not completely hairless and margins indistinct, but always with obvious difference compared with rest of elytra 26

\- Elytra pilose posterior to shoulder and base.....................32

26\. Apices of elytra hairless..27

\- Apices of elytra pilose...28

27\. Elytra with apices widely emarginate, strongly and acutely spinose and hairless, horizontally margined with a line of dense pubescence (Fig. 3.74), triangular hairless patch posterior to shoulder margined with line of dense pubescence; pronotum strigate at about basal third and apex (Fig. 3.150); ventral surface of femur with groove (male) filled with dense pubescence; male genitalia as in Fig. 3.39 (see also couplets 28 and 30)........... ....*triangularis* Hope

- Elytra with apices narrowly emarginate and weakly spinose, with hairless patch at apices obliquely marginated with dense pubescence (Fig. 3.69); pronotum strongly strigate from base to apex across the midline but becoming irregular or circularly rugose about middle (Fig. 3.145); ventral surface of femur densely pilose..pallens Hope

28. Elytra with a triangular hairless patch posterior to shoulder....29

- Elytra with 3 hairless patches at base (one humeral, one median and one sutural), remainder densely pilose, moderately punctate, widely emarginate and acutely spinose (Fig. 3.79)

  [pronotum with sides angular about middle and dilated near apex, strongly strigate from base to apex across the midline but becoming irregular about middle, binodose across middle and widely tuberculate near base, pilosity as longitudinal bands at post lateral sides (Fig. 3.154); muzzle moderate (length about 1/2-3/4 times width); clypeus triangular and convex; antennae as long as body, with segments 4-10 slightly produced on one side at apex].... ....fuscocinereus White

29. Margins of triangular patch on elytra indistinct, area partially pilose...30

- Margins of triangular hairless patch on elytra distinct, with marginal line of pubescence as on adjacent parts; apices of elytra dark in colour, outer tooth much longer than the proximal one (Fig. 3.75)

  [pronotum with sides angular about middle, weakly strigate and binodose across middle, densely pilose; muzzle short (length about 1/3-1/2 times width); clypeus semicircular; antennae with segments 5-10 produced on one side at apex, segment 11 divided by feeble suture (i.e. appearing 2 segmented); T7 rounded but notched (Fig. 3.114); male genitalia as in Fig. 3.40 (also see couplets 27 & 31). ....triangularis var.A Lea

30. Pronotum with sides angular about middle, slightly tapering, pilosity dense or sparse...31

- Pronotum with sides widely rounded about middle, strongly tapering apically and depressed near base, strigate from base to apex across the midline but becoming curved about middle, pilosity as 2 longitudinal bands at each post lateral side (Fig. 3.155)

  [elytra with apices narrowly emarginate and more acutely spinose proximally than outer corner, with 3 feeble elevated

lines, pilosity concentrated in regular longitudinal lines (sublineate) (Fig. 3.80); muzzle long (length about same as width); clypeus triangular; antennae shorter than body, with segments 5-10 angularly produced on one side at apex, segment 11 divided by feeble suture (i.e. appearing 2-segmented); T7 rounded but notched (Fig. 3.119); pilosity pale yellow and grey; male genitalia as in Fig. 3.46; length 25-37mm, width 5-8mm]............regalis McKeown

31. Humeral patch almost hairless with marginal line of denser and paler pubescence than those on adjacent area, apices also darker than adjacent parts, proximal spines long than outside one; pronotum sparsely pilose; muzzle long (length about same as width); male genitalia as in Fig. 3.41 (see also couplet 27)...... ....triangularis var. B Lea

\- Humeral patch almost hairless patch with margining line of pubescence as on adjacent parts, apices are the same colour as adjacent parts, proximal spine as longer as outside one; pronotum densely pilose; muzzle short (length about 1/3-1/2 times width); male genitalia as in Fig. 3.42 (see also couplet 27).............. ....triangularis var.C Lea

32. Elytra with pilosity uniformly dense or sparse..................33

\- Elytra with pilosity condensed into numerous small fascicles, apices widely emarginate strongly and acutely spinose (Fig. 3.54)

[pronotum strigate from base to apex across the midline but becoming slightly curved about middle, pilosity with 2 post lateral bands of dense pubescence on each side which become fused about middle, binodose across middle (Fig. 3.131); muzzle long (length about same as width); clypeus semicircular; antennae shorter than body with segments 5-10 flat and produced on one side of apex; T7 rounded but notched in middle (Fig. 3.93); male genitalia as in Fig. 3.24].....................cryptophagus Oliff

33. Pronotum short (length about same as basal width), sparsely pilose, sides widely rounded about middle and strongly depressed either posteriorly or anteriorly, binodose across middle and strongly tuberculate on both sides near base (Fig. 3.140; elytra sparsely pilose, sides narrowing regularly, apices squarely emarginate and acutely spinose (Fig. 3.63); clypeus semicircular and depressed; antennae longer than body; T7 truncate (Fig. 3.102); body black-redbrown, pilosity white; male genitalia as in Fig. 3.30; length 46-52mm, width 10-12mm (also see couplet 5)........... ....gigas Lea

- Pronotum long (length about 1 1/2 times basal width), densely pilose, strigate at base and apex across the midline (Fig. 3.159); elytra densely pilose, sides parallel, apices semicircularly emarginate, corners slightly spinose (Fig. 3.84); clypeus triangular and flat; antennae shorter than body, segments 3-11 thin; T7 rounded (Fig. 3.123); body reddish-brown, pilosity pale yellow; length 17-18mm, width 2.7-3mm................<u>parallelus</u> Lea

34. Apices of elytra truncate or with single tooth or spine (e.g. Figs. 3.57 & 3.65)..35

- Apices of elytra notched (e.g. Figs. 3.51 & 3.58)................38

35. Apices of elytra truncate, without pronounced spine (e.g. Figs. 3.57 & 3.66)...36

- Apices of elytra somewhat truncate, but with a pronounced proximal spine (e.g. Figs. 3.65 & 3.82)..........................37

36. Pronotum with 2 longitudinal postlateral bands of dense pubescence on each side, irregularly strigate or vermiculate from base to apex, binodose across middle and with 2 wide tubercles near base (Fig. 3.142); elytra coarsely punctate, with 3 or 4 elevated lines, sparsely and finely pilose; clypeus semicircular; abdomen densely pilose; male genitalia as in Fig. 3.33............ ....<u>loranthi</u> Lea

- Pronotum unevenly pilose, tuberculate near the base, remainder smooth (Fig. 3.134); elytra semicircularly depressed just before the tip, unevenly pilose, with a square almost hairless patch about middle, pilosity dense at tip; clypeus triangular; abdomen sparsely pilose, S 3 and S 4 with hairless patches; male genitalia as in Fig. 3.27.......................<u>frogatti</u> Blackburn

37. Body reddish-black; pronotum irregularly strigate, strongly tuberculate near base and binodose across middle (Fig. 3.157); elytra evenly and densely pilose, with white pubescence along margin, remainder pale yellow, apices widely truncate (Fig. 3.82); clypeus triangular and flat; antennae shorter than body, segments 6-8 feebly produce on one side at apex, segment 11 divided by feeble suture (i.e. appearing 2-segmented); abdomen densely pilose but with hairless patches on S 1-4; male genitalia as in Fig. 3.48...................................<u>fuscostriatus</u> McKeown

- Body reddish-brown, pronotum regularly strigate from base to apex (Fig. 3.141); elytra with 2 to 3 elevated lines, unevenly pilose with pale yellow pubescence, apices narrowly truncate (Fig. 3.65); clypeus semicircular; antennae longer than body, segments 4-10

flat and triangularly produced on one side at apex; abdomen densely and uniformly pilose; male genitalia as in Fig. 3.32..... ....longicornis Lea

38. Elytral pilosity sublineate.......................................39
- Elytral pilosity uniform or uneven but without lines............40

39. Elytra with almost hairless patch at shoulder and remainder with numerous longitudinal thin lines of pubescence, moderately punctate toward the base, apices rounded in middle, a small narrow notch present between middle and apical end of suture (Fig. 3.58); pronotum strigate at base and apex, unevenly pilose (Fig. 3.135); clypeus semicircular; antennae shorter than body; T7 rounded (Fig. 3.97); male genitalia as in Fig. 3.28............ ....fuscus Lea
- Elytra pilose at shoulder, with 2 longitudinal bands of dense white pubescence (one along suture and one along margin) interspersed with thin sparse pilose space, finely punctate, apices widely notched between middle and apical end of suture; pronotum strongly strigate from base to apex across the midline but becoming curved about middle, pilosity as a longitudinal band on each post lateral side which disappear before apex (Fig. 3.147); clypeus triangular; antennae longer than body; T7 truncate (Fig. 3.110); male genitalia as in Fig. 3.36 (also see couplet 15)......................................marginellus Hope

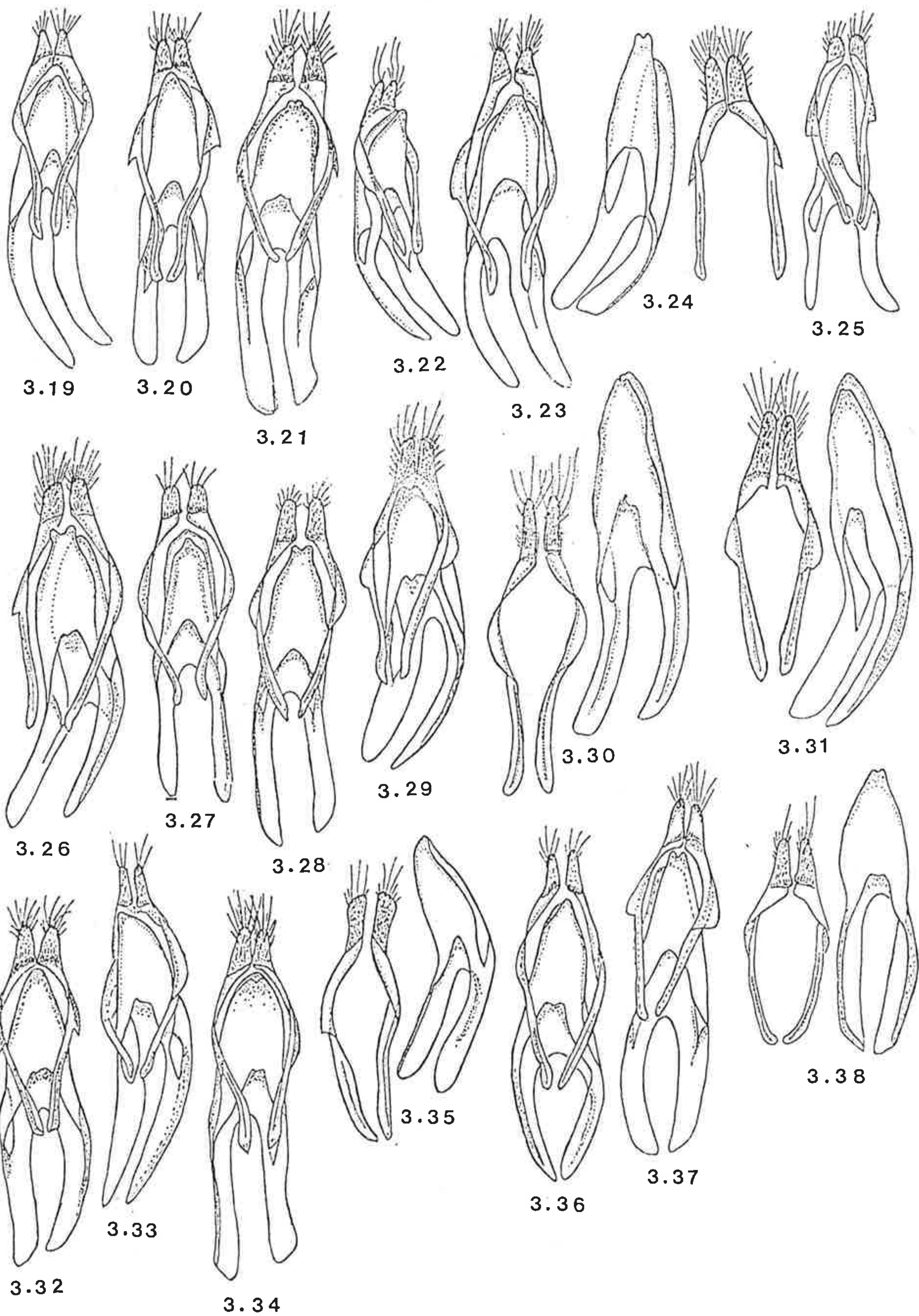
40. Body reddish-brown and pilosity white and pale yellow...........41
- Body reddish-black or almost black and pilosity white [pronotum with sides rounded about middle and strongly depressed posteriorly, strongly strigate from base to apex across the midline, and sparsely pilose (Fig. 3.128); elytra coarsely punctate towards the base, sparsely pilose, apices rounded in middle, notched and weakly spinose proximally (Fig. 3.51); clypeus semicircular; antennae longer than body, with segments 4-10 flat and triangularly produced on one side at apex; T7 truncate (Fig. 3.90); male genitalia as in Fig. 3.21].....ater Lea

41. Pronotum short (length shorter than basal width), strigate at base and apex across the midline (Fig. 3.130); apices of elytra with a narrow small notch proximally (Fig. 3.53); clypeus triangular and depressed anteriorly; antennae with segments 5-10 flat and triangularly produced on one side at apex; male genitalia as in Fig. 3.23........................corrugicollis Lea

- Pronotum long (length longer than basal width), strongly strigate from base to apex across the midline but becoming irregular about middle (Fig. 3.148); elytra with apices widely notched proximally (Fig. 3.72); clypeus semi-circular; antennae with segments 5-10 produced on one side at apex; male genitalia as in Fig. 3.37...simulans Pascoe

Figs. 3.19 - 3.38: Adult Uracanthus spp.: male genitalia, ventral and ventrolateral view, showing the aedeagus (the combined median lobe and tegmen).

3.19 acutus; 3.20 albatus; 3.21 ater; 3.22 bivitta; 3.23 corrugicollis; 3.24 cryptophagus (median lobe separated from tegmen; 3.25 discicollis; 3.26 dubius; 3.27 froggatti; 3.28 fuscus; 3.29 lateroalbus; 3.30 gigas (median lobe separated from tegmen); 3.31 gigas var. A (median lobe separated from tegmen); 3.32 longicornis; 3.33 loranthi; 3.34 maleficus; 3.35 pertenuis (median lobe separated from tegmen); 3.36 marginellus; 3.37 simulans; 3.38 strigosus (median lobe separated from tegmen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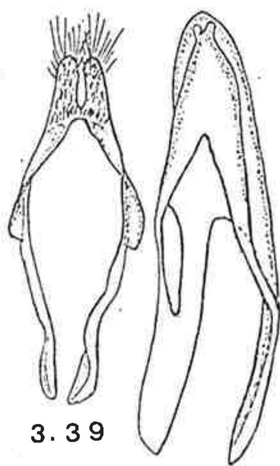
Figs. 3.39 – 3.48: Adult *Uracanthus* spp.:
male genitalia, ventral and ventrolateral view, showing the aedeagus (combined median lobe and tegmen).

3.39 *triangularis* (median lobe separated from tegmen); 3.40 *triangularis* var. A (median lobe separated from tegmen); 3.41 *triangularis* var. B; 3.42 *triangularis* var. C; 3.43 *suturalis*; 3.44 *ventralis*; 3.45 *tropicus*; 3.46 *regalis*; 3.47 *multilineatus*; 3.48 *fuscostriatus*



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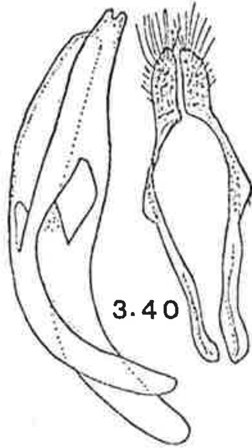

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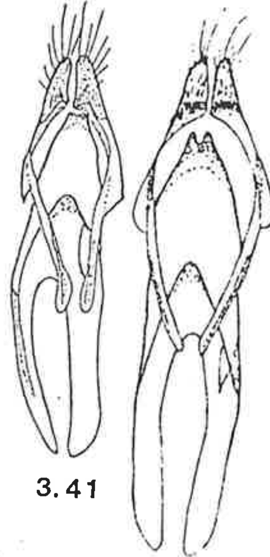

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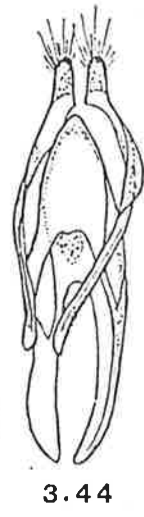

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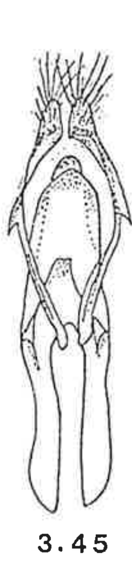

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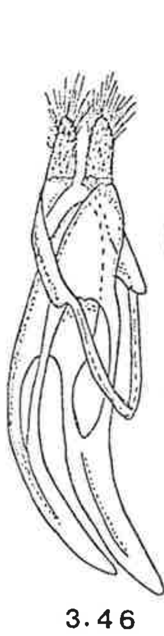

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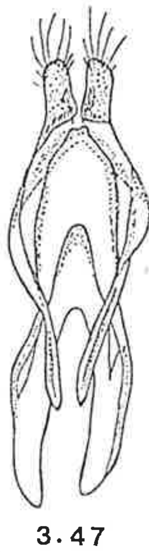

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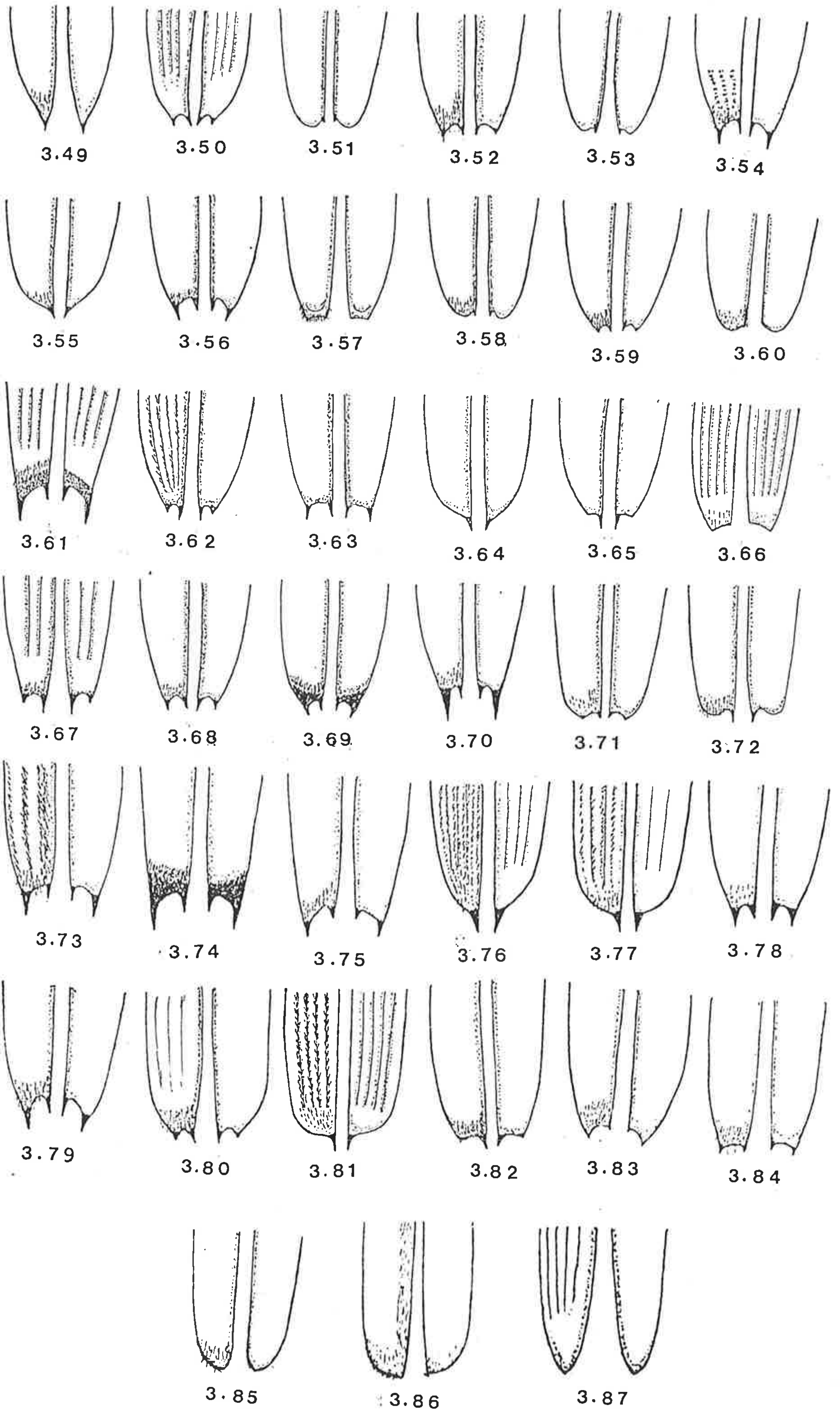
Figs. 3.49 - 3.87: Adult Uracanthus spp.: apices of elytra of male (except Figs. 3.61, 3.78, 3.79 and 3.85 which are females), showing imargination of apices and sculpturing.

3.49 acutus; 3.50 albatus; 3.51 ater; 3.52 bivitta; 3.53 corrugicollis; 3.54 cryptophagus; 3.55 discicollis; 3.56 dubius; 3.57 froggatti; 3.58 fuscus; 3.59 lateroalbus; 3.60 leai; 3.61 insignis; 3.62 glabrilineatus; 3.63 gigas; 3.64 gigas var. A; 3.65 longcornis; 3.66 loranthi; 3.67 maleficus; 3.68 parvus; 3.69 pallens; 3.70 pertenuis; 3.71 marginellus; 3.72 simulans; 3.73 strigosus; 3.74 triangularis; 3.75 triangularis var. A; 3.76 suturalis; 3.77 ventralis; 3.78 tropicus; 3.79 fuscocinereus; 3.80 regalis; 3.81 multilineatus; 3.82 fuscostriatus; 3.83 dentiapicalis; 3.84 parallelus; 3.85 minatus; 3.86 inermis; 3.87 cupressiana.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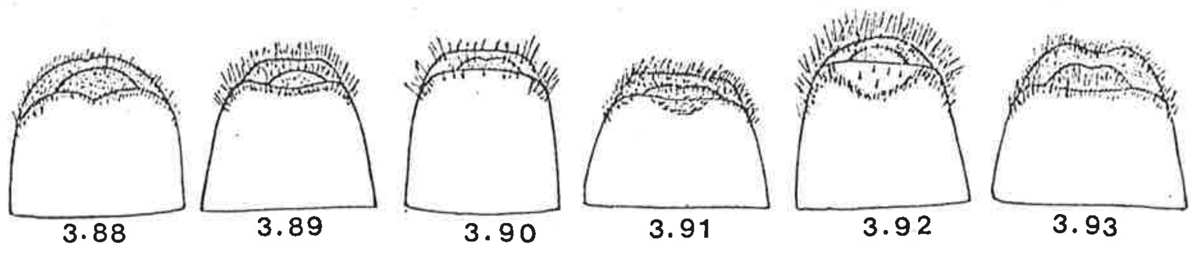
Figs. 3.88 - 3.125: Adult *Uracanthus* spp., terminal segments of abdomen of male (except Figs.3.100. 3.117, 3.118 and 3.124 which are females), showing imargination of S7, T7 and T8.

3.88 *acutus*; 3.89 *albatus*; 3.90 *ater*; 3.91 *bivitta*; 3.92 *corrugicollis*; 3.93 *cryptophagus*; 3.94 *discicollis*; 3.95 *dubius*; 3.96 *froggatti*; 3.97 *fuscus*; 3.98 *lateroalbus*; 3.99 *leai*; 3.100 *insignis*; 3.101 *glabrilineatus*; 3.102 *gigas*; 3.103 *gigas* var. A; 3.104 *longicornis*; 3.105 *loranthi*; 3.106 *maleficus*; 3.107 *parvus*; 3.108 *pallens*; 3.109 *pertenuis*; 3.110 *marginellus*; 3.111 *simulans*; 3.112 *strigosus*; 3.113 *triangularis*; 3.114 *triangularis* var. A; 3.115 *suturalis*; 3.116 *ventralis*; 3.117 *tropicus*; 3.118 *fuscocinereus*; 3.119 *regalis*; 3.120 *multilineatus*; 3.121 *fuscostriatus*; 3.122 *dentiapicalis*; 3.123 *parallelus*; 3.124 *minatus*; 3.125 *inermis*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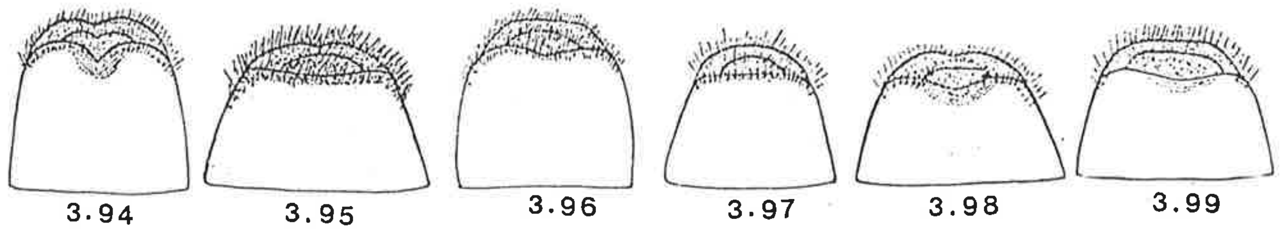
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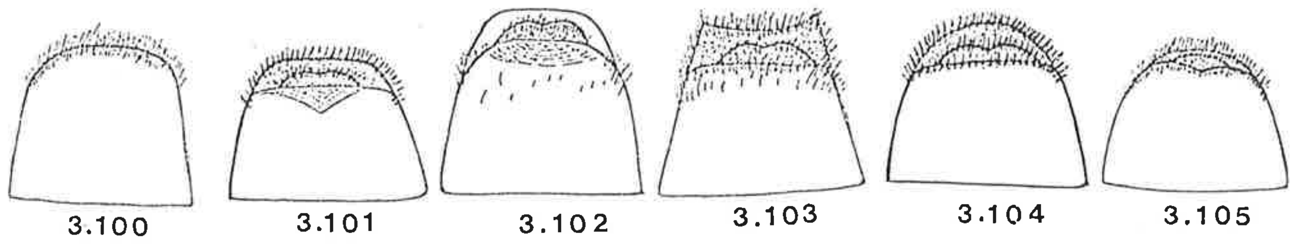
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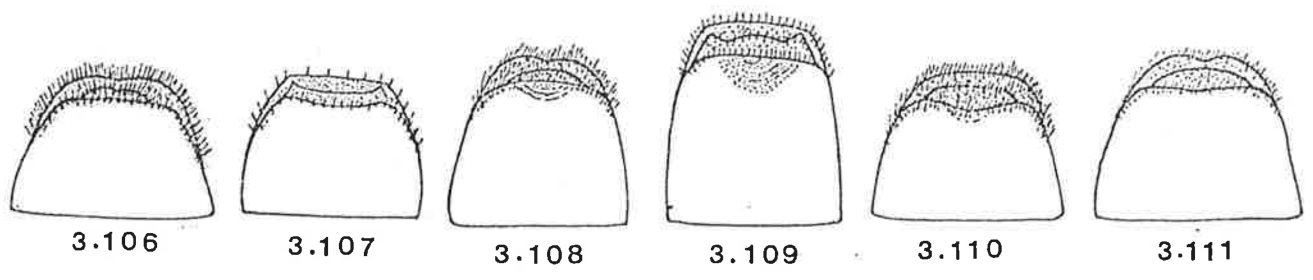
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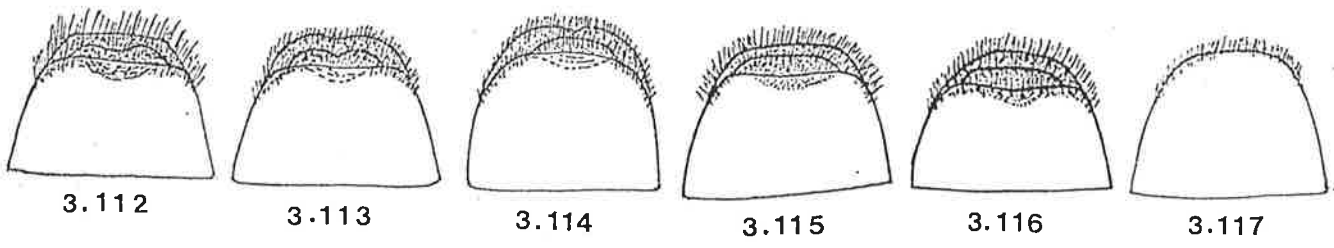
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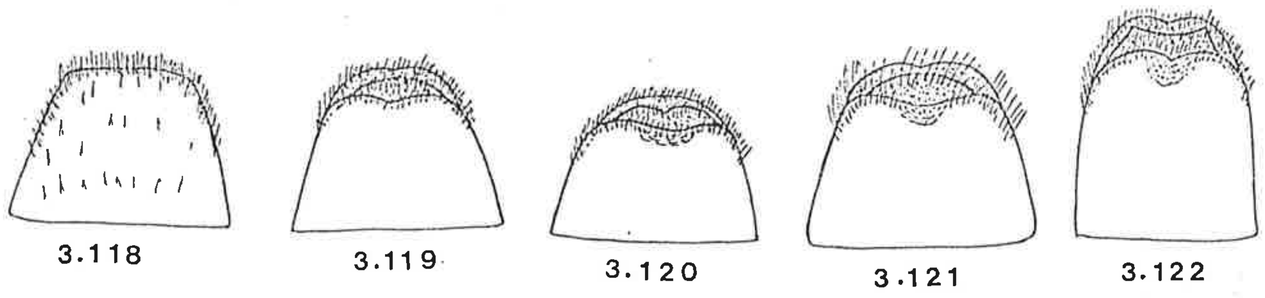
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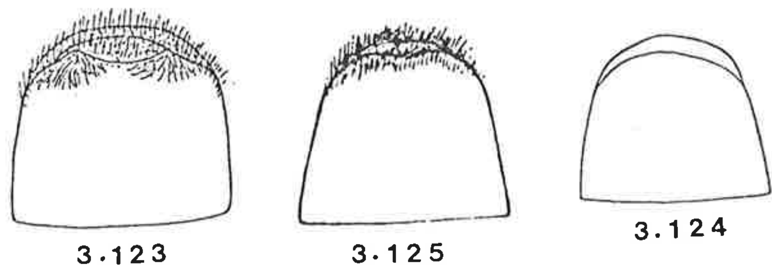
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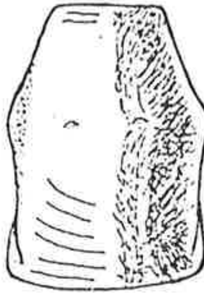
Figs. 3.126 - 3.145: Adult *Uracanthus* spp.
showing shape, pilosity (right side) and
sculpturing (left side) of pronotum.

3.126 *acutus*; 3.127 *albatus*; 3.128 *ater*; 3.129 *bivitta*; 3.130 *corrugicollis*; 3.131 *cryptophagus*; 3.132 *discicollis*; 3.133 *dubius*; 3.134 *froggatti*; 3.135 *fuscus*; 3.136 *lateroalbus*; 3.137 *leai*; 3.138 *insignis*; 3.139 *glabrilineatus*; 3.140 *gigas*; 3.141 *longicornis*; 3.142 *loranthi*; 3.143 *maleficus*; 3.144 *parvus*; 3.145 *pallens*.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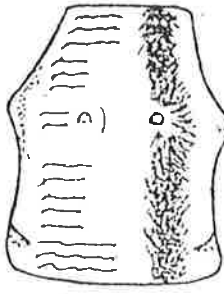
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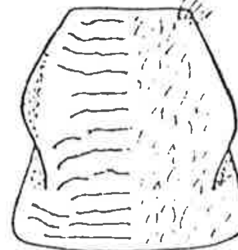
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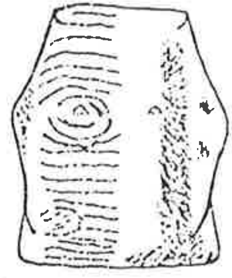
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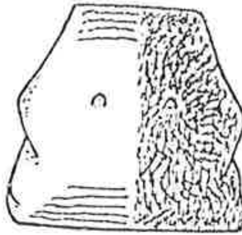
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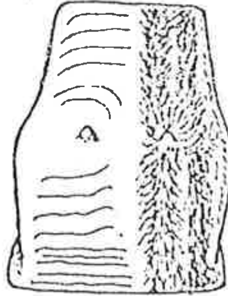
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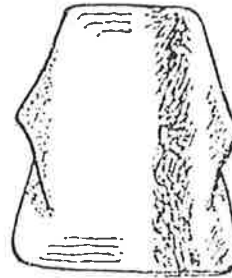
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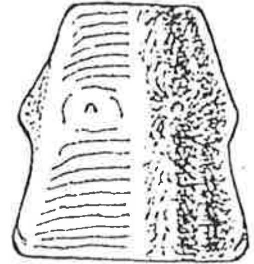
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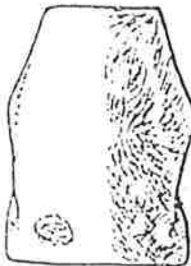
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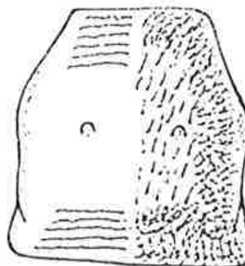
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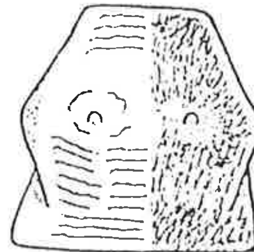
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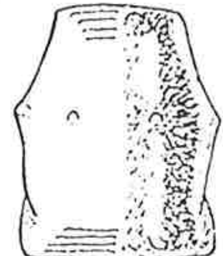
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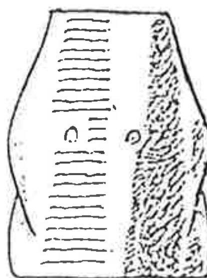
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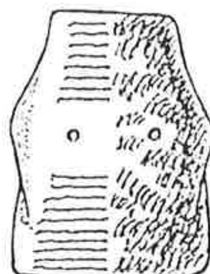
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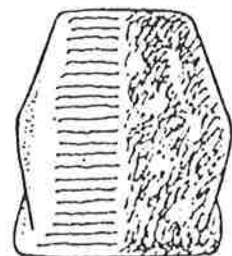
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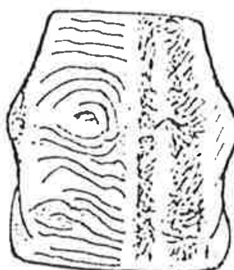
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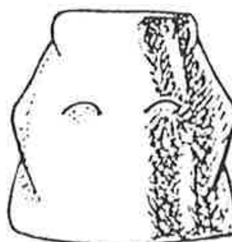
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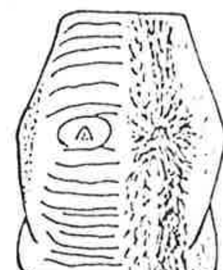
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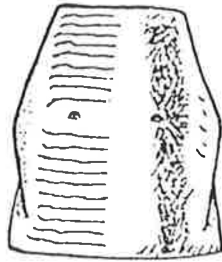
Figs. 3.146 - 3.161: Adult *Uracanthus* spp. showing shape, pilosity (right side) and sculpturing (left side) of pronotum.

3.146 *pertenuis*; 3.147 *marginellus*; 3.148 *simulans*; 3.149 *strigosus*; 3.150 *triangularis*; 3.151 *suturalis*; 3.152 *ventralis*; 3.153 *tropicus*; 3.154 *fuscocinereus*; 3.155 *regalis*;; 3.156 *multilineatus*; 3.157 *fuscostriatus*; 3.158 *dentiapicalis*; 3.159 *parallelus*; 3.160 *minatus*; 3.161 *inermis*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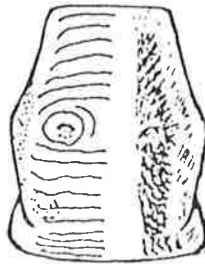
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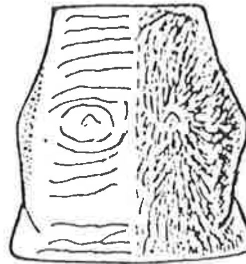
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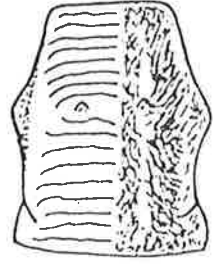
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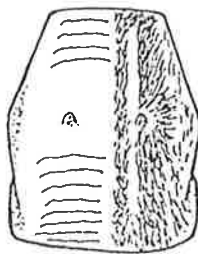
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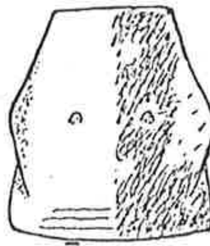
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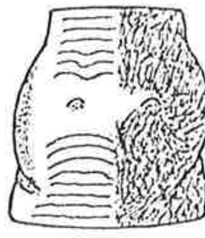
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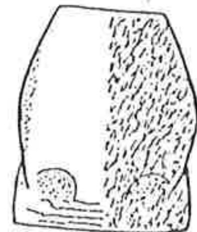
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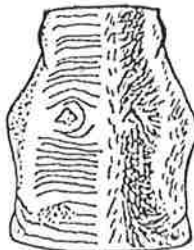
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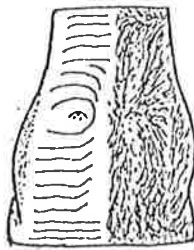
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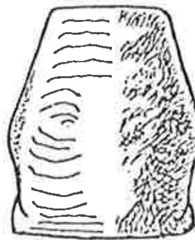
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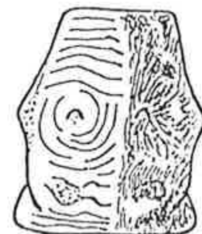
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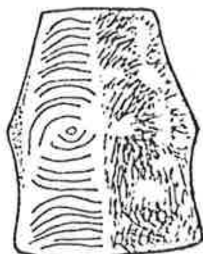
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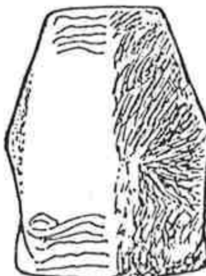
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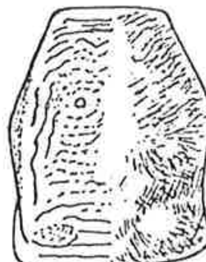
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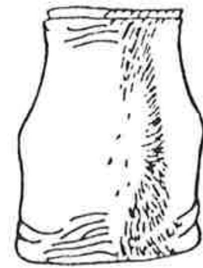
3.161

Appendix 2. Means of daily air temperatures (°C) recorded at WARI in 1983 to 1986

Month	Maximum				Minimum				1/2(Max. + Min.)			
	1983	1984	1985	1986	1983	1984	1985	1986	1983	1984	1985	1986
January	27.3	26.4	28.1	26.5	15.2	15.8	16.1	14.8	21.3	21.1	22.1	20.7
February	31.2	27.9	27.9	26.7	19.5	16.4	16.6	15.6	25.4	22.1	22.2	21.2
March	25.3	24.6	27.0	28.4	15.9	15.1	17.0	16.7	20.6	19.9	22.0	22.6
April	19.1	21.1	22.4	21.2	12.2	12.3	13.8	13.0	15.7	16.7	18.1	17.1
May	17.8	19.1	18.1	18.1	11.0	12.1	11.1	11.5	14.4	15.6	14.6	14.8
June	15.3	15.8	14.8	14.9	8.5	8.7	9.0	9.1	11.9	12.2	11.9	12.0
July	13.5	13.1	14.8	13.2	7.7	7.3	8.9	8.1	10.6	10.2	11.8	10.6
August	16.3	14.7	15.0	15.0	9.4	9.3	9.0	8.9	12.8	12.0	12.0	11.9
September	17.6	15.4	16.6	16.8	10.0	8.8	8.9	9.7	13.8	12.1	12.8	13.2
October	20.9	20.7	20.7	18.6	11.4	11.3	12.1	10.2	16.3	16.0	16.4	14.4
November	23.8	22.9	23.0	23.5	13.5	14.1	13.6	12.5	18.7	18.5	18.3	18.0
December	27.7	25.8	23.3	23.9	15.8	15.5	13.9	14.1	21.8	20.7	18.6	19.0
Annual Mean	21.3	20.6	21.0	20.7	12.5	12.2	12.5	12.0	16.9	16.4	16.7	16.3

Appendix 3. Means of daily rainfall (mm) and relative humidity (%) recorded at WARI in 1982 to 1986

	rainfall (mm)/relative humidity (%)				
Month	1982	1983	1984	1985	1986
January	24.6/50.3	22.4/53.4	42.8/56.7	1.6/49.0	10.2/54.0
February	7.0/54.2	1.8/46.8	2.6/54.9	3.2/49.4	1.6/57.8
March	54.2/56.6	105.6/64.9	32.4/52.7	49.4/55.6	1.8/50.6
April	81.2/62.1	99.0/62.3	26.2/64.9	55.6/59.2	75.6/62.0
May	63.2/71.4	76.6/74.5	62.4/64.4	100.2/69.3	57.4/69.7
June	62.6/76.3	34.0/75.3	48.8/72.4	65.2/76.0	46.8/75.6
July	38.6/70.4	127.6/80.1	103.6/82.8	58.6/66.6	168.2/78.2
August	24.6/57.0	90.6/69.3	134.4/78.2	94.0/75.3	129.8/70.5
September	32.0/60.6	77.0/69.0	63.6/65.8	71.6/61.7	77.6/69.7
October	16.0/55.5	56.8/60.0	25.8/54.0	37.8/60.6	62.2/62.1
November	3.4/43.9	10.6/55.3	54.4/59.0	27.4/60.8	10.0/50.1
December	20.0/49.5	20.0/49.5	9.0/52.2	59.6/59.6	42.0/57.5
Annual Mean	35.0/58.3	60.2/63.5	50.5/63.2	52.0/53.3	56.9/63.2

Appendix 4. Distribution of body length (mm) in U. cupressiana larvae of different instars

Instar	I	II	III	IV	V	VI	VII
	1.45-1	2.50-3	5.0 -4	7.03-3	10.50-2	14.00-2	18.00-3
	1.54-3	2.75-1	5.23-4	7.50-5	10.70-7	14.53-3	18.23-2
	1.64-2	2.86-2	5.63-2	7.95-2	10.85-6	14.78-2	18.75-2
	1.73-6	2.95-2	5.77-2	8.23-4	11.00-2	15.45-4	19.38-2
	1.82-3	3.00-2	5.88-2	8.28-2	11.45-4	15.63-1	19.63-2
	1.91-3	3.13-3	6.32-2	8.85-2	11.90-2	15.78-1	20.20-2
	2.05-5	3.25-3	6.48-1	9.34-2	12.03-3	15.85-4	20.70-1
	2.09-2	3.64-2	6.78-1	9.48-2	12.13-4	17.85-3	21.25-2
	2.18-8	3.75-1	6.88-2	9.53-3	12.50-3	17.95-4	21.35-3
	2.27-1	3.85-2	6.95-2	9.63-1	12.90-7		21.88-1
	2.36-3	3.90-1	6.98-4	10.30-2	13.85-2		22.50-2
	2.45-1			10.48-1			23.28-4
				10.88-2			23.75-1
							24.00-4
							25.00-2
							25.35-1
							25.73-3
							26.98-1
							28.85-1
							29.00-1
							30.40-2
							30.88-1
							31.98-1
Mean	1.96	3.25	6.24	9.04	11.72	15.76	23.79
Range	1.45 to 2.45	2.50 to 3.90	5.0 to 6.98	7.03 to 10.88	10.40 to 13.85	14.0 to 17.85	18.0 to 31.98
N	38	23	24	31	43	24	43

Figures are: body length (mm) - the number of larvae
N: The total number of larvae in each instar

Appendix 5. Number of emergence holes in relation to twig size (diameter)

Number of hole	n	Twig size (mm)	P value
1	47	Mean: 9.30±0.41 Range: 5.38-17.50	<0.01
2	40	Mean: 5.98±0.21 Range: 3.0 -9.38	

T test.

Appendix 6. Twig size, larval mine, and larval weight of L7 of U.cupressiana

Twig diameter (mm)	Larval weight (mg)	Length of mine (mm)	Width of mine (mm)
5	90.15	300	3.64
6	148.7	260	3.75
8	148.3	300	3.86
8	100.2	370	4.09
5	66.4	300	3.64
6	65.7	370	3.41
7	50.3	230	3.41
8	40.6	300	3.64
6	58.6	390	2.95
6	127.4	360	3.64
13	157.2	280	4.09
12	125.1	380	3.64
3	90.5	250	3.41
8	133.7	240	3.64
9	161.4	420	4.09
5	61.7	300	3.64
7	61.5	440	3.64
3	95.0	200	3.18
4	79.8	320	3.64
6	49.6	200	2.73
4	76.5	270	3.18
5	65.4	390	3.64
6	77.8	320	3.41
5	83.0	280	3.18
7	62.2	360	3.18
6	85.5	280	3.18
5	86.7	300	2.95
4	63.3	150	2.95
4	60.4	250	2.95
10	112.3	300	3.18
6	76.6	490	2.73
5	99.3	350	3.86
4	88.3	250	3.64
5	149.1	300	3.41
6	52.2	130	4.09
5	109.7	230	3.86
6	55.0	340	3.18
7	98.6	390	3.86
5	136.3	290	3.41
5	92.5	270	3.64
8	99.6	500	4.32
5	69.8	240	2.73

continued.

continued.

Twig diameter (mm)	Larval weight (mg)	Length of mine (mm)	Width of mine (mm)
10	92.8	330	3.64
7	98.2	470	3.86
8	92.0	370	3.64
3	121.5	340	3.86
6	72.5	130	2.73
7	90.5	320	3.64
10	56.8	320	3.18
6	99.6	410	3.64
8	67.5	240	3.64
5.5	70.5	350	3.64
5	100.6	240	3.18
4	100.6	220	3.18
8	100.2	380	4.09
10	125	310	3.41
5	90.3	230	2.95
10	88.0	350	2.95
5	138.0	190	4.09
5	100.4	300	3.18
8	115.7	360	3.86
5	75.1	200	3.18
6	55.6	410	3.18
6	96.0	350	3.64
6	88.7	360	4.55
10	143.7	430	3.18
10	185.4	220	3.64
8	78.5	380	3.86
8	41.2	320	3.41
5	113.3	350	3.64
10	77.6	225	3.18
7	109.2	390	3.18
7	91.5	410	3.41
9	84.4	300	3.86
5	53.5	340	3.86
10	73.5	510	3.86
10	168.7	280	3.64
4	83.7	350	3.41
4	110.3	280	3.18

Appendix 7. Time required (in weeks) for the completion of diapause development of larvae of *U. cupressiana* at 15 and 20°C CTR *

15°C Week – N (30)	20°C Week – N (27)
24 – 2	26 – 2
25 – 1	27 – 1
26 – 3	28 – 4
28 – 3	30 – 2
29 – 1	32 – 3
30 – 3	33 – 1
32 – 3	34 – 2
34 – 2	35 – 1
36 – 2	36 – 2
37 – 1	38 – 2
38 – 3	40 – 2
40 – 2	76 – 2
72 – 2	80 – 1
74 – 1	
76 – 1	

* The experiment was terminated after 20 months.

Appendix 8. Time required (weeks) by the end of diapause development of larvae initially exposed to 10°C, then kept at 15 and 20°C and those maintained at 15 and 20°C for 9 months

Control		Exposed to 10±C	
15°C (N=14)	20°C (N=13)	15°C (N=13)	20°C (N=12)
24 - 1	26 - 2	22 - 3	18 - 2
25 - 1	27 - 2	23 - 1	20 - 4
26 - 2	28 - 3	24 - 1	22 - 2
28 - 4	30 - 3	25 - 1	23 - 1
29 - 2	31 - 1	26 - 2	24 - 2
30 - 2	32 - 2	28 - 2	26 - 1
32 - 1		30 - 1	
36 - 1		32 - 1	

Appendix 9. Time required (weeks) by the end of diapause development of larvae of U. cupressiana after initially exposed to 25°C for 6 and 12 months, then kept at 15°C *

Control (N=14)	Initially exposed to 25°C	
(15°C)	6 months(N=12)	12 months(N=9)
24 - 1	60 - 1	64 - 1
26 - 2	62 - 2	66 - 2
28 - 2	64 - 2	68 - 3
30 - 1	65 - 1	70 - 2
32 - 2	66 - 2	72 - 1
36 - 2	70 - 2	
40 - 2	71 - 1	
70 - 1	72 - 1	
72 - 1		

* The experiment was terminated after 18 months).

Appendix 10. The duration of pupal development (days) for 3 stages in constant temperatures

Temperature (°C)	Stage I M	Stage I F	Stage II M	Stage II F	Stage III M	Stage III F	Total M	Total F
15	14	15	14	14	9	12	37	41
	12	14	17	14	10	12	39	40
	14	16	14	14	10	12	38	42
	13	14	17	18	10	10	40	42
	14	15	15	17	10	10	40	42
	14	13	17	20	10	14	41	47
	13	16	14	17	9	10	36	43
	14	14	15	17	12	17	41	48
	12	15	17	20	10	14	39	49
	14	14	16	17	9	16	39	47
		15		16		14		45
		14		14		12		40
		13		17		17		47
20	7	7	8	10	6	6	21	23
	6	7	8	8	5	7	19	22
	7	8	7	7	6	7	20	22
	7	7	7	7	6	7	20	21
	6	7	7	8	5	7	18	22
	7	8	8	7	6	7	21	22
	6	7	7	10	5	6	18	23
	7	7	8	11	5	7	20	25
		8		10		7		25

M: Male
F: Female.

Appendix 11. The number of beetles emerged from field collected twigs under laboratory conditions during 1984/1985, 12985/1986, and 1986/1987

	1984/1985		1985/1986		1986/1987	
	M	F	M	F	M	F
Sept.	3	0	0	0	0	0
Oct.	96	42	90	36	4	0
Nop.	132	96	142	147	214	186
Dec.	21	51	84	103	50	64
Jan.	30	42	63	71	26	84
Feb.	0	0	0	2	2	10
Total	282	231	379	359	296	344

M: Male, F: Female

Appendix 12. Potential fecundity of female U. cupressiana in relation to body weight and size

NED	NO	Total	BW	LB	WB
28	39	67	59.25	18	3.4
3	57	60	45.70	18	3.4
5	85	90	65.80	22	3.8
6	34	40	41.00	16	2.7
2	66	68	89.80	18	3.8
24	24	48	43.70	18	2.7
2	32	34	28.50	15	2.1
28	26	54	45.50	16	2.7
17	35	52	37.30	16	2.5
0	50	50	47.60	16	3
3	71	74	89.30	19	3.5
6	44	50	39.30	16	2.7
5	38	43	70.80	16	2.7
1	42	43	49.30	16	2.8
0	56	56	100.30	18	3
0	66	66	65.20	18	3.2
0	60	60	63.00	18	3
0	42	42	34.00	16	2.7
0	56	56	68,50	18	3.8
0	52	52	58.80	16	3
3	13	16	64.60	17	2.3
0	84	84	122.00	19	3.3
0	44	44	60.60	15	3
0	20	20	20.70	12	1.5
0	16	16	20.50	12	1.8
7	23	30	42.60	14	2.5
0	52	52	58.20	16	2.8
0	60	60	75.00	18	3
0	58	58	85.00	18	3.4
0	63	63	89.60	19	3.3
10	14	24	50.10	18	3
13	46	59	50.50	19	3
6	37	43	46.60	16	2.7
8	32	40	38.30	16	2.6
Average		46.65	58.03	16.85	2.8

NED: Number of eggs deposited
NO: Number of remaining ova within abdomen
BW: Body weight (mg)
BL: Body length (mm)
BW: Body width (mm).

Appendix 13. Spatial distribution of eggs on potted plant of _C. sempervirens_

Strata	Mean number of eggs	F	P
Lower	8.5a	8.3649*	< 0.1
Mid	9a		
Upper	4b		

Means followed different letters are significantly different (P < 0.5; Tukey's test)

Appendix 14. Time spent (seconds) and distance travelled (cm) by males of various ages (days) from source of stimuli of female

Male number	0		1-3		4-7		8-14	
	T	D	T	D	T	D	T	D
1	120	100	10	50	30	150	300	175
2	80	100	12	60	36	150	300	180
3	90	100	12	75	10	125	210	100
4	110	100	6	65	12	100	110	100
5	40	100	5	0	7	60	120	125
6	60	150	21	0	8	75	180	150
7	50	150	31	0	10	80	150	50
8	30	150	38	0	12	40	50	50
9	55	175	15	0	14	30		
10	58	175	16	0	6	75		
11	38	175	21	0	8	60		
12	30	75	6	35	12	50		
13	32	50	7	30	15	0		
14	15	80	9	40	26	0		
15			12	30	30	0		

T: time spent
D: distance travelled

Appendix 15. Time spent (seconds) and distance travelled (cm) by females of various ages (days) from source of stimuli of male

Female number	0		1-3		4-7		>7	
	T	D	T	D	T	D	T	D
1	120	35	5	40	30	100	180	175
2	90	150	6	50	50	150	300	165
3	300	100	7	0	60	50		
4	240	100	10	0	120	50		
5	200	80	12	0	15	65		
6	180	135	15	0	36	75		
7	150	65	30	0	40	165		
8	38	75	36	50	80	150		
9	50	175	25	100	180	175		
10	48	180	20	125	300	100		
11			15	60	26	0		
12			30	40	6	0		
13			40	30	8	0		
14			45	35	10	35		
15			60	0	9	25		

T: time spent
D: distance travelled

Appendix 16. Mating time in relation to single pair mating (max. observation time 30 minutes, N = 108)

Time (second)	Frequency
0 - 30	4
31 - 60	35
61 - 90	34
91 - 120	10
121 - 150	6
151 - 180	2
181 - 210	2
211 - 240	3
241 - 270	2
270 - 300	2
301 - 330	1
331 - 360	1
361 - 390	1
391 - 420	1
421 - 450	1
451 - 480	1
481 - 510	1
511 - 540	0
541 - 570	0
571 - 600	0
601 - 630	1
> 30 minutes	2
> 60 minutes	2

Mating times > 30 minutes not included in calculation.

Appendix 17. Frequency of males on multiple mating with one female (N = 36)

Number of mating	Frequency
1	4
2	12
3	8
4	5
5	3
6	3
7	1

Appendix 18. Frequency of males (of different ages) on matings with different females

Number of females to be copulated	Number of males 0-3 days	> 3 days
1	0	6
2	2	8
3	6	1
4	3	
5	2	
6	1	
7	1	

Appendix 19. Mating time in relation to multiple choice matings

Time (second)	Frequency
0 - 60	8
61 - 90	15
91 - 120	8
121 - 150	7
151 - 180	4
181 - 210	4
211 - 240	5
241 - 270	3
271 - 300	1
301 - 330	2
331 - 360	1
361 - 390	1
391 - 420	1
421 - 450	2
451 - 480	1
481 - 510	1
511 - 540	0
541 - 570	1
571 - 600	1
601 - 630	0
631 - 660	0
661 - 690	0
691 - 720	1
721 - 750	1
751 - 780	1
1280	2
> 30 minutes	2

Frequency value of > 30 minutes not included in calculation.

Appendix 20. Diameter of simulated twigs, time spent on twigs, and number of eggs deposited by five females for five minute observations

TD	Time spent F1	F2	F3	F4	F5	No. eggs deposited F1	F2	F3	F4	F5
2mm	300	300	300	300	300	0	2	2	1	0
	300	30	300	37	300	2	2	1	0	2
	66	300	156	300	300	0	2	1	2	1
	300	300	30	30	300	2	2	0	2	2
	300	300	300	300	300	2	1	2	1	2
	300	300	32	300	300	2	2	0	1	1
	300	300	28	91	300	2	1	0	2	1
	38	300	34	32	28	0	0	0	0	0
	300	300	26	300	300	2	0	0	1	1
	300	300	300	300	300	1	0	0	0	1
4mm	300	124	300	60	33	2	0	0	0	0
	300	32	300	24	92	2	0	2	0	0
	300	300	152	22	300	2	2	0	0	2
	300	34	27	300	300	2	0	0	2	2
	38	300	26	36	28	0	2	0	0	0
	300	300	32	300	300	2	1	0	2	2
	120	36	34	62	300	0	0	0	0	2
	31	300	30	66	300	0	1	0	0	1
	28	24	92	300	300	0	0	0	1	1
	126	300	300	300	300	1	1	1	1	0
8mm	300	30	300	32	90	0	0	0	0	0
	300	300	300	24	60	1	1	1	0	0
	92	24	210	26	60	0	0	0	0	0
	152	300	122	30	122	0	1	0	0	0
	20	22	24	300	92	0	0	0	1	0
	30	210	30	24	120	0	0	0	0	0
	300	24	20	26	300	1	0	0	0	1
	24	22	26	28	30	0	0	0	0	0
	22	56	24	30	24	0	0	0	0	0
	20	300	22	60	23	0	1	0	0	0

TD, Tree diameter
F1-F5, Female no. 1 to no. 5.

Appendix 21. Number of attacked twigs for N0, N1, N2, N3, and N4 within 3 strata of the trees and within 4 zones; tree shape and measurement

Area	QE	QN	T#	Top N0	N1	N2	N3	N4	Middle N0	N1	N2	N3	N4	Bottom N0	N1	N2	N3	N4	Height	Width	Shape
1	13	2	1	10	14	12	6	3	6	2	3	1	2	2	21	0	0	0	6	1.4	cone
	13	2	2	15	20	22	15	24	8	0	20	4	0	8	2	0	0	0	8	2.5	cone
	15	3	1	12	30	15	11	17	18	4	12	10	5	5	4	0	4	1	10	1.5	cone
	15	3	2	10	12	15	4	10	8	6	3	6	0	0	0	0	0	0	6	2	cone
	16	3	1	20	36	12	4	11	10	6	9	6	1	5	2	0	4	0	10	2.5	cone
	16	3	2	18	32	22	10	22	26	6	6	10	2	6	2	1	4	1	10	2.5	cone
	17	6	1	30	15	12	12	12	18	0	4	4	0	3	8	0	0	0	7	2.5	oval
	17	6	2	12	16	15	8	13	11	2	12	12	1	8	10	0	0	0	7	2.8	oval
	18	10	1	6	10	9	0	5	12	0	1	5	1	0	4	0	0	0	10	2	cone
	18	10	2	11	20	8	5	11	5	1	4	2	0	1	2	0	0	0	11	1.8	cone
	5	7	1	4	13	4	1	4	2	1	0	1	0	0	0	0	0	0	5	2.5	oval
	5	7	2	4	14	7	1	8	1	0	1	3	0	1	1	0	0	0	3.5	2.5	oval
	4	8	1	8	42	58	5	26	34	0	10	16	0	6	0	0	0	0	12	2.5	cone
	4	8	2	8	16	12	0	4	1	0	2	1	0	0	0	0	0	0	8	2	cone
	1	9	1	8	16	8	8	9	6	0	2	2	1	1	0	0	0	0	9.5	2	cone
	1	9	2	5	10	6	3	4	6	1	2	1	0	0	0	0	0	0	9	2	cone
	8	12	1	6	6	4	2	6	5	0	1	1	2	2	0	0	0	0	4	1.6	cylinder
	8	12	2	4	12	6	6	8	3	1	2	3	1	0	1	0	0	0	4	1.6	cylinder
	12	10	1	4	8	16	3	12	8	1	6	0	0	0	0	0	0	0	8	2	cone
	12	10	2	6	8	6	4	12	2	0	7	4	0	2	2	0	0	0	10	1.8	cone
2	32	8	1	20	62	22	0	12	2	0	6	0	0	3	0	1	2	0	11	2	oval
	32	8	2	10	18	32	1	4	5	0	4	0	0	1	0	0	0	0	12	2	cone
	31	10	1	0	12	17	0	4	2	0	2	1	0	0	0	0	0	0	6	2	oval
	31	10	2	0	12	4	0	4	2	0	2	0	0	0	0	0	0	0	5	1.2	cone

Area	QE	QN	T#	Top NO	N1	N2	N3	N4	Middle NO	N1	N2	N3	N4	Bottom NO	N1	N2	N3	N4	Height	Width	Shape
	32	10	1	96	108	112	24	48	76	9	26	48	8	6	12	4	12	6	11.5	1.6	oval
	32	10	2	36	54	24	4	16	6	0	4	2	0	0	0	0	0	0	10	2	cone
	33	11	1	21	144	90	18	118	54	15	48	36	36	24	15	4	18	2	11.5	3	cone
	33	11	2	36	61	42	12	15	18	2	6	9	1	2	3	0	0	0	10	2.5	cone
	29	11	1	10	24	8	6	10	4	4	2	5	0	1	0	0	0	0	7.5	1	cone
	29	11	2	12	14	12	4	8	10	2	8	4	0	4	0	0	2	0	6	1	oval
	30	3	1	7	10	10	4	6	7	4	5	5	2	3	3	0	0	0	5	4	cone
	30	3	2	5	9	6	2	4	2	0	2	8	0	0	0	0	0	0	6	3.6	cone
	29	4	1	5	6	6	0	3	5	1	0	0	0	0	0	0	0	0	7	1	cone
	29	4	2	5	12	15	1	5	5	0	2	1	0	0	0	0	0	0	8	1.2	cone
	27	6	1	3	3	2	2	3	0	0	0	0	0	0	0	0	0	0	4	1.2	cylinder
	27	6	2	72	108	96	12	36	45	3	21	27	3	8	12	0	2	1	9	3.5	oval
	25	9	1	6	10	15	3	5	1	0	2	1	0	0	0	0	0	0	6	1.2	cone
	25	9	2	12	12	10	0	6	6	5	10	5	1	1	0	0	0	0	7	1.2	cone
	22	12	1	96	102	106	54	132	112	12	32	65	0	12	2	0	2	2	10	3.5	cone
	22	12	2	45	115	195	24	76	93	9	32	45	2	3	3	0	2	2	8	1.5	oval
3	49	2	1	56	33	37	20	18	10	3	13	12	4	4	4	4	4	2	6.5	1.4	oval
	49	2	2	4	2	16	4	5	0	0	2	0	0	0	0	0	0	0	4	0.8	cone
	50	3	1	10	13	19	3	3	13	5	9	4	1	5	2	0	2	0	6	2	cylinder
	50	3	2	7	7	7	1	3	4	1	2	3	1	3	2	0	0	0	5	0.9	cylinder
	47	5	1	25	56	77	13	13	26	10	13	9	8	10	7	2	3	2	4	1.8	cylinder
	47	5	2	26	34	43	10	20	17	11	10	19	6	8	10	2	4	3	4	1.6	cylinder
	48	10	1	60	35	70	13	10	10	8	7	8	7	7	5	2	3	1	3.5	1.6	cylinder
	48	10	2	43	49	66	6	10	18	5	9	15	5	3	3	5	3	1	3.6	1.4	cylinder
	46	13	1	63	57	46	25	36	27	20	25	16	10	12	13	5	6	5	9.5	1.6	cone
	46	13	2	145	166	157	52	112	83	62	93	82	25	64	33	8	12	13	9.5	2.8	cone
	43	13	1	10	12	21	4	3	5	2	3	4	0	0	0	0	0	0	2.5	1.2	cylinder

Area	QE	QN	T#	Top					Middle					Bottom					Height	Width	Shape
				NO	N1	N2	N3	N4	NO	N1	N2	N3	N4	NO	N1	N2	N3	N4			
	43	13	2	5	15	26	5	6	10	2	4	5	0	0	0	0	0	0	3	1.2	cone
	42	2	1	14	38	32	5	15	14	0	4	8	0	0	5	0	0	0	5	1.5	cylinder
	42	2	2	20	20	8	8	4	6	0	6	4	0	2	2	0	0	0	3	1.2	cylinder
	42	6	1	124	168	216	42	72	121	45	54	72	32	45	59	15	25	29	11.5	2	cone
	42	6	2	51	87	124	18	39	36	18	24	30	15	21	18	2	3	3	9.5	1.6	oval
	39	8	1	64	55	66	35	47	46	11	23	25	11	24	25	10	8	7	6.5	1.8	oval
	39	8	2	62	75	45	15	36	24	12	18	24	15	21	18	3	8	5	6.5	1.8	oval
	40	11	1	0	0	8	0	0	6	0	0	3	0	0	0	0	0	0	5	2	cone
	40	11	2	0	15	20	0	0	16	2	3	10	2	1	9	0	0	0	9	2.2	cone
4	66	4	1	7	26	25	6	10	5	0	10	5	5	5	0	4	2	0	5	1.6	cylinder
	66	4	2	5	26	51	4	15	14	4	18	3	2	10	3	2	2	4	10	1.8	cone
	67	4	1	39	29	31	17	29	16	11	15	12	18	9	10	1	5	9	5	1.8	cylinder
	67	4	2	20	48	40	24	23	20	12	25	19	5	14	11	1	5	4	5	1.8	cylinder
	60	3	1	0	15	12	0	7	2	0	0	0	0	0	0	0	0	0	6	1.5	cone
	60	3	2	17	18	22	0	3	13	3	8	5	7	8	0	0	3	0	7	1.4	cone
	61	4	1	6	18	30	2	5	9	1	2	8	0	4	3	0	0	0	9	1.8	cone
	61	4	2	1	29	23	1	9	10	4	8	2	4	6	8	0	4	2	8.5	1.6	cone
	58	2	1	5	17	12	0	4	5	0	3	0	0	0	0	0	0	0	10	1.6	cone
	58	2	2	0	14	4	0	2	6	0	1	4	0	3	2	0	0	0	10	1.4	cone
	67	2	1	7	20	64	4	14	5	6	16	8	6	1	9	5	2	3	5	1.6	cone
	67	2	2	10	32	37	6	4	8	5	5	3	1	1	0	0	0	0	4	1.2	cylinder
	66	1	1	11	29	47	11	13	12	7	9	21	6	7	9	2	6	2	6	1.8	cone
	66	1	2	12	24	37	5	20	4	5	10	6	4	5	6	3	3	2	6	2	cone
	57	4	1	2	11	9	0	1	2	0	0	2	0	0	0	0	0	0	6	1.2	cone
	57	4	2	10	28	30	3	6	12	2	6	7	0	0	3	0	0	0	3	1	cone
	54	2	1	13	75	65	13	14	30	11	8	20	10	16	5	6	8	3	6	1.6	cylinder
	54	2	2	20	66	87	5	22	23	3	16	21	3	7	12	0	5	3	10	1.8	cone
	56	2	1	11	30	29	4	13	11	3	7	10	0	2	2	0	0	0	2.5	1.2	cylinder
	56	2	2	21	30	25	10	13	10	9	3	2	0	0	3	0	0	0	2.5	1.2	cylinder

QN: Quadrat North; QE: Quadrat East
NO-N4: Current growth generation to Very old generation

Appendix 22. Number of eggs deposited on trees maintained at constant pot weight, 0, 4, 8, and 12 days after initial cessation of watering (see text)

Trial (day)	Replicate 1	2	3	4	5	6	7	8
0	13	22	12	9	4	8	3	7
4	22	3	20	7	3	4	7	2
8	11	2	14	9	5	20	10	2
12	3	3	5	12	26	4	11	1

Appendix 23. Proportion of survival on host trees featuring in appendix 22

Trial (day)	Replicate 1	2	3	4	5	6	7	8
0	.62	.40	.42	.46	.35	.38	.33	.35
4	.50	.67	.60	.57	.53	.55	.51	.60
8	.65	.68	.67	.67	.60	.85	.70	.64
12	.73	.99	.80	.75	.79	.80	.73	.99

Appendix 24. RMC of C. sempervirens twigs cut from trees featuring in Appendix 22

Trial (day)	Replicate							
	1	2	3	4	5	6	7	8
0	.74	.75	.78	.76	.75	.74	.74	.73
4	.71	.69	.69	.70	.70	.70	.69	.67
8	.61	.49	.61	.61	.61	.61	.48	.62
12	.38	.46	.38	.39	.48	.39	.46	.40

Appendix 25. Number of eggs deposited within strata on _C. sempervirens_ trees featuring in Appendix 22

Trial (day)	Strata on tree			
	Lower	Middle	Upper	Total
0	23	45	10	78
4	25	36	8	69
8	29	31	13	73
12	22	35	8	65

Appendix 26. Total free amino-nitrogen (mg/gm dried material) of twigs of *C. sempervirens* trees featuring in Appendix 22

Trial (day)	Replicate				
	1	2	3	4	5
0	28.97	42.98	28.62	24.96	24.40
4	20.05	20.92	21.34	22.44	20.16
8	20.89	20.19	19.14	20.22	20.61
12	17.31	17.67	10.58	18.22	17.73

Appendix 27. Total carbohydrate (mg/g dried material) of <u>C. sempervirens</u> twigs cut from trees featuring in Appendix 22

Trial (day)	Replicate				
	1	2	3	4	5
0	33.36	37.14	46.39	43.71	39.70
4	33.60	37.00	41.88	38.16	36.53
8	44.81	66.02	49.68	38.23	34.82
12	43.59	25.92	45.79	42.26	40.90

Appendix 28. Total carbohydrate (mg/g dried material) of <u>C. sempervirens</u> twigs within strata of trees featuring in Appendix 22

Strata on trees	Replicate				
	1	2	3	4	5
upper	34.08	39.93	49.07	46.04	49.01
middle	44.81	66.02	49.68	38.23	34.82
lower	28.35	44.07	50.66	49.33	42.14

Appendix 29. Total crude lipids (mg/g dried material) of *C. sempervirens* twigs cut from trees featuring in Appendix 22

Trial (day)	Replicate				
	1	2	3	4	5
0	37	64.9	35.9	50.8	59
4	39.4	45.7	37.2	52	60
8	53.9	89.3	58.8	44.8	67.1
12	51.8	45	39.4	45.8	53.2

Appendix 30. Total crude lipids (mg/g dried material) of *C. sempervirens* twigs within strata of trees featuring in Appendix 22

Strata on trees	Replicate				
	1	2	3	4	5
Upper	57.3	70.5	61.3	76.1	70.2
Middle	53.9	69.3	58.8	44.8	67.1
Lower	49.3	68.8	49.4	54.8	60.9

Appendix 31. Total free amino-nitrogen (mg/g dried material) of _C. sempervirens_ twigs within strata on trees weighed eight days after cessation of watering

Strata on trees	Replicate				
	1	2	3	4	5
upper	49.79	25.66	29.21	29.31	30.15
middle	20.89	20.19	19.14	20.22	20.61
lower	23.56	21.52	8.13	16.26	23.21

Appendix 32. RMC (%) of _C. sempervirens_ twigs within strata on trees weighed eight days after cessation of watering

Strata on trees	Replicate							
	1	2	3	4	5	6	7	8
upper	73.33	70.58	73.33	72.22	70.58	70.83	73.68	75.00
middle	61.11	48.57	60.96	61.42	36.66	36.66	48.43	61.90
lower	66.66	51.72	74.28	57.14	53.33	57.77	51.42	52.00

Appendix 33. Length of mine and weight of larval _U. cupressiana_ within strata on trees featuring in appendix 22

Strata on trees	Larval length (mm)	Larval weight (mg)
upper	360	21.2
	100	10.14
	350	35.0
	280	22.8
	300	20.5
Middle	300	29.3
	405	16.8
	330	53.9
	360	26.3
	210	10.8
	410	60.4
	440	20.5
	300	38.2
	500	30.4
	260	24.9
	360	21.2
	140	20.8
	250	30.2
Lower	470	121.4
	460	92.2
	430	96.4
	590	95.4
	480	95.2
	480	38.5
	380	28.8
	420	102.7
	560	69.3
	450	50.1
	330	41.0
	440	69.0
	440	56.4
	520	62.6
	420	42.3
	420	73.4
	650	47.3
	320	34.5
	570	69.0
	630	37.3
	520	63.3
	450	31.3
	700	84.3
	300	19.5
	300	33.2
	700	34.4

Appendix 34. Weight and length of mine of larval _U. cupressiana_ (L6 & L7) reared in _C. sempervirens_ trees featuring in Appendix 22

Trial (day)	Larval weight (mg)	Length of mine (mm)	Instar
daily	34.5	470	L6
	20.5	360	L6
	26.3	300	L6
	69.3	460	L6
	10.8	140	L6
	37.3	430	L6
	63.3	590	L7
	60.4	405	L6
	31.3	480	L6
	84.3	480	L7
	19.0	360	L6
4	19.5	420	L6
	56.4	560	L6
	29.3	330	L6
	62.6	450	L6
	16.8	300	L6
	73.4	440	L7
	53.4	360	L6
	42.3	520	L6
	47.3	420	L6
8	92.2	420	L7
	121.4	650	L7
	38.2	210	L6
	33.2	320	L6
	96.4	570	L7
	30.4	410	L6
	24.9	440	L6
	102.7	630	L7
12	69.0	520	L7
	34.4	550	L6
	50.1	700	L6
	20.8	600	L6
	21.8	600	L6
	30.2	500	L6
	41.0	660	L6
	38.5	700	L6

Appendix 35. Number of eggs deposited on trees of various water status (watered daily or periodically 4, 8, and 12 days) grown either on soil (recycled) or soil+sand (soil sand ratio 1:2)*

	Watered (day)	Replicates 1	2	3	4	5	6
Soil:							
	daily	18	31	17	24	20	32
	4	22	14	3	24	14	2
	8	19	8	9	25	33	28
	12	12	14	16	18	17	5
Soil+sand:							
	daily	29	27	26	18	16	11
	4	8	7	27	10	12	3
	8	10	7	8	8	18	4
	12	16	15	12	12	15	2

*See text.

Appendix 36. Reading of water potential (bars) (measuring water deficit) of twigs of *C. sempervirens* trees featuring in appendix 35

	Watered (day)	Replicates 1	2	3	4
Soil:					
	daily	4.6	5.0	4.4	4.2
	4	10.0	7.0	7.0	7.0
	8	21.0	20.0	18.0	20.0
	12	40.0	39.2	39.6	39.0
Soil+sand:					
	daily	6.0	6.0	6.0	6.0
	4	11.0	12.0	9.6	12.2
	8	22.0	22.0	22.4	22.0
	12	39.6	40.0	39.2	39.0

Appendix 37. Larval mortality and water status of trees featuring in appendix 35

Watered (day)	Replicate 1	2	3	4	5	6
Soil:						
daily	.33	.29	.41	.29	.20	.25
4	.27	.21	.25	.17	.14	.25
8	.11	.13	.00	.12	.09	.04
12	.00	.00	.00	.00	.00	.00
Soil+Sand:						
daily	.26	.26	.24	.33	.31	.36
4	.25	.14	.11	.20	.25	.23
8	.10	.14	.00	.00	.00	.00
12	.00	.00	.00	.00	.00	.00

Appendix 38. Pupation site, length of mine, and weight of larval *U. cupressiana* in relation to water status of tree *C. sempervirens* after 20 months

Well watered tree			Poorly watered tree		
Length of mine	Larval weight	Pupation site*	Length of mine	Larval weight	Pupation site*
44	88.4	0	40	91.4	0
25	147.8	0	60	100.3	40
53	243.0	10**	88	186.4	50
14	145.0	0	56	84.0	15
32	35.5	0	50	-	13
37	-	0	62	184.0	30
57	165.0	13**	65	145.0	30
25	60.2	7*	80	-	10
24	121.5	0	63	142.0	30
27	125.1	5	66	-	10
43	142.2	0	66	-	10
40	-	30**	68	121.0	30
16	78.5	0			
45	-	0			

- no weighing (larvae had been crushed)
* (distance from girdling site in cm)
** girdled trees.

Appendix 39. Number of eggs deposited on trees of *C. sempervirens* under various fertilizer regimes (0, 15, 30, and 45g fertilizer mixture per 10 litres of water)

Fertilizer mixture (g/10) 1	Replicate							
	1	2	3	4	5	6	7	8
0	11	9	15	13	7	8	14	17
15	14	17	9	16	13	11	10	8
30	26	12	19	11	5	10	20	14
45	21	20	29	23	6	15	26	10

Appendix 40. Percent Nitrogen (per gram dry weight) in twigs of *C. sempervirens* grown under various fertilizer regimes (0, 15, 30, and 45g fertilizer mixture per 10 litres of water)

Fertilizer mixture (g/101)	Replicate							
	1	2	3	4	5	6	7	8
0	1.04	1.18	1.29	1.12	1.12	1.18	1.18	1.09
15	2.07	2.04	2.16	2.02	1.93	1.93	2.13	2.44
30	2.52	2.58	2.58	2.52	2.80	2.66	2.39	2.52
45	2.58	3.7	2.63	2.77	2.55	2.86	2.57	2.63

Appendix 41. Larval weight and length of mine in relation to fertilizing regime in C. sempervirens

Fertilizer mixture (g/101)	Weight (mg)	Mine (cm)	Instar
0 (control)	84.5	600	L6
	110	620	L7
	89	570	L6
	51	580	L6
	71.5	700	L6
	112	700	L7
15	140	320	L7
	156	340	L7
	60	420	L6
	76	440	L6
	102.5	440	L7
	112	570	L7
	71	410	L6
	61.5	210	L6
	106	620	L7
	93	600	L6
	102	360	L7
30	76	320	L6
	56.6	300	L6
	119.5	250	L7
	77.5	260	L6
	164.5	360	L7
	105	420	L6
	77.5	420	L6
	74	440	L6
	107	330	L6
	109.5	420	L6
	222.5	320	L7
	114	340	L7
	113	300	L7
45	59	300	L6
	60.5	140	L6
	64	150	L6
	121.5	175	L7
	205.5	320	L7
	201	360	L7
	89	420	L6
	133	300	L7
	72	340	L6
	75	120	L6
	65	150	L6
	112	220	L7
	89	200	L7
	117.5	180	L7
	101	150	L6
	126.5	180	L7
	179.5	260	L7

Appendix 42. Survival of larval *U. cupressiana* reared in trees under various fertilizing regimes (0, 15, 30 and 45g fertilizer mixture per 10 litres of water)

Fertilizer mixture	Replicate							
	1	2	3	4	5	6	7	8
0	.27	.33	.27	.23	.14	.50	.29	.29
15	.14	.24	.22	.31	.67	.45	.20	.63
30	.15	.16	.37	.27	.40	.30	.30	.29
45	.24	.20	.17	.13	.67	.09	.15	.30

Appendix 43. Number of eggs deposited by female *U. cupressiana* on potted trees of various *Cupressus* spp.

Host species	Replicate						
	1	2	3	4	5	6	7
horizontalis	0	1	2	2	2	6	6
bruniana	0	1	1	2	3	2	2
horizontalis Aurea	0	7	3	10	10	1	6
sempervirens	11	6	5	4	2	3	4
tolurosa	5	2	1	0	11	3	10
glabra	0	4	4	1	11	1	1
cashmeriana	3	4	9	6	7	2	1

Appendix 44. Growth, development, and weight of larval _U. cupressiana_ reared on various _Cupressus_ spp.

Host species	Larval weight(mg)	Instar
sempervirens	179.5	L7
	207.5	L7
	91.5	L6
	66.5	L6
	118	L7
	66.5	L6
	105.4	L7
	81.5	L6
	115	L7
	72	L6
cashmeriana	76	L6
	104.5	L7
	135.5	L7
	66.5	L6
	111	L7
	115	L7
	81.5	L6
	59	L6
glabra	192.5	L7
	222.5	L7
	131	L7
	93	L6
	100	L7
tolurosa	80.5	L6
	104.7	L7
	76	L6
	104.5	L7
	93	L6
	131	L7
horizontalis	102	L7
	110.5	L7
	79.5	L6
	79.5	L6
	52.5	L6
bruniana	138	L7
	90.5	L7
horizontalis Aurea	176.5	L7
	72.5	L6
	66.5	L6
	90.5	L7
	118.5	L7
	91.5	L7

Appendix 45. RMC (%) of twigs taken from low rainfall area (coastal area) on the Adelaide Plain in summer 1985/1986

Tree number	Sample 1	2	3	4	Average
1	41.2	46.1	48.2	44.1	44.9±1.49
2	51.2	49.2	48.1	50.6	49.7±0.70
3	60.3	62.1	66.1	65.3	63.5±1.36
4	50.6	51.1	56.2	54.3	53.1±1.33
5	62.2	63.4	66.7	64.9	64.3±0.97
6	42.3	44.1	41.9	45.6	43.5±0.85
7	59.2	57.6	56.2	52.1	56.3±1.52
8	49.3	48.1	51.2	53.6	50.5±1.2
9	42.6	43.1	45.7	47.1	44.6±1.06
10	59.1	58.2	57.3	56.9	57.9±0.49

Appendix 46. RMC (%) of twigs taken from high rainfall area (foothills area) on the Adelaide Plain in summer 1985/1986

Tree number	Sample 1	2	3	4	Average
1	83.3	79.9	81.2	80.9	81.3±0.71
2	73.9	75.6	78.3	76.3	76.3±0.91
3	79.3	78.6	76.5	75.9	77.6±0.82
4	82.9	81.6	80.3	79.8	81.2±0.70
5	72.9	71.6	74.2	70.5	72.3±0.80
6	73.2	71.8	70.9	74.4	72.6±0.77
7	83.1	80.1	79.9	82.9	80.5±0.91
8	80.9	81.7	79.2	78.9	80.2±0.67
9	69.5	68.9	66.9	64.7	67.5±1.08
10	67.9	70.1	71.2	69.9	69.8±0.69

Appendix 47. Analysis of variance of number of eggs deposited on twig cut 0, 1, 2, 3, 4, and 5 days

Source	SS	DF	MEAN SQ	F	P
Treatments	450.89	5	90.18	.69	>0.05
Residual	3910	30	130.33		
Total	4360.89	35	124.6		

Means of Groups:
Group 1 = 7.5
Group 2 = 11.67
Group 3 = 13.5
Group 4 = 9.67
Group 5 = 3.83
Group 6 = 4.5

Appendix 48. Analysis of variance on number of eggs deposited on twigs cut 0, 2, 4, 6, and 8 days

Source	SS	DF	MEAN SQ	F	P
Treatments	173.12	4	43.28	1.74	>0.05
Residual	1121.7	45	24.93		
Total	1294.82	49	26.42		

Means of Groups:
Group 01 = 2.5
Group 02 = 2.8
Group 03 = 5.8
Group 04 = 2.4
Group 05 = 6.8

Appendix 49. Two-way analysis of variance (replicates in cells) of number of eggs deposited on trees with various watering regimes (row) for different types of soil (column)

Source	SS	DF	MEAN SQ	F	P
Total	3951.31	47	84.07		
Rows	1223.23	3	407.74	3.43	>0.05
Columns	305.02	1	305.02	5.19	>0.05
Residual	70.23	3	23.41		
Reps	2352.83	40	58.82		

Column Means:
1 17.71
2 12.67
Row means:
3 23.75
4 10.75
5 13.58
6. 12.67

Appendix 50. Two-way analysis of variance of water potential reading on twigs with various watering regimes (row) for different type of soil (column)

Source	SS	DF	MEAN SQ	F	P
Total	5674.68	31	183.05		
Rows	5618.93	3	1872.98	2378.38	<0.001
Columns	25.21	1	25.2	32.01	<0.001
Residual	11.65	3	3.88		
Reps	18.9	24	.79		

Column Means:
1 17.88
2 19.65
Row Means:
3 5.28
4 9.48
5 20.8
6 39.5

Appendix 51. Two-way analysis of variance (arcsin transformation) of mortality percentage and watering regimes (0, 4, 8, and 12 days periodically)

Source	SS	DF	Mean Square	F	P
Total	9404.34	47	200.09		
Rows	7984.40	3	2661.47	87.01	<0.001
Columns	74.70	1	74.7	2.44	
Residual	121.69	3	40.56		
Reps	1223.55	40	30.59		

Column Means:

1	18.78
2	16.29

Row Means:

3	32.53
4	26.86
5	10.75
6	0

Column: type of soil
Row: watering regimes

Appendix 52. Analysis of variance (arcsin transformation) of proportion surviving and various water status trees (watered 0, 4, 8, and 12 days after initial cessation of watering)

Source	SS	DF	Mean Square	F	P
Treatments	3431.02	3	1143.67	19.27	<0.001
Residual	1662.13	28	59.36		
Total	5093.15	31	164.3		

Means of groups:
Group 01 = 39.90
Group 02 = 48.87
Group 03 = 55.90
Group 04 = 68.23

Appendix 53. Regression Analysis of number of attacked twigs of N0 against number of attacked twigs of N1

Regression Coefficients:

	Estimate	SE	T
Constant	23.70	5.92	4.01
Twigs2	1.58	0.083	19.06

Analysis of Variance:

	DF	SS	MS
Regression	1	645925	645925
Residual	78	138622	1777
Total	79	784548	9931
Change	-1	-645925	645925

Percentage Variance accounted for 82.1
Variance = 363.49
$P < 0.1$

Appendix 54. Regression Analysis of number of attacked twigs of NO against surface area of conical trees

Regression Coefficients:

	Estimate	SE	T
Constant	-21.6	31.8	-0.68
Area	3.86	1.00	3.86

Analysis of Variance:

	DF	SS	MS
Regression	1	143935	143935
Residual	45	435155	9670
Total	46	579090	12589
Change	-1	-143935	143935

Percentage Variance accounted for 23.2
Variance = 11.44
$P < 0.001$

Appendix 55. Two-way analysis of variance (replicates in cells) of density of attacked twigs of N3 horizontally within areas (zones) (column) and vertically within trees (row)

Source	SS	DF	MEAN SQ	F	P
Total	209.02	239	.87		
Rows	2.57	2	1.28	1.64	>0.05
Columns	26.49	3	8.83	11.28	<0.001
Residual	1.40	6	.23		
Reps	178.56	228	.78		

Column Means:
1 .2285
2 .2306
3 1.0209
4 .6722
Row means:
5 .6703
6 .5261
7 .4178

Appendix 56. Two-way analysis of variance (replicate in cells) of densityof attacked twigs of NO horizontally within areas (zones) and vertically within trees

Source	SS	DF	MEAN SQ	F	P
Total	3838.22	239	16.06		
Rows	39.91	2	19.96	1.446	>0.05
Columns	575.68	3	191.89	13.90	<0.001
Residual	75.08	6	12.51		
Reps	3147.55	228	13.81		

Column Means:

1	1.5635
2	3.4496
3	5.9115
4	3.982

Row means:

5	4.2447
6	3.687
7	3.2482

Appendix 57. Daily air temperatures (°C) recorded at WARI in November 1984, 1985 and 1986 and number of beetles *U. cupressiana* emerged

Date	Temp.(°C) Max.	Min.	No. of Beetles	Temp.(°C) Max.	Min.	No. of Beetles	Temp. (°C) Max.	Min.	No. of Beetles
1	28.5	12.6	3	26.0	13.0	6	17.0	10.6	0
2	19.4	12.4	0	25.8	15.4	4	25.5	8.9	5
3	20.0	10.0	2	28.7	15.3	26	31.6	14.7	34
4	17.0	12.2	0	26.0	19.9	23	33.2	24.1	38
5	18.5	8.8	0	26.0	17.0	24	25.2	20.9	22
6	24.4	9.6	5	21.5	14.2	9	18.3	12.6	3
7	29.5	13.8	19	23.6	12.2	6	17.6	9.4	2
8	31.9	23.2	43	23.9	11.6	9	19.1	7.5	2
9	30.0	25.7	32	30.2	12.7	36	26.1	10.6	19
10	19.5	15.0	5	19.6	18.3	3	28.7	17.4	23
11	16.7	12.5	0	22.6	15.3	4	21.8	16.4	14
12	17.1	11.8	0	28.4	13.6	27	19.0	9.8	1
13	18.5	11.8	0	33.2	18.8	39	23.5	10.7	13
14	19.3	11.1	0	19.5	14.0	5	28.2	12.5	23
15	22.2	12.0	0	19.8	11.2	9	24.2	13.0	16
16	29.0	13.4	5	19.4	10.7	2	23.2	15.7	14
17	34.0	19.4	15	17.9	10.3	0	19.6	12.8	6
18	35.3	26.7	25	16.6	10.2	0	15.4	8.8	0
19	19.6	15.5	5	18.2	9.3	2	16.2	10.5	0
20	21.5	13.2	15	21.2	11.1	7	19.5	9.1	3
21	18.7	13.9	3	20.0	11.7	2	23.5	10.2	19
22	15.4	9.6	0	24.4	10.7	7	26.7	12.9	24
23	16.4	9.7	0	30.5	14.9	19	22.7	9.0	9
24	23.3	10.2	5	23.3	17.0	14	28.0	11.1	26
25	29.8	15.0	12	18.0	13.2	0	36.7	17.8	35
26	35.8	23.1	21	18.4	12.7	0	18.2	13.4	5
27	21.5	15.6	5	21.1	13.3	2	19.0	9.3	3
28	28.3	11.3	5	19.5	14.2	0	22.4	9.3	5
29	21.1	12.4	3	23.7	11.4	2	25.5	12.6	14
30	21.0	11.7	0	23.3	15.8	2	30.7	14.4	22
Average	18.5			18.3			18.0		
Total			228			289			400

Appendix 58. Twig density per square metre surface area of tree for conical, cylindrical, and ellipsoidal trees of _C. sempervirens_

Tree number	Tree shape conical	cylindrical	ellipsoidal
1	54	50	56
2	42	50	42
3	64	84	48
4	34	36	32
5	52	76	30
6	48	48	54
7	64	56	46
8	42	48	46
9	38	46	76
10	60	74	34
11	34	52	80
12	40	70	28
13	56	56	56
14	28	34	52
15	50	80	42
16	36	40	42
17	32	72	22
18	96	62	36
19	22	38	52
20	40	50	68