A LIFE SYSTEM STUDY OF *CRYPTOPHLEBIA OMBRODELTA* (LOWER) (LEPIDOPTERA : TORTRICIDAE) IN SOUTHEAST QUEENSLAND

by

Eric Russell Sinclair, B.Sc.Agr.(Honours I)

Department of Entomology

University of Queensland

Brisbane, Australia

Submitted as partial fulfilment of the requirements for the degree of Doctor of Philosophy

September, 1974

VOLUME ONE

ABSTRACT

The larval stages of *Cryptophlebia ombrodelta* (Lower) (Lepidoptera: Tortricidae), the macadamia nut borer, a native to Australia, has been recorded as a pest of *Macadamia* spp. in Australia. *Macadamia* spp. (commonly known as "macadamia") yielding edible nuts are Australian native trees grown commercially. The industry is presently undergoing expansion.

This study, based on macadamia orchards in Southeast Queensland, was undertaken to investigate the damage caused to the crop by the insect, establish factors contributing to the insect's abundance, and to provide a sound base from which future studies may be directed. To maintain direction, each part was envisaged as contributing to a computer model which would summarize current knowledge of the life system. The study developed in three main sections - the host plants, the subject insect, and its natural enemies. These were then investigated as interacting subsystems of the whole.

Host plants: 46 species of host plants (from six botanical families) are known. Most, although not natives, are now found in Australia. Macadamia trees were studied to establish the number of plant parts, their stability, and distribution within the tree for sampling purposes. Nut numbers decline from a maximum early in the season (October) with two well defined periods of fall, coinciding with natural crop thinning, and maturity. Other plant parts were considered stable for the purposes of this study. Distribution of nuts within trees was very variable. Nut crop development was studied to determine the effect of insect attack at different times. Processing size is achieved in October, November. Nut shells harden in December, and kernels mature in February; each event is

well defined. Alternative hosts occur in abundance only near housing settlements. Overlapping of fruiting periods ensures food supply throughout the year.

Cryptophlebia ombrodelta was reared satisfactorily on an artificial medium. The use of head capsule widths to identify larval instars was complicated by the variable number of instars (five or six). A computer programme assisted in determining instars of field collected larvae. The physiological time (hour degrees) of development of each immature stage was determined and appears to depend on daylength. The main field sampling unit for population studies was one fruit. Population trends were consistent from season to season but results were imprecise, due to the relatively low numbers of insects per fruit. Examination requirements limited the sample size. In macadamia, populations increased rapidly in late December, declining gradually after February. In the alternative hosts population intensity was usually much greater and infestation periods shorter. A pheromone lure proved effective in trapping males. Traps for females were ineffective. Studies on the biology and behaviour revealed a marked preference for oviposition on damaged nuts. Fruit entry by young larvae is easier on damaged nuts. A considerable proportion of mature larvae leave the fruit in search of pupation sites.

Natural enemies: Six parasites of the immature stages were recorded with an overall average species apparent percent parasitism of 0.05% to 12.20%. One hyperparasite was found. Observed predation was negligible; no disease factor was discovered.

The interactions: The alternative hosts were important sources of *C. ombrodelta*. In macadamia, partial budgets indicated that mortality was important in population regulation. Two of the most important factors

are probably larval establishment mortality, and death of mature larvae leaving the nuts. Parasitism is probably more important than the average percent parasitism figures indicate. Crop damage is caused by direct kernel damage and husk damage before and after maximum kernel maturity. At one site it was estimated that *C. ombrodelta* reduced potential crop value by approximately 20%.

The computer model explained and summarized the population processes as they are understood. Although not suitable for predicting the outcome of commercial management practices, it is a useful teaching tool.

The study concluded that it is essential for the industry to define product quality more clearly, and to conduct population studies in specific commercial areas. If new orchards are to be planted, an area isolated from housing settlements would be preferable. Otherwise a natural enemy, reducing *C. ombrodelta* populations in alternative hosts, is likely to provide the most acceptable control.

ACKNOWLEDGEMENTS

I wish to express appreciation to my supervisor Dr P.R. Blood, Senior Lecturer, Department of Entomology, University of Queensland, for his approval of the study, discussions and assistance during its development, and reading of the draft. I am also grateful to Dr T. E. Woodward, Reader, Department of Entomology, University of Queensland, for his criticism of the draft, and advice on its arrangement.

A number of people have provided assistance during the thesis preparation, for which I am most grateful. Advice on statistical aspects of the work was received from; Mr D.R. Strong, CSR Ltd., Sydney (who also made some valuable suggestions on the first draft), Mr R. Sandland, CSIRO Cunningham Laboratories, Brisbane, and from the University of Queensland, Mr H.M. Finucan, Reader, Department of Mathematics, Mr I. Horton, Senior Lecturer in Biometrics, Department of Agriculture, and Mr A.W. Beatty, Senior Lecturer in Biometrics, Department of Animal Husbandry. In developing the computer population model, I was assisted by discussions with Dr J. Munro, Senior Lecturer, Department of Biology and Environmental Sciences, Queensland Institute of Technology, Brisbane, Dr K.T. Glasziou, Mr D. Tovey, and Dr T. Bull of the David North Plant Research Centre, Brisbane, and Professor C. Rose, and Mr D. Able of the School of Australian Environmental Studies, Griffith University, Brisbane. Mr W. Goodman of the Department of Agriculture, University of Queensland, provided invaluable assistance in preparing the two computer programmes presented.

Dr I.F.B. Common and Dr E.F. Riek, of the Division of Entomology,

CSIRO, Canberra, and Mr I.D. Galloway, Department of Primary Industries, Brisbane, identified insect specimens. The staff of the Herbarium, Department of Primary Industries, Brisbane, assisted by identifying plants and providing information about the hosts of *C. ombrodelta*. Mr R. Teakle, Department of Primary Industries, conducted trials to determine the presence of pathogens in a sample of dead larvae.

Valuable material assistance was received from a number of people and organizations.

I am grateful to the following orchardists for allowing me access to their properties: Mr A. Armanasco, Blunder Road, Inala, CSR Ltd. at their Beerwah orchard, where the farm manager, Mr S. Henry provided every assistance, and in particular to Mr H.S. Yorsten, Dorville Road, Aspley who gave me the unrestricted use of his entire orchard.

Dr K.T. Glasziou, Manager of the David North Plant Research Centre provided the use of two constant environment rooms, and arranged that my plant material be cared for. Dr A.R. Brimblecombe, then the Director of the Entomology Branch, Department of Primary Industries, provided the use of their multitemperature cabinets, in their Brisbane office. Professor W.C. Mitchell, Department of Entomology, University of Hawaii, kindly supplied a number of pheromone lures, and sticky traps, for tests during 1972-73. The Zoecon Corporation, Palo Alto, California, donated 100 Orfamone II lures to my trapping programme in 1973. Bush Boake Allen Australia Ltd. supplied quantities of Terpinyl Acetate, Safrole, and Citral for use in the bait trap trials, and J. Wildridge and Sinclair Pty. Ltd. (Brisbane), assisted with the necessary welding in the construction of flight traps and field trays.

The Entomology Department, University of Queensland, provided most of the facilities required for the study which was mainly funded by grants from the Australian Universities Commission.

I am most grateful to my wife, Penelope, for her encouragement, and assistance in typing the first draft of the thesis and in helping to check the final draft.

My sincere appreciation is expressed to CSR Ltd. for supporting me financially throughout this study, and assisting with funding and facilities where necessary. I am grateful to Mr P.E. Robinson, the Chief Technical Field Officer, for his interest and assistance at all stages.

TABLE OF CONTENTS

Page

VOLUME TWO

LIST OF TABLES

TABLE Page

LIST OF FIGURES

FIGURE FACING PAGE

STATEMENT OF SOURCES

The experimental work presented in this thesis is the result of original research by the author. When used, the techniques and results of other workers have been acknowledged.

The research comprising this thesis has not been submitted previously either to the University of Queensland or to any other institute for any degree.

Eric Sinclair
.....

SECTION I

INTRODUCTION

CHAPTER 1

PURPOSE OF THE STUDY

Cryptophlebia ombrodelta (Lower) (Lepidoptera: Tortricidae), the macadamia nut borer, has been reported as a significant pest of macadamia, only in Australia.

Until the mid 1960's macadamia plantings in Australia were limited in size and extent, and few growers relied on the crop to provide a significant proportion of their income. However, there is now a rapid expansion of plantings and a large proportion of these are monocultures of more than 50 ha. Most of the large orchards should be bearing by 1978.

In this rapidly expanding macadamia industry the extent of the loss which may be experienced from *C. ombrodelta* attack is uncertain. The pest has been shown to be severely damaging in certain cases, although the particular conditions were not clearly defined. There is little information on the damage caused by *C. ombrodelta* to the new varieties, and none on how its populations will behave in the new, large, uniform plantings of macadamia.

With the exception of the work of Ironside (1974) the infrequent publications on the commercial importance of *C. ombrodelta* in macadamia have amounted to little more than defining spray applications. There has been no understanding of the pest's ecology. Whilst still having an interest in chemical control Ironside (1970 unpublished report) undertook the first work which recognizes the need for biological studies and a broader view of the ecology of the pest. Ironside explained that any control method for this pest, relying entirely on chemicals, will certainly be very expensive and probably unsatisfactory.

The present work is an extension of Ironside's study, defining more precisely the life system of *C. ombrodelta* in Southeast Queensland,

and the insect's impact on macadamia. It also shows the direction which further research should take.

The aims of the present study were:

(i) to define the damage caused by *C. ombrodelta* to macadamia;

(ii) to establish the range of factors which contribute to the establishment and persistence of *C. ombrodelta* in macadamia plantings;

(iii) to show the direction subsequent research should take.

CHAPTER 2

REVIEW OF THE SITUATION TO 1971

Information available at the beginning of this study, related to the crop and the insect, is presented below.

1. MACADAMIA

(i) The Species

"Macadamia" is one of the common names of the commercial nut producing species of the botanical genus *Macadamia*. Other common Australian names are the "Queensland Nut", "Bush Nut" and "Bopple Nut". In this thesis, unless referring to the genus *Macadamia*, or to a particular species of that genus, macadamia will be used as a common name.

Storey (1965) reported that there are 10 species in the genus *Macadamia*, which is a member of the family Proteaceae. Six of these are Australian, three New Caledonian and one is from the Celebes. These ten species fall into four intrageneric groups - only one of which is of commercial interest. This latter group comprises three of the extra-tropical Australian species, viz.

Macadamia ternifolia

Macadamia integrifolia

Macadamia tetraphylla

M. ternifolia is the species on which the genus was established in 1858 (Storey 1965). Until 1956 there was much confusion as to specific nomenclature. Maiden and Betche described the new species *integrifolia* in 1896 (Maiden and Betche 1896) but later decided that it was *M. ternifolia* var. *integrifolia* (Maiden and Betche 1899). Bailey

(1910, 1911) introduced the species names *M. minor* and *M. lowii*.

Taxonomic work in the 1950's cleared the confusion regarding naming of the commercial species. Johnson (1954) described *M. tetraphylla* as being one of the major economic species and in 1956 Smith showed that there were three distinct species - *ternifolia, integrifolia* and *tetraphylla*. Edible nuts are produced only on *M. integrifolia* and *M. tetraphylla* or hybrids of these, which are common in nature (Smith 1956).

Storey (1965) described the commercial species as follows:

M. integrifolia occurs naturally in coastal and mountainous rainforests on the eastern slopes of the Great Dividing Range. Its range is about 440 km from just south of the New South Wales, Queensland border to the lower Mary River (28^{o}-25^{o}S). Some crop is carried throughout the year although there is a peak maturity period between March and June.

M. tetraphylla has a natural range of only 120 km in the rainforests of the eastern slopes of the Great Dividing Range - from the Richmond River in New South Wales to the Coomera River in southern Queensland (29^{o}-28^{o}S). Crop maturity is restricted to the period March to June.

(ii) The Industry

Macadamia has been introduced to many tropical and sub-tropical regions. To date Hawaii is the only area with significant commercial production, plantings are large (1292 ha in 1966 and expanding (Scott 1969)) and techniques advanced.

In 1961 the Australian plantings consisted of many small orchards, mainly of seedling trees, amounting to 61 ha in Queensland (Officers of the Department of Agriculture and Stock 1961) - probably of the order of 12,000 trees, with a similar number in northern New South Wales. A considerable

proportion of the crop also came from garden trees. Expansion has been rapid recently[1] and there are now some orchards greater than 50 ha in size, although most are not yet bearing fully.

Early plantings of macadamia in both Australia and Hawaii were non-grafted trees of the two edible species and hybrids between them.

Seedling trees are inherently variable in nut characteristics and bearing capacity and of little value for commercial production (Ripperton *et al.* 1938, Hamilton and Storey 1956, Officers of the Department of Agriculture and Stock 1961).

The Hawaiians recognized that *integrifolia* type seedlings were the most suitable (e.g. Ripperton *et al.* 1938), and since the late 1930's only these types have been planted in Hawaii. All the Hawaiian varieties established by clonal propagation are of this type (Hamilton and Storey 1956).

In Australia, a variety selection programme was begun in 1948 (Officers of the Department of Agriculture and Stock 1961). However, as recently as 1965, of 16 Australian varieties recommended, nine were of the *tetraphylla* type, four *integrifolia* type and three were hybrids (Anon 1965, "Macadamia Nut" roneoed pamphlet, Horticulture Branch, Queensland Department of Primary Industries).

However, most of the recent commercial plantings in Australia (since 1965) have been of *integrifolia* types - mostly Hawaiian varieties, with a reasonably well defined fruiting period. *Tetraphylla* types have fallen from favour because of their usually thinner shells allowing nut deterioration and increased insect attack, thus creating processing problems; there is also a general enchantment with Hawaiian varieties.

---

1. By 1972 the tree numbers had risen to 100,000 in Queensland (reported by Ironside (1974)), or approximately 500 ha. Increases have also occurred in New South Wales.

(iii) The Tree

Macadamia trees when fully grown, are approximately 12 m high with a spread of nine metres and have a dense leafy canopy. Most orchard trees are pruned to the "central leader" type of growth. Planting distances vary from 4.5 to 12 m so that when mature the trees touch each other, and the orchard is said to "cover in". Cann (1965) stated that the trees, if planted too closely, do not bear a heavy crop and insect pests are hard to control.

Most orchards have a ground cover of grass and herbacious plants. This cover is mowed periodically and many growers, using herbicides, maintain the area under the drip line of the tree in a bare condition to facilitate harvesting. It has been observed that in orchards which have covered in, ground vegetation is virtually absent.

(iv) The Crop

In the common commercial varieties in Queensland flowering occurs in August and September. Flowers are borne on racemes which are fairly evenly distributed throughout the inside of the leafy tree canopy, on wood two or more years old. The racemes may be up to 30 cm long with as many as 300 buds each. Each of these buds is capable of developing into a fruit which Hartung and Storey (1939) and Storey (1968) described as a follicle. The edible part, the kernel, is enclosed in a very hard testa - commonly referred to as the shell. Around the shell is the green pericarp, the husk.

In October to December there is a heavy natural shedding of crop and few varieties carry more than two or three fruit per raceme to maturity. The fruits mature in March and in most varieties there is a further heavy drop of fruit in March and April.

Cann (1965) stated that trees start to bear when six or seven

years old. At eight to ten years yield should be 4.5-14 kg of nuts in shell (i.e. husk removed) per tree each year, or approximately 600 to 1,800 nuts per tree. From twelve to fourteen years one expects up to 27 kg nuts per tree or up to 3,600 nuts. In one season 113.5 kg of nuts in shell have been taken from a particular tree.

Yields from the commercial trees on the islands of Hawaii varied from a maximum of 4.5 kg of nuts in shell per tree in trees aged five years to 45-49 kg per tree for fourteen year old trees and 45-68 kg for twenty year old trees (Keeler and Fukunaga 1968).

Factors affecting crop quality and quantity include, flower pollination and variety of tree (Shiguera 1967); soil moisture (Warner 1966; nutrient supply - e.g. phosphorus (Cooil *et al.* 1966) and insect attack e.g. in Hawaii *Cryptophlebia illepida* (Butler) (Namba 1957a, Hamilton and Fukunaga 1959) and *Nezara viridula* (L.) (Mitchell 1965).

In Australia, Ironside and Davis (1969) reported "....[insects damaging macadamia] that commonly cause serious damage, although not in every district, are as follows: on the flowers, macadamia flower caterpillar [*Homoeosoma vagella* Zell.]; on the nuts, macadamia nut borer [*C. ombrodelta* (Lower)], fruit spotting bug [mainly *Amblypelta nitida* Stal.], and yellow peach moth [*Dichocrocis punctiferalis* (Guen.)]; on the foliage, macadamia twig girdler [*Neodrepta luteotactella* (Walk.)], and macadamia leaf miner [*Acrocercops chionosema* Turn.]." Few Australian orchardists take regular control measures against insect pests. However, with larger orchards involving better management, the situation is likely to change.

(v) Harvest

Harvest in Hawaii consists of picking the nuts from the ground either by hand or with the use of various mechanical devices (Keeler and Fukunaga 1968). Experiments are in progress in net harvesting and tree

shaking (Wilson 1971, H. Ooka[1] pers. comm.).

In Australia at the present time, all harvesting is by hand. Most nuts are picked up from the ground after fall, although some varieties need to be hand stripped because the nuts deteriorate in the tree before they fall.

The period between harvests is important, as the kernel quality deteriorates when nuts are left on the ground (Keeler and Fukunaga 1968). Hamilton and Storey (1956) recommended a pick up every five to six weeks in dry weather and every three weeks in wet. Cann (1965) believed harvest should be every two weeks as did Keeler and Fukunaga (1968).

2. *C. OMBRODELTA*

(i) Taxonomy

Much confusion has existed over the identity and taxonomy of the macadamia nut borer.

Lower first described the species as *Arotrophora (?) ombrodelta* from Australia (Lower 1898). Meyrick (1910) synonymised both *A. ombrodelta* and *Cryptophlebia carpophaga* (described by Walsingham (1899) from India) with the Hawaiian species *Teras illepida* Butler, 1882, now known as *Cryptophlebia illepida* (Butler). Meyrick transferred this species to the genus *Argyroploce* Hübner, in the family Eucosmidae.

Swezey and Zimmerman (1946) agreed with Meyrick's generic placement but disagreed with his synonymy, upholding the specific distinctness of *illepida* and *carpophaga* on adult colour, setation and genitalia.

Bradley (1953), in a study of the genus *Cryptophlebia*, examined colour, markings, secondary sexual characteristics, and genitalia. He

---

1. Mr H. Ooka, Field Superintendent, Royal Hawaiian Macadamia Nut Co., Hilo.

showed that the species described by Lower (1898) and Walsingham (1899) are conspecific, i.e. *Cryptophlebia carpophaga* Walsingham is a junior synonym of *Cryptophlebia ombrodelta* (Lower), which is specifically distinct from *C. illepida* (Butler). He placed the genus in the Olethreutidae.

Common (1970, p.801) placed the species in Subfamily Olethreutinae, Family Tortricidae.

(ii) Distribution

Concurrent with the confusion over specific nomenclature, there has been confusion over the origin and distribution of the insect.

Froggatt (1897) and Lower (1898) first recorded the species, in Australia. In 1899 Walsingham recorded it in India (from Swezey and Zimmerman 1946, Bradley 1953). Meyrick (1910) also recorded it from India but after grouping the two species (at present known as *ombrodelta* and *illepida*), he described the distribution of the insect as: Australia, India and South Africa. Lever (1938) also stated that specimens obtained by him in Fiji were the same species as that from South Africa, India, Australia, South China and Hawaii. Swezey and Zimmerman (1946) examined specimens from Hawaii and Guam. Their work showed that *C. ombrodelta* (recorded as *Agyroploce carpophaga*) did not occur in Hawaii but did occur in Guam.

Bradley's work (1953) has established that the South African and Chinese species are distinct from *ombrodelta*. Bradley gave the distribution of *C. ombrodelta* (Lower) as: "South India, Ceylon, Formosa, Indonesia (Java), Siam, Philippine Is., Guam, Dampier I., Australia (Queensland, New South Wales and the Northern Territory)."[1]

Ironside (1970 unpublished report) stated that in Queensland, the species occurs throughout coastal Queensland and has been found in the

---

1. Dr V.P. Rao, Commonwealth Institute of Biological Control, Bangalore, India, has collected the species from Northern India (1970 unpublished report).

South Burnett District. Elevated regions (more than 300 m above sea level) appeared to be largely exempt from *C. ombrodelta* infestations. He also stated that the insect occurred more frequently in older orchards than in young ones, even when both were relatively close to each other. From this he speculated that the moth may be comparatively sedentary, mating and ovipositing in the same locality as it fed as a larva (most orchards in the region where Ironside was working have some nuts throughout the year).

C. ombrodelta apparently has been established in the State of Hawaii since 1958 (e.g. Beardsley 1962, Davis 1962, Chong 1964, Nakao 1966).

(iii) Description of the Life Stages

Descriptions of the adults are given by Bradley (1953) and Ironside (1974). The latter author also gives brief descriptions of the immature stages.

Briefly these are:

The imago: up to 25 mm across the expanded wings, and about 12 mm long. The female is usually larger than the male. The forewing of the female is reddish brown with a distinct triangular shaped dark brown mark on the hind margin. The male wings are lighter in colour and the triangular mark is much less distinct or even absent.

The egg: eggs are placed singly or slightly overlapping in small groups. The egg is flattened, elliptical and approximately 1.0 x 0.8 mm in size. The surface of the chorion is finely reticulate. At oviposition, it is ivory white to pale yellow, with pale orange to red spots appearing and coalescing to form a reddish suffusion as incubation progresses. The head capsule is clearly visible before hatching.

The larvae: at eclosion the larva chews its way through the chorion leaving it mainly intact. The young larva is approximately 1 mm long,

light orange in colour with a dark brown head capsule. It tunnels into the fruit.

Later instars are mainly white, with dark brown to black head capsules and distinctive small round spots on the thoracic and abdominal segments. The full grown larva is up to 20 mm long, and stout bodied. The head capsule and prothoracic shield is brown, the body greenish grey to pink.

Galloway (1971) studied certain morphological features of *C. ombrodelta*, in a comparison of this species with *Isotenes miserana* (Walker) (Lepidoptera: Tortricidae). Briefly his findings for *C. ombrodelta* larvae were: mandibles bluntly dentate, six ocelli on each side of the head capsule, spiracles elliptical, crochets uniordinal, anal shield rounded posteriorly, no anal fork. Galloway stated that such anatomical features are typical of boring Lepidopterous larvae.

The pupa: is firstly light brown, darkening before the moth emerges. At emergence the pupa wriggles two-thirds of the way out of the cocoon and the moth emerges, leaving the pupal case protruding from the exit hole.

(iv) Development Times of the Immature Stages

Ironside (1970 unpublished report) reported the following development times for *C. ombrodelta* on macadamia nut husks:

	(A) Ambient temperature 20 individuals	(B) Constant 26.1°C 5 individuals
Eggs	4 days	4-5 days
Larvae	21-28 days including 2-3 days pre-pupae	29-34 days
Pupae	8-10 days	11-12 days

Ironside found that the number of larval instars was variable,

being either five or six.

(v) Fecundity

One female reared by Ironside (*loc. cit.*), fed on 10% honey solution, laid 232 eggs over a 14 day period.

3. HOST PLANTS

Fletcher (1920) and Bradley (1953) published records of host plants for *C. ombrodelta*.

The appearance of the species in Hawaii resulted in an extension of the host record (Davis 1962, Sherman for Habeck 1962, Chong 1964, Hamilton 1964, Beardsley 1965, Shiroma 1965a, 1965b, Nakao 1966, Au for Bianchi 1968).

In Australia, the following host plants had been recorded: *Leguminosae - Acacia farnesiana* (Froggatt 1897), *Bauhinia galpinii, Bauhinia* sp., *Caesalpinia pulcherrima, Cassia fistula, C. pulcherrima, Delonix regia, Schotia brachypetala* (Ironside 1970 unpublished report); *Proteaceae - Macadamia integrifolia, M. tetraphylla* (Officers of the Department of Agriculture and Stock 1951, Cann 1965, Ironside and Davis 1969); *Sapindaceae - Cupaniopsis anacardioides* (Common, pers. comm.) *Litchi chinensis* (Ironside 1970 unpublished report).

The records from all countries included 33 species, plus three plants recorded by genus only, from six botanical families:

Leguminosae	21 species, plus 3 recorded by genus only
Palmae	1 species
Polygonaceae	1 species
Proteaceae	2 species
Rutaceae	3 species
Sapindaceae	5 species.

The complete host plant record is shown in Table 3.

4. NATURAL ENEMIES

Ironside (1970 unpublished report) reported that the following species have been recorded attacking *C. ombrodelta* in Queensland.

Braconidae *Apanteles* sp. (mycloenta group)

Ichneumonidae *Echthromorpha incidiator* Sm.

Gotra sp.

Reduviidae *Pristhesancus papuensis* Stal.

Ironside stated that *Gotra* sp. was found to be more numerous than any other.

Because of the limited species range, and low numbers of each species observed, he believed that the importance of these natural enemies in population regulation was not great.

In India, three parasites are known from *C. ombrodelta:*

Bethylidae	*Goniozus trissomalus fulvicornis* Rohw. (Muesebeck 1940)
Braconidae	*Euagathis cryptophlebiae* Vier. (Thompson 1943)
Ichneumonidae	*Cremastus flavo-orbitalis* Cam. (Thompson 1943)

Both the *Cremastus* sp. and the *Goniozus* sp. are polyphagous. All three are larval parasites.

5. SEASONAL INCIDENCE IN AUSTRALIA

Infestations of *C. ombrodelta* in *A. farnesiana* in northern New South Wales were studied by Froggatt (1897). He stated "The pupae [*sic:* larvae (?)] are plentiful in the seeds about May, and were pupating towards the end of June, the first moths emerging in August, but a great number still in the cocoons."

Ironside (1970 unpublished report) reported that in Queensland successive generations occur in orchards of *M. integrifolia* seedlings, as nuts are available throughout the year; larvae are found in nuts every month.

6. SURVEY TECHNIQUES

(i) Immatures

Most of the publications appear to deal with casual collections. Damaged plants were observed, and a collection of the damaged part was made. In some cases, investigation of the type of damage occurring has been made by dissection of the material. In addition Ironside (1970 unpublished report) carried out relatively detailed surveys to determine seasonal incidence of the pest. He also presented quantitative data (in terms of numbers of nuts damaged by *C. ombrodelta*) compiled from the collection and dissection of nuts at intervals to show the variation in damage under insecticide treatments and between varieties.

(ii) Adults

Meyrick (1910) caught the species in India, at a light. Ironside (1970 unpublished report) stated that males are more readily attracted to mercury vapour light than females.

Mitchell (1971 unpublished report) tested 36 chemicals as lures for *C. ombrodelta*. He caught 7 males in a trap with the lure Cis-8-dodecenyl acetate and one female in a trap containing Cis-5-tetradecenyl acetate. He reported that the catches occurred when field populations were low.

7. REARING TECHNIQUES

No attempts to rear *C. ombrodelta* on an artificial diet have been reported. Rearing of the species has been mainly for the purposes of identification of the adult. For example, Meyrick (1910) bred the adult from litchi fruit, and it was reared from the terminal branches of seedling *Sapindus saponaria* by Bianchi (Au for Bianchi 1968).

Ironside (1970 unpublished report) reared the insect in the laboratory using macadamia husks as food, with the husks being changed as necessary.

8. DAMAGE

C. ombrodelta has been recorded periodically as a pest of macadamia in Australia. A report in 1951 (Officers of the Department of Agriculture and Stock 1951) stated that holes may be found in the shell and husks of many nuts at harvest. The kernel of each of these nuts will be inedible. Other nuts may be damaged without showing external signs. This report also stated that some crops may be entirely destroyed and it is pointed out that even light attacks necessitate a very careful grading of the crop at harvest.

Cann (1965) reported that damage by the macadamia nut borer is only detected as the nuts are approaching maturity, when examination will reveal a small hole in the shell, and a completely spoiled kernel.

In an unpublished report, Rand[1] (1966) stated that "...[the] larva tunnels into the young nut where it feeds on the developing kernel. ...Occasionally the larva attacks the nut when the shell has begun to

---

1. Mr J. Rand, then a Research Student, Department of Entomology, University of Queensland, St Lucia, Queensland 4067

harden and then feeding is confined to the husk."

Ironside and Davis (1969) also reported that the nut borer larvae tunnel into the kernel if the nuts are attacked at an early stage, but later, after the shells have hardened, damage is mainly confined to the husk. These nuts may fall prematurely.

In his unpublished report of 1970 Ironside gave a more detailed description of the damage. "Fruits as small as 10 mm in diameter may be infested but heaviest infestations occur when fruits are 20 mm or more in diameter..... While the shell is soft enough to permit easy entry, larvae feed on kernels. Rarely is a kernel completely destroyed, but immaturity and invasion by secondary organisms....mostly result in complete loss.... Infested fruits often fall from the trees before the moth emerges but with some varieties damaged fruits remain on the tree until most of the crop has fallen."

"Larvae occasionally...enter hardened shells but..usually..via the hilum or micropile.. Thin shelled nuts and rough shelled *tetraphylla* types are more readily entered once the shell is fully hardened."

"When damage is confined to the husk, crop loss occurs as a result of premature fall and reduction of kernel quality. ...Husk damage to near mature fruits is unimportant as kernels are then of acceptable quality. Fruits not in contact with others appear to be just as readily infested as those occurring in clusters."

"*C. ombrodelta* not only reduces yields and quality of macadamia nuts but also increases the cost of processing by necessitating extra sorting and grading of kernels."

Ironside stated that nuts are most vulnerable between November and February.

He compared nut fall from untreated trees with that from trees treated with different chemicals. It appeared that although a small number of nuts fall whether they are damaged or not, *C. ombrodelta* was,

in this trial, a major factor in causing nuts to fall prematurely. He also showed that there was a marked difference in varietal susceptibility to the insect and consequent loss of nuts.

In Hawaii, the only other region with both extensive macadamia plantations and *C. ombrodelta*, the insect apparently has not caused appreciable economic damage, although it has been recorded in macadamia on these islands in 1961 and 1962 (Chong 1964).

Damage to other plant species occurs in both fruit and shoots (Table 3). It is probably most significant in the fruits of litchi and tamarind.

9. CONTROL MEASURES

The only recommended control measures for *C. ombrodelta* are from Australia.

A 0.2% DDT spray, repeated after two weeks, was recommended for control in 1951 (Officers of the Department of Agriculture and Stock 1951).

Cann (1965) also recommended DDT. He remarked that because of the dense foliage a high pressure spray unit was necessary.

0.1% DDT was recommended by Ironside and Davis (1969), who stated that control measures are usually required from December to March.

Following trials using monocrotophos, carbaryl, methidithion, azinphos methyl, DDT, and trichlorphon, Ironside (1970 unpublished report) suggested 0.1% carbaryl as a control measure for *C. ombrodelta* in macadamia. In reaching this decision Ironside considered effectiveness, cost, human safety, phytotoxicity and the effect on non-target organisms. He believed that the number of applications could be reduced to two or three over the season, according to the infestation level and the variety.

Ironside considered that insecticidal control of *C. ombrodelta*

may be very costly because of the difficulty of applying chemicals to the large densely foliated trees, and the long period of insecticidal coverage that is necessary. This period includes some of the wettest months of the year.

CHAPTER 3

THE APPROACH TO THE PROBLEM

It is important for the developing Australian Macadamia Industry to know the extent to which *C. ombrodelta* is likely to be economically important, and what steps should be taken to control it, if this occurs.

The development of the macadamia crop during the period of *C. ombrodelta* attack must be investigated in detail, so that a precise evaluation of the pest impact may be made.

To predict or prevent outbreaks of a pest a thorough understanding of its biology and ecology is essential (e.g. Geier 1966, Pimentel, 1966, p.15, Clark *et al.* 1967, p.165, 204).

Several theoretical approaches have been proposed to assist in the acquisition of the detailed knowledge required: e.g. Bakker (1964), Watt (1966, p.6) and Clark *et al.* (1967, p.5). Each recognized that the particular problem should initially be conceived in its broadest terms with a minimum of detail of its limits, and the interactions and relationships within it. The researcher progresses from the general to the detail and his views on the relationships, and the data required should remain flexible, and subject to the feedback of the data collected.

In practice some limit has to be set on the amount of data collected and processed. Elton and Miller (1954) and Stark (1966, p.40) suggested that a lone investigator would be too limited in resources to complete such a study, although he could make a worthwhile contribution to it.

The present study was undertaken to establish the outline for a full ecological and biological study of *C. ombrodelta*, similar to that undertaken by Stark (1966) for *Dendroctonus brevicomis* LeConte.

In its broadest terms, the study was of the life system (Clark

et al. 1967, p.5) of *C. ombrodelta* in Southeast Queensland.

To maintain direction in the study, each part was designed so that all parts could be integrated correctly at the completion of the programme (Watt 1966, p.2-3).

This integration was to be achieved by the construction of an "open ended" model of the system, such as Watt's (1968, p.253) Type 4 model. In this, any degree of complexity can be achieved by adding to the model, environmental and biotic factors as data are accumulated.

Thus modelling served to direct the study. The final model was not only to show quantitatively how much was understood about the life system of *C. ombrodelta*, but also to act as the basis for further experimentation to add to this knowledge.

Initially only a verbal model could be constructed to summarize the processes believed to be involved and to assist in the collection of the data. Later, mathematical models could be constructed and tested. Their construction helped to indicate deficiencies of the data.

Thus the study may be seen as being the early stages of Holling's (1963) "experimental component analysis" which he stated directed research in logical steps, producing a model describing and explaining events, and expressing their interrelationships mathematically. Watt (1968, p.271) stated that in this approach experimentation and mathematical model construction are conducted as two interlocking parts of an integrated programme.

Following the thoughts of Beer (1965) the whole system was divided into interacting subsystems, and the role of these investigated in the behaviour of the whole. The broad divisions were:

1. *The Host Plants*

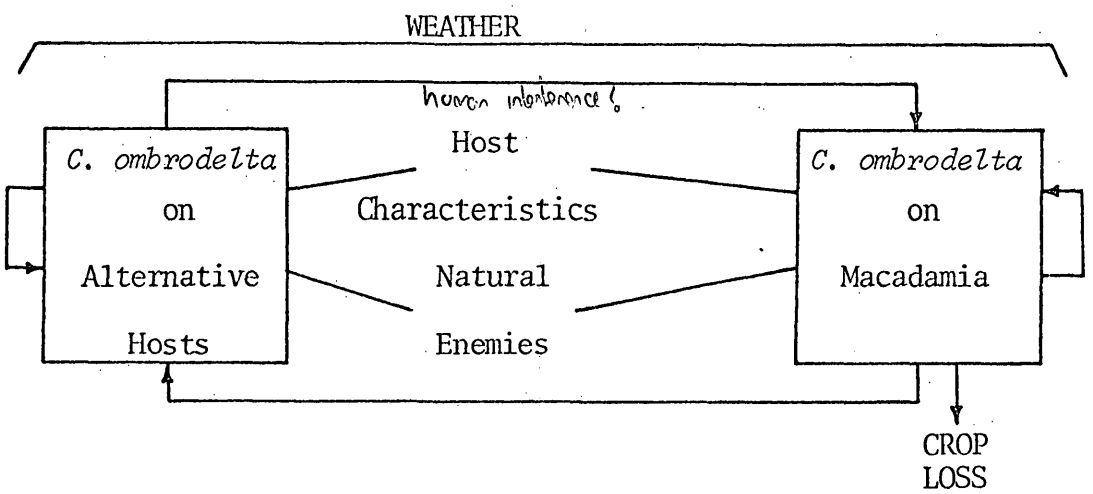
   (i) Macadamia - definition of parts for use in the sampling programme
   - definition of the development of the crop

(ii) Alternative hosts - definition of parts for use in the sampling programme
- investigation of geographic and temporal distribution.

2. *The Subject Species* - *C. ombrodelta*
- investigation of rearing and sampling techniques
- investigation of biology and life cycle
- investigation of behaviour and mortality.

3. *The Natural Enemies of C. ombrodelta*
- identification of the diversity of species
- estimation of intensity of attack on the subject species.

The data accumulated from these sections were then to be examined as a set of interacting sub-systems influenced by certain climatic conditions:



In practical terms, it was necessary to:

(i) develop techniques for obtaining data

(ii) accumulate data

(iii) formulate hypotheses as to cause and effect

(iv) construct a model incorporating these hypotheses and the data

The main effort was directed to a study of the subject species (*C. ombrodelta*) and the crop (macadamia). Because of time and resource limitations it was not possible to study the other aspects of the system in such detail.

For the same reasons it was not practical to prove or disprove individual hypotheses of cause and effect. This is a similar situation to that encountered by Clark (1963) where he found that proof of such hypotheses was not practical. This approach is consistent with the thoughts of Richards (1959).

CHAPTER 4

THE STUDY SITES

This study was conducted in Southeast Queensland and to a minor extent, northeastern New South Wales. The area is illustrated in Figure 1.

In studies of insect population dynamics, it is necessary to establish one or more sites from which regular samples may be taken. Ideally several sites should be established. Clark *et al.* (1967) stated that this allows adequate replication within a reasonable time. In addition, the contribution of spatial and temporal effects to population fluctuations may be determined.

However, Varley and Gradwell (1970) emphasized the danger of not being able to obtain any adequate data if resources were spread over too many sites. In a situation of scarce resources, they suggested that study at a single site is to be preferred.

It was expected that in this study, resources would not be adequate to study more than one site. However, insufficient was known of the geographic region, and the subject insect to predict which sites would have reasonable pest populations during the study period. Thus the selection of two sites was considered essential.

As the emphasis was on the pest-crop interaction, the main study sites were to be macadamia orchards.

Preferably the site chosen would be:

- consistently subject to attack by *C. ombrodelta*;
- owned by a co-operative grower, who would not carry out orchard operations detrimental to the study. It should be unsprayed, at least during the fruiting period;
- of sufficient size that the pest populations may behave as

orchard populations rather than populations of isolated hosts;

- bearing close to, or at a maximum, so that year to year variations in crop would be minimal, and within any one year the crop would be sufficient for pest increase and for sampling;
- of currently popular varieties, so that results may have relevance to the current Australian situation. This implies that the trees would be grafted - these may be expected to be less variable in bearing than seedling trees;
- reasonably close to the working base, Brisbane, to avoid excessive travelling time.

The area was surveyed during the early months of 1971. None of the orchards inspected met all the requirements. The best two were chosen for study in the 1971-72 season.

These were INALA and ASPLEY. The former site consisted of two adjacent orchards - Armanasco and Circus. At the end of the first season, the INALA orchards were dropped because of low pest populations. A new site was then selected and in 1972-73 studies were carried out at ASPLEY and BEERWAH. In 1973-74, only the ASPLEY orchard was used as *C. ombrodelta* populations were very low at Beerwah in that season.

Figures 2 and 3 show the orchard areas for INALA and ASPLEY respectively.

INALA is 17 km south of Brisbane City. The surrounding area is largely native bush (i.e. trees and shrubs of predominantly Myrtaceae, Proteaceae and Leguminosae), with scattered farmland and housing. The nearest suburban housing is 1.5 km to the north and west, and 11 km to the east.

C. ombrodelta infestation has been observed in the host plants in suburban gardens. Elsewhere around this orchard, hosts are rare, and infestation has not been observed.

The orchards: originally one orchard (of approximately 2 ha) it has been divided into two. The trees, all seedlings, are approximately 30 years old. Planting distances vary but approximate to an 8.0 metre square.

ARMANASCO is the northerly portion consisting of 56 trees. Adjoining the macadamia block on the north and east there are oranges, lemons, mangoes and pecan nuts, and on the west, bush.

CIRCUS consists of 68 trees bounded on the east, south and west by bush.

Insect pests: *Homoeosoma vagella*, the flower-eating caterpillar caused slight damage in 1971, and the owner stated that it was usually not sufficiently troublesome to spray. *Amblypelta nitida*, the fruit-spotting bug was not observed. *C. ombrodelta* infestation was about 20% of fallen nuts in the 1970-71 season.

Past care: ARMANASCO had been regularly watered, fertilized and mowed. Pruning had been minimal. Spraying had been irregular with the last spray being an application of parathion in 1969. CIRCUS had had no care for at least ten years.

During the study: watering, fertilizing and mowing continued in ARMANASCO. No spray was applied. CIRCUS was partly mowed once.

Sampling: each tree was numbered along the east-west rows. Numbers for sampling trees on each date were drawn from a random numbers table (e.g. Steel and Torrie 1960, p.428-431).

ASPLEY is 13.7 km north of Brisbane City and 30.7 km north of INALA.

The orchard: is 2 ha in area, with 213 trees planted in 11 rows, at a within row spacing of 7.0 m. The rows are 9.2 m apart. In 1971 the trees were ten years old.

The trees consist of five Australian grafted varieties and some

seedling trees. The varieties are planted in blocks, the number of trees in each variety being:

S1	H2	D8	M2	H3	Seedling
99	72	12	5	8	17

S1 and H2 are *integrifolia* types. D8, M2, and H3 are *tetraphylla* types which flower later than the S1 and H2 and are highly susceptible to insect attack; their crop was negligible in each of the study years.

Insect pests: in each year the flowering was heavily attacked by *H. vagella*. *C. ombrodelta* infestations were as high as 50% of tree nuts in the 1970-71 season. *A. nitida* infestation was negligible in 1971-72 and 1972-73, but in 1973-74 it reached a very high level and considerable crop damage resulted.

Past care: during its early years the orchard was watered, fertilized and mowed frequently. In latter years care has been reduced. Before the present study, the last spray applied was dimethoate in April 1969.

During the study: the orchard was mowed and pruned infrequently. In 1972 each tree was fertilized with an unknown quantity of nitrogenous fertilizer. In 1973-74 trees showed signs of nutrient deficiency.

The owner sprayed the entire orchard with white oil in 1972. Following the heavy damage to flowers in 1971, the author sprayed the flowers in 1972, and 1973 with *Bacillus thuringiensis* at 560 and 1,120 g per hectare.

Sampling: in 1971-72, the trees in the two main varieties were numbered 1-99 (S1) and 1-72 (H2). A completely random sample of trees was drawn from a random numbers table on each sampling date.

In the 1972-73, and 1973-74 seasons, each variety was stratified by rows - outside, inside and border (Figure 3). Within each row stratum, trees without appreciable crop - those on each end of the rows, and those

used for fallen nut counts (p.37) were not considered for sampling. However, in calculating absolute populations all trees were considered, except those without appreciable crop. Rows 2 and 5 of the S1's were not sampled, but they were included in absolute population calculations. They were used for other experiments.

BEERWAH is approximately 64 km north of Brisbane.

A village borders the east and south boundaries of the orchard. The country to the north is wallum (swamp and sandy heath) and elsewhere there is farmland, Eucalypt and *Pinus* forest.

The orchard: is 2.5 ha in area, and has approximately 400 trees ranging in age from 5 to 20 years. In 1972, the modal age was 10 to 12 years. There are approximately 10 grafted varieties - both Australian and Hawaiian, and also some seedling trees.

Insect pests: the most important pests at Beerwah were *H. vagella*, *A. nitida* and *C. ombrodelta*. Spray applications against each of these pests were usually necessary.

Past care: The orchard has always received intensive care, with regular watering, fertilizing, pruning, mowing and spraying.

During the study: care continued. The orchard, except for the trees used in this study, was sprayed twice with Gardona ^{R} for *C. ombrodelta* control during the 1972-73 season. The sampled trees were sprayed only in the first week of the study, with trichlorphon for *A. nitida* control.

Sampling: only two trees were used, consequently a figure of the orchard is not presented. These trees were 10 year old 246 variety (Hawaiian). . Each tree was sampled every week.

Climatic Data

Table 1 shows long term climatic data for the Brisbane City, compiled by the Bureau of Meteorology, Brisbane. This was the nearest centre to the ASPLEY and INALA orchards compiling such data. Table 2 shows long term average data for the Beerwah area, compiled by the Department of Forestry Research Station at Beerwah.

Climatic data recorded within the ASPLEY and INALA orchards during the study were restricted by the equipment available, to temperatures and humidities. Rainfall data were available for centres close to the orchards. At the Beerwah orchard, daily records were kept of temperature, humidity and rainfall, by the orchard manager.

ASPLEY. In each season, temperature and humidity records were recorded on an OTA KEIKI SEISAKUSHO thermohygrograph. From the 30.X.71 to 13.XI.71 this instrument was sheltered from direct sunlight and rain in a makeshift screen. Thereafter it was housed in a Standard Stevenson Screen.

Rainfall records are those supplied by the Bald Hills Post Office, 3.2 km to the north-west of the orchard.

Figures 4, 5, and 6 show the daily maximum and minimum temperatures recorded in the ASPLEY orchard and the daily rainfall at Bald Hills for the 1971-72, 1972-73 and 1973-74 seasons respectively. In 1971-72 (Figure 4) the break in temperature data from 17.I.71 to 6.II.72 was caused by a breakdown of the equipment.

INALA 1971-72. Temperatures and humidities were recorded on an OTA KEIKI

SEISAKUSHO thermohygrograph in a Standard Stevenson Screen. Figure 7 shows the daily maximum and minimum temperatures recorded in the orchard and rainfall recorded daily at Archerfield 6.5 km to the north.

BEERWAH 1972-73. Temperatures and humidities were recorded on a LAMBRECHT thermohygrograph in a screen at 30 cm height. Figure 8 shows the daily maximum and minimum temperatures and daily rainfall recorded at the orchard.

CHAPTER 5

STATISTICAL METHODS

A number of statistical techniques have been used throughout this study. Authority for their use is given in the appropriate places.

Some general explanation of the use of statistics is given below.

(i) Presentation of Data

In many cases, sample data are presented as sample mean ± standard error. It is emphasized that unless stated to the contrary this standard error is that of the sample(s) (Steel and Torrie 1960, p.17) and is not the standard error of the sample mean ($s_{\bar{x}}$) (Steel and Torrie 1960, p.49).

(ii) Transformation of Data

Southwood (1966, p.8) pointed out that the dispersion pattern (or distribution) of the individuals of a population is seldom normal. The results of samples taken during this study, and described in the following chapters, show that *C. ombrodelta* and its hosts are no exception.

The statistical formulae and methods by which estimates and inferences may be drawn about populations have been developed for data which have "normal" or Gaussian distribution. Non-normality in data can usually be corrected by an appropriate transformation of the original data (e.g. Steel and Torrie 1960, p.157-158, Southwood 1966, p.11). However, where interest lies in an estimate of numbers, e.g. leaves per tree, eggs per orchard, the transformed data have no relevance to the real world situation.

Southwood (1966, p.11) stated that there is justification for

using arithmetic (untransformed) means in insect population studies, as the use of transformations can lead to difficulties in comparing means, if these are based on different transformations. It is common practice to use arithmetic means, for example, the works of LeRoux and Reimer (1959), LeRoux (1961), Harcourt (1961a), Geier (1963), Berryman (1968) and MacLellan (1973).

In this study, it has been decided that when statistical tests of significance within data groups are to be carried out, the original data should be transformed where population distributions appear to be anormal.

However, when estimating population numbers it has been decided that untransformed data may be used.

(iii) Precision of Estimates

To define the precision of population numbers estimated from samples, the length of the confidence interval (Steel and Torrie 1960, p.22) expressed as a percentage of the estimate has been used. A confidence interval length of 10% or 20% of the estimate has been chosen as a suitable level of precision. The first length is slightly less precise than the criterion of standard error of 10% of the mean, generally accepted by entomologists (e.g. Morris 1955, Harcourt 1961a, 1969, Southwood 1966, p.19), as the confidence interval length is usually a lower percentage of the mean than is the standard error(s).

Confidence intervals were calculated using the untransformed standard error of the mean. Steel and Torrie (1960, p.53) stated that even if a parent distribution is considerably anormal the distribution of means of random samples from it approaches the normal distribution as the sample size increases. D.R. strong[1] (pers. comm.) recommended that

---

1. Mr D.R. Strong, Statistician, CSR Ltd., Sydney.

unless dealing with very small samples, it would be safe to assume normality of sample means.

In some cases samples were small, and the distributions from which they came highly skewed. I. Horton[1] (pers. comm.) suggested that use of the untransformed data would probably be adequate in these cases, as the back transformed confidence interval of the mean did not fall across that mean. For example, in the case of the sampling stick results (p.46) the original mean leaf numbers/sample was 52.02; the back-transformed (from log(x+1)) limits of the 95% confidence interval of the mean were 10.74 to 29.54.

On only one occasion have confidence intervals been estimated from transformed data, and their limits retransformed. This was for comparison with asymmetrical confidence intervals obtained from tables (Table 65).

(iv) Statistical Formulae

Following the usual practice unless otherwise stated, the statistical formulae used are those for continuous data; although most of the data examined were discrete.

---

1. Mr I. Horton, Senior Lecturer in Biometrics, Department of Agriculture, University of Queensland.

SECTION II

THE HOST PLANTS OF *CRYPTOPHLEBIA OMBRODELTA*

CHAPTER 6

SPECIES OF HOST PLANTS

To date, forty one species of plants have been confirmed as carrying infestations of *C. ombrodelta*. These are shown in Table 3.

For some of these it is not clear whether *C. ombrodelta* can develop from egg to fertile adult on that plant alone. Some collections may have been chance occurrences; e.g. the case of *Cocos nucifera*. Gutierrez *et al.* (1971) considered findings of *Aphis* spp. on plants not normally believed to be hosts fortuitous, and due to unusually high populations of the insect in the region. During the course of the present study *C. ombrodelta* eggs were found on custard apple fruit (*Annona squamosa*, Family Annonaceae) in the Beerwah orchard. On hatching, the larvae entered the fruit but died soon afterwards. It is supposed that oviposition on these fruits was fortuitous, and similar to the situation discussed by Gutierrez *et al.*

In the plant host *Acacia podalyriifolia*, infestation by *C. ombrodelta* apparently only occurs in those pods infested by the fungus *Uromycladium robinsoni*[1]. Normal pods are flat but infested pods grow into grotesque galls (Figure 30B).

At least thirty one of the host plants listed are now found in Australia, but only six have been confirmed as being Australian natives (S.L. Everist[2] 1973 pers. comm.).

Common (1972 pers. comm.) believes that *C. ombrodelta* is native to northern and eastern Australia so it is probable that there may be

---

1. Identified by Dr R.F. Langdon, Department of Botany, University of Queensland.

2. Mr S.L.Everist, Director Botany Branch, Department of Primary Industries, Meiers Rd., Indooroopilly, Queensland.

other as yet unrecorded Australian native hosts. In these regions of Australia rainforest was common, and is still to be found. Francis (1951) listed 14 Leguminosae, 11 Proteaceae, 29 Rutaceae, 32 Sapindaceae and four Palmae, which occur as tree species in the eastern Australian rainforests. Coaldrake (1961) conducted a faunal survey of the lowlands of the Southeast Queensland coast. He recorded that the native shrub layer is conspicuously Leguminous in many forest communities; in the heaths the obvious families included Proteaceae and Rutaceae. The species he collected during this survey included 41 Leguminosae, 9 Rutaceae, and 3 Sapindaceae (one of which was *Cupaniopsis anacardioides*).

Thus even if only a small proportion of these Australian species were suitable as hosts for *C. ombrodelta* there would probably have been a continuous food supply for the insect in the virgin flora.

In Australia, the only commercially exploited host plants of *C. ombrodelta* are *Macadamia integrifolia* and *M. tetraphylla*, and their hybrids. For the purposes of this study, orchard macadamia are regarded as the main host, all other host plants, including extra-orchard macadamia are regarded as alternative hosts.

CHAPTER 7

MACADAMIA. I. ESTIMATES OF PLANT PART NUMBERS, THEIR DYNAMICS AND DISTRIBUTION

During the course of the study, it was found that the fruit, leaves and branches of the host trees of *C. ombrodelta* were habitats for certain life stages of the insect.

So that budgets, using absolute populations of the insect, could be constructed, it was necessary to estimate the number of each of these plant parts present in the sampling area, on each of the sampling dates (Southwood, 1966, p.3).

Sample units should be stable, but if not, their lack of stability must be measured (Southwood, 1966, p.18). Thus the dynamics of the plant parts were investigated.

If stratified sampling is employed it is also necessary to know the distribution of sample units (fruit, leaves etc.) between the strata, so that samples can be drawn proportionally (LeRoux 1961, Sampford 1962, p.77). Alternatively the absolute populations can be estimated for each stratum and added for a total population estimate (Morris 1955).

A. METHODS

It will be shown in later sections that the fruit is the most important habitat for *C. ombrodelta* populations in macadamia; consequently, most effort was devoted to establishing the required parameters for fruit. Estimates made of leaf numbers and branch lengths were sufficient only to indicate the proportion of insect population found in these habitats.

Estimates of the dynamics of the plant parts were made without

the benefit of any study of macadamia physiology. Thus the estimates were measures of effect. The partitioning of this effect between various causes was complicated. In the case of the nut for instance, the possibility of fall was believed to be proportional, in certain parts of the season, to insect attack (Ironside 1970 unpublished report). Generally, in this section, the falling fruit was distinguished as having no *C. ombrodelta* damage (although eggs may be present), and damaged, i.e. with present or past *C. ombrodelta* activity. Further discussion on the role of *C. ombrodelta* in causing nut fall will be presented in Section V.

The leaves and branches were considered to be stable in numbers over the entire duration of this study because of the small proportion of population using the habitats, and the low precision of estimates made of these plant parts.

(i) Direct Counts

Trees were selected at random, except at Beerwah where only two trees were studied. Nuts in all, or part of the canopy were counted by direct observation. Divisions of the tree canopy were made as follows:

Levels: the canopy was bissected into upper and lower level.

Quadrants: within each level a division into four quadrants was made along the north-east to south-west line, and north-west to south-east line. Thus each tree contained eight quadrants:

Upper north, Upper east, Upper south, Upper west, Lower north, Lower east, Lower south, Lower west.

To assist the count, strings were threaded through the trees along these dividing lines.

This method provided an estimate of total nuts and an estimate of the within tree distribution of nuts.

(ii) Tagged Racemes

Racemes were selected randomly, marked, and inspected at intervals. Counts of the nuts present at each inspection showed the nut loss that occurred.

Racemes were marked with a Dymo Tape ^{R} label, tied on with a cotton thread or fuse wire. These labels remained attached and in good condition throughout the inspection period.

This method only supplied details of nut loss within a period, and thus had to be combined with a direct count to provide an estimate of nuts at any date.

(iii) Fallen Nut Count

Trees were initially selected at random, except at Beerwah, and these same trees were used on each subsequent estimation date.

The nuts which had fallen between each inspection were counted and removed. At the end of the season, any nuts remaining on the tree were stripped and counted. Thus the total nuts per tree on each inspection date could be estimated by adding the number fallen after this date to the number stripped off the tree. If the tree had been sampled - i.e. removing nuts from the tree for larval estimates - these nuts also had to be included.

At Beerwah, the ground under each of the study trees was free of vegetative cover, so that fallen nuts were easily seen.

At Aspley the ground cover was heavy, and nuts were difficult to find. Hessian sheet or synthetic fibre net was spread beneath each of the selected trees (Figure 9) and vegetative cover was reduced by periodic applications of paraquat dimethyl sulphate. Because of the expense and time involved only five trees in each of the Aspley S1 and H2 could be used.

These trees at Aspley were not included in the normal sampling programme. It was assumed that the tree growth and insect populations, and thus nut fall, in these trees was similar to that of other trees in the orchard.

This assumption should be treated cautiously. In 1973-74 it was observed that these trees appeared healthier and more vigorous than the others, probably because weed competition for nutrients was reduced. Also, because fallen nuts were removed frequently *C. ombrodelta* attack rate in these trees may have been reduced. However, populations appeared to be as high as in other trees; movement of adults between trees was apparently quite common.

This method only provided an estimate of total nuts per tree.

(iv) Sampling Stick

The sampling stick consisted of a light pole, with two or more cross pieces (Figure 10). The stick illustrated was 200 cm in length, each of the long cross pieces was 50 cm, and the shorter cross pieces 25 cm in length.

The tree to be examined was seen as a regular geometric volume (Figure 11).

The sampling stick was placed at random points within this volume and rotated to describe a cylindrical volume; the number of plant parts within this volume was counted. Since the volumes of the tree and the sampling stick were known, the number of parts in the total tree could be estimated.

Random placement of the sampling stick was achieved by drawing two numbers from a random numbers table. The first referred to horizontal displacement, the second to vertical displacement.

Horizontal displacement: a 7 x 7 grid was painted on a large piece of netting which was moved from tree to tree. Each square of the grid

was 50 x 50 cm, and the intersections were numbered 1 to 49 (this is seen in Figure 10).

Vertical displacement: points on the operator's body at 50 cm distance were noted, and also marked on the handle of the stick.

Figure 10 shows the sampling stick in use. It was very difficult to use with only one operator, and on most occasions help was enlisted.

Error control could be assisted by restricting the tree "volume" to the main part of the canopy, thus reducing the number of zero samples, and by the use of different sized sampling stick volumes.

In these trials one "50 cm" volume and two "25 cm" volumes were counted for each placement of the stick, these are referred to as "large" and "small" sampling stick samples. If the method were developed further each estimate should be randomized to avoid systematic bias.

The method provides an estimate of all plant parts. If sampling were to be stratified, it would provide an estimate of within tree distribution of those parts.

Its main use was for the approximate estimation of leaf and branch populations. Random branch sampling, as described by Jessen (1955) was also considered for this purpose, but was not attempted as it would have been too time consuming.

In general, too few resources were devoted to the estimation of plant parts, to achieve narrow error limits. As the study was of a limited nature, no further time could be allowed. The estimates are fairly consistent between and within seasons and are thus considered adequate at this stage.

The combinations of methods used in each year and at each site were:

1971-72. At Aspley and Inala sites a direct count of nuts in sections of randomly selected trees was followed by periodic inspections of tagged racemes.

1972-73. At Beerwah fallen nut counts were made for each tree, for each week of the sampling period. Direct counts of nut numbers were made three times on each tree, including the stripping of trees at the end of the season. The sampling stick was used in sections of each tree on two occasions.

At Aspley fallen nut counts were made on each of five trees per variety, in the inside rows, each week. Direct counts were made on these five trees four times (including the end of season stripping) and on five trees in the outside row of each variety on three occasions, including stripping. Lack of time prevented direct counts being made on trees in the border rows. Visual assessment indicated that the number of nuts per tree in these rows was similar to that in trees in the inside rows.

1973-74. Aspley: the same five trees in inside and outside rows of each variety that were used in 1972-73 were used again. Fallen nut counts each week were made on these inside row trees, and a direct count was performed at stripping. Direct counts of the outside row trees were performed twice (including stripping).

B. RESULTS AND DISCUSSION

1. PLANT PART ESTIMATES

(i) Nut Numbers

1971-72

ALL SITES. Tables 4 and 5 show the estimates of nut numbers in

each Inala orchard and each Aspley variety at various dates throughout the season.

1972-73

BEERWAH. Table 6 shows the estimates of nuts per tree for each of the study trees and illustrates the method by which nuts per tree calculations were made by fallen nut counts.

ASPLEY S1 AND H2. The partial stratification of the orchard, and the different methods of counting, complicated the estimate of total nuts per variety. Therefore the following calculations were required.

a Comparison of nuts per tree between rows

The analysis of the difference of nuts per tree in inside and outside rows is described on p. 51. It is shown that in each variety the outside row had significantly (P=0.01) fewer nuts per tree than the inside row; this difference was maintained on all dates. Therefore nut estimates are calculated for each row.

b Comparison of estimates made by direct counts and fallen nut counts

The estimates of total nuts in each Aspley variety is based partly on direct counts (outside rows) and partly on fallen nut counts (other rows). The two methods were compared.

Direct counts are onerous and difficult; fallen nut counts are quite quick and easy, and the nuts are removed when counted so that estimates can be easily checked. Thus fallen nut counts were considered accurate and direct count estimates are compared to these.

Comparisons were possible on three dates in each of the Aspley

varieties (Table 7). Also included for interest, are the two dates at Beerwah on which a comparison was possible.

The percentage deficiencies of direct counts shown in Table 7, were transformed to arcsin $\sqrt{x}$ and analysed for each variety separately.

The analysis was of the form:

Source	df	Expected mean square
Dates	(d-1)	$\sigma^2 + \frac{t}{(d-1)} \Sigma\delta^2$
Trees	(t-1)	$\sigma^2 + \frac{d}{(t-1)} \Sigma\tau^2$
Dates x Trees	(d-1)(t-1)	$\sigma^2 + \frac{1}{(d-1)(t-1)} \Sigma(\delta\tau)^2$
TOTAL	dt-1	

No estimate of error variance was possible and the main effects mean squares were compared to the interaction mean square. In future studies of this type it would be desirable to design an experiment with replication, so a true estimate of error could be obtained.

A summary of the relevant results arising from the analyses is shown in Table 8. It can be seen that the analyses do not refute the hypothesis that the deficiency of estimate by direct counts compared to fallen nut estimates is constant from tree to tree and throughout the season. The deficiency is probably a property of the observer.

The deficiency at Beerwah was not statistically different from that in each of the Aspley varieties ("t" test, Steel and Torrie (1960, p.81)). The apparent higher Beerwah deficiency may be related to the larger tree size and greater difficulty in sighting nuts.

Following a policy of treating each site separately, the estimates of nuts in Aspley S1 and H2 outside rows made by direct counts should be increased by "observer deficiency", 21.0% and 22.0% respectively to obtain

true estimates. Direct counts were not used for absolute population estimates at Beerwah.

c Calculating the total Aspley S1 and H2 crop

Following the calculations shown above, an estimate of the total crop in each variety was possible.

Firstly an estimate of nuts per tree for the inside and border rows was calculated from fallen nut counts for each week. These figures are presented in Table 9. The table also shows the number of trees which should have been observed for a confidence interval of the estimate to be only 10% or 20% of the mean, calculated by: $n = (t_1^2 s^2)/d^2$, where n = the number of trees required; t_1 = tabular "t" for the desired confidence level and degrees of freedom of the initial sample; s^2 = the sample variance; d = the half width of the desired confidence interval. (Steel and Torrie 1960, p.81).

The required number of trees is in most cases, larger than the number available. However, if the number of trees sampled were increased, the sample would constitute an appreciable proportion of the tree population and it would be necessary to use the finite population correction - (N-n)/N, where N is the population size, n the sample size (Steel and Torrie 1960, p.416), in the calculation of standard error of the mean ($s_{\bar{x}} = \sqrt{(\frac{s^2}{n} (\frac{N-n}{N}))}$). Thus as n approached N, the confidence interval of the mean would approach zero.

In the outside rows estimates of the number of nuts per tree each week were obtained graphically. The nuts per tree for inside rows for each week (Table 9) were plotted against time (Figures 12 and 13). They formed a relatively smooth curve. The direct count estimates of outside rows on 10.XII.72 and 3.II.73 (Tables 27 and 28) were converted

to nuts per tree, increased by the relevant observer deficiency and plotted also. The estimate for the 3.IV.73 was plotted without increase as it was obtained by stripping the nuts from the tree, and was accurate.

A line following that described by the inside row estimates, but running through the estimated points for outside row was drawn, and the weekly estimates read from this. These are shown in Table 10.

For the final estimate of nuts in each variety each week, the figures of nuts per tree in the inside rows (Table 9) and outside rows (Table 10) were multiplied by the respective number of nut bearing trees, and the two figures added. This is shown in Table 11. No estimate of error was available for these variety totals. However, the standard errors shown in Table 9 indicate the variability of the estimates.

1973-74

The same methods described for Aspley 1972-73 were used.

Table 12 gives the mean estimates of nuts per tree and the standard errors for the five trees whose populations were estimated by fallen nut counts. Also shown are the graphically obtained estimate of nuts per tree for the outside row of each variety.

Finally Table 13 shows the estimate of total nuts in each variety for each week of the season.

Sampling Stick Method for Estimating Nut Numbers

Table 14 shows the results of the sampling stick trials for estimating nuts.

It was considered that an analysis of the data to detect differences between varieties and trees within varieties was not worthwhile because of the high percentage of zero readings. The data were treated as having been drawn from a homogeneous universe.

Table 15 shows the relevant statistics used in judging the method's effectiveness.

To determine whether the large sample or small sample gave the better estimate of variance for an equal cost, the method of computing the inverse of the product of cost of sampling and variance for each method on a common basis (that of the smaller unit) is used (Southwood 1966, p.19). The higher the value the greater the precision for the same cost. The larger unit was more efficient.

It can be seen that the number of samples taken in this test provided an inadequate estimate of nut numbers.

The number of samples required for a precision of estimate such that the 95% confidence interval of the mean was no more than 10% or 20% of the mean, was impractical. In the time required to take the sample an adequate number of trees could have been examined for fallen nut counts.

In summary: nut numbers vary throughout the season in a regular pattern. The large numbers early in the season are reduced rapidly until December when a stable level is maintained until late January or early February. Nut numbers decline rapidly again in March.

Figure 14 shows the nut numbers estimated at Aspley and Inala in the 1971-72 season. and Figure 15, the nut numbers at Aspley in 1972-73 and 1973-74. Beerwah data are omitted as they were complicated by heavy sampling.

(ii) Leaf numbers

Table 16 shows the number of leaves per sample for each sized sampling stick sample. Table 17 gives estimates of leaves per tree at Aspley and Beerwah, and indicates the effectiveness of the method.

It can be seen that the larger unit is slightly better as an estimating method.

The best estimates of leaf numbers per tree were: Beerwah, 30,137 and Aspley, 11,500 (the weighted mean of large and small sampling stick estimates).

(iii) Branch numbers

Table 18 shows the centimetres of branch per sample for each sized sampling stick sample. Table 19 gives the estimates of total centimetres of branch per tree and tests the effectiveness of the sampling stick method for estimating this. The larger unit is the more efficient of the two sizes tested.

At Aspley the weighted average of the large and small estimates was used for an approximate estimate of total branch per tree: viz:- 19,375 cm. At Beerwah, total branch length per tree was estimated as 78,057 cm.

Table 20 shows the total estimate of branch length classified by diameter sizes in the proportions measured in the samples at Aspley, and gives the estimated number of branch junctions at each site.

2. NUT DYNAMICS - THE STABILITY OF NUTS DURING THE SEASON

From the inspection of tagged racemes in 1971-72, and the fallen nut counts in each of the following seasons, it was possible to estimate the number of nuts which fell between inspection periods.

To overcome the variability of fall due to variation in number of nuts available for fall in different trees and different seasons, and to overcome the effect that heavy sampling probably had on fall from Beerwah trees, a figure of "percent likelihood of fall" is calculated:

$$\text{Percent likelihood of fall} = \frac{\text{No. of nuts which fall in a period}}{\text{No. of nuts in tree at start of the period}} \times \frac{100}{1}$$

As an indication of the contribution that *C. ombrodelta* may have made to nut fall, the proportion of fallen nuts damaged (i.e. with some larval boring) is shown in the relevant tables of nut fall. Standard errors for the mean percentage damage are also shown. These have been calculated from the formula:

$$s_p = \sqrt{\left(\frac{p(1-p)}{n} \cdot \frac{(N-n)}{(N-1)}\right)} \cdot 100\%$$

(M.M. Prentice[1] pers. comm.)

Where; p = the proportion of nuts damaged, n = the number of nuts sampled, N = the number of nuts which fell.

If a standard error is not shown, either the mean percentage damaged was 0 or 100%, or the whole population of fallen nuts was sampled.

A discussion on the magnitude of this effect is given in Section V. Here no assumptions are made concerning the role of the pest.

After falling, tagged nuts were lost in the ground cover so that it was not always clear whether the fallen nuts were affected by *C.*

---

1. Dr M.M. Prentice, Lecturer, Department of Mathematics, University of Queensland.

ombrodelta. Thus the results presented for 1971-72 do not show the proportion of the crop affected by the borer.

Figure 16 shows the percent likelihood of fall of nuts at each site in 1971-72.

The inspection dates in 1971-72, covered the period from the time nuts were first formed up to the time mature fall occurred. This was found to be an unnecessarily long period, and in subsequent years examination did not begin until later in the crop cycle.

Table 21 shows the actual nut fall recorded by fallen nut counts, for each of the Beerwah trees in 1972-73. Figure 17 shows the weekly percent likelihood of fall of nuts from both Beerwah trees.

Tables 22 and 23 show the nut fall at Aspley (from five trees in each variety) estimated by fallen nut counts for the 1972-73, and 1973-74 seasons respectively. Figure 18 shows the percent likelihood of fall of nuts for both varieties at Aspley for the 1972-73, and 1973-74 seasons.

It can be seen that the change in percent likelihood of fall follows a pattern which is similar for each site and each year.

The data for Aspley in 1972-73 and 1973-74 were used for the following four analyses of variance of the pattern of fall:

1972-73	S1	5 trees x 23 weeks
	H2	5 trees x 23 weeks
1973-74	S1	5 trees x 18 weeks
	H2	5 trees x 18 weeks

Original data of % likelihood of fall were transformed to arcsin $\sqrt{x}$. Table 24 shows the transformed weekly mean and standard error(s) for each variety in 1972-73; Table 25, the same parameters for each variety in 1973-74.

Within each of the four groups of data, a Bartlett's test of homogeneity of variance (Sokal and Rohlf 1969, p.370) was conducted. In all but H2, 1973-74, some division of the data was required before

analysis. The divisions are indicated in Tables 24 and 25.

In measuring lack of stability, the most appropriate standard of reference is the point of greatest stability, i.e. the lowest percent likelihood of fall between the periods of observed instability. Thus weekly means were examined in relation to this lowest mean, either by a least significant difference (LSD) (0.05) (Steel and Torrie 1960, p.106) for the means included with the lowest in the analysis, or by a "t" test for means outside this group. The means not significantly greater than the lowest in each analysis are shown in Tables 24 and 25.

The general bimodal pattern of macadamia nut fall is well known. The early high likelihood of fall is known as "natural thinning". The macadamia tree appears to set many more nuts than it can carry through to maturity. The later increased likelihood of fall coincides with the normal drop of mature nuts.

The analysis of percent likelihood of fall for the Aspley trees indicates that natural thinning was complete in early to mid-December, and a period of relative stability then existed for five to ten weeks before fall increased again - probably due to increasing maturity, but possibly also because of increased insect attack. These conclusions were supported by inspection of the graphs of percent likelihood of fall for Beerwah 1972-73 and the data for 1971-72 all sites.

More precise estimates of the stability of nuts cannot be made until the role of *C. ombrodelta* in causing fall is investigated.

3. THE DISTRIBUTION OF NUTS WITHIN THE TREE CANOPY

The direct counts of tree nuts in the 1972-73 season were analysed, to determine whether there was any regularity in the distribution of nuts within the tree canopy.

The counts were:

BEERWAH: three dates of counting, two trees, two levels, and four quadrants.

The original data are shown in Table 26.

ASPLEY S1: three dates of counting, five trees, two levels, and four quadrants.

Counts were taken in the outside and inside rows (Table 27).

ASPLEY H2: as for Aspley S1 (Table 28).

It can be seen from these tables that there were discrepancies in the data; viz. - certain quadrants on the second date had a greater number of nuts than on the first date. There was negligible (if any) recruitment of nuts in this period; the error arose because the strings delineating the quadrants had moved between the counts.

Labour requirements of direct counts prevented replication. Thus in the factorial analyses, no true estimate of error was available, as all factors were fixed, or crossed. The highest order interaction was used as the best available estimate of error.

BEERWAH. The Beerwah data, after transformation to $\log(x+1)$, were analysed with the aid of a desk calculator. Table 29 shows the results of this analysis. Tests were conducted from the second highest order interactions up to the main effects, and non-significant interaction effects were accumulated as the test continued.

ASPLEY. Mr Strong of the CSR Ltd. assisted with the preparation of the data and their computer analysis. The programme required that each variate be multiplied by 10 and zeros replaced with 0.001. The means and error mean squares were corrected for the multiplication after analysis. Because of the complexity of the result non-significant effects were not accumulated.

Initially each row count was analysed separately; i.e. the four analyses were: Aspley S1 outside row, Aspley S1 inside rows (Table 30), Aspley H2 outside row, Aspley H2 inside rows (Table 31).

Within each Aspley variety, the third order interactions (each with 24 degrees of freedom) for both rows were homogeneous, and the two analyses were combined, to test row differences. In each variety, the outside row had significantly (P=0.01) fewer nuts than the inside rows, over all dates. Subsequent examination of the results was made for each separate analysis; viz. Beerwah, Aspley S1 outside row, Aspley S1 inside rows, Aspley H2 outside row, Aspley H2 inside rows.

The Beerwah trial was relatively straight forward. Dates was the only main effect that was significant. The two way tables of means for the significant first order interactions are shown in Table 32, together with the LSD's for mean differences. Also shown are the main effects means averaged over the interactions.

The four Aspley analyses were more complicated. All main effects were significant, as were most of the first order interactions, and some of the second order interactions. This reveals a very complex situation which could be understood only after much more experimentation with replication, both within and between time and place. It also shows that the use of the third order interaction mean square as a source of error is not very satisfactory.

Accepting the limitations of these non-replicated trials the results are of interest and are discussed below.

Tables 33, 34, 35 and 36 show the two way tables of means for the significant first order interactions in S1 outside row, S1 inside rows, H2 outside row, H2 inside rows, respectively.

(i) Tree effects

The main interaction effects, not involving "dates", are believed to indicate differences in the growth habit and pruning practices at each site.

Normal growth of macadamia can produce trees of various shapes depending on variety, wind and light exposure, and probably other effects which are not well understood. Pruning practices aim at achieving a uniform shape, but even so variations occur, and wind damage, to which macadamia are susceptible, can produce asymmetry.

a Tree differences

At Beerwah these were not significant. The trees had been selected for uniformity. However, the tree x quadrants interaction was significant, due partly to small differences in shape, but also to a large branch having been broken out of the west quadrant in tree 146 during high wind.

Aspley tree main effects were significant (the trees had been selected at random). The significance of all "tree" interactions, with the exception of trees x quadrants in H2 inside rows, and trees x levels x quadrants in S1 outside row, probably reflects the comparative lack of pruning that trees in this orchard received.

b Level differences

At Beerwah, levels were not significantly different. For each of the Aspley analyses, however, the upper level had significantly fewer nuts than the lower.

The Aspley trees were younger, and smaller than those at Beerwah, and had in this season, received fertilizer for the first time

for some years. Thus they were increasing their size more rapidly than those at Beerwah. Nuts are only borne on wood of two years or more in age, and Aspley trees had a high proportion of new wood in their upper levels.

An examination of levels x quadrants interaction at Aspley, reveals that in S1 upper quadrants, the north had significantly more nuts than the others in both rows; in S1 lower, north and west had more nuts in outside row, and north, west and east in inside rows. In H2 upper, west had the highest population in both rows, and in the lower quadrants north and west had the highest in both rows. The pattern of nut set appears to be reasonably consistent as, at Beerwah, upper north and lower west also had the highest nut populations. The reasons for this are not known but the pattern may be affected by light and wind conditions at flowering or during tree growth. However, at Aspley trees x levels x quadrants interaction is significant for all but S1 inside rows, indicating that the situation is complex.

(ii) Date Effects

At every site dates main effect was significant. Nut numbers declined slightly, or not at all between the first two dates, and sharply between the second and third - the latter period being that of increased probability of nut fall.

Dates x trees was significant in all five analyses. At Beerwah the tree which had significantly fewer nuts on the first two dates, had significantly more than the other finally. This could have been due to differential insect attack, or physiological features. At Aspley, the situation was less marked but trees lost nuts at different rates, especially between the last two counting dates.

Dates x levels was not significant in either S1 row or in H2 outside row. However, the significance of dates x trees x levels in

S1 outside row and H2 outside row indicates a complexity.

At Beerwah the upper level, which on the first two dates had only slightly fewer nuts than the lower level, finished with significantly more nuts than the lower level. In Aspley H2 inside rows a greater proportion of nuts in the upper level fell than in the lower.

The reasons for these differences are not clear.

It is apparent that no clear decision can be reached on the distribution of nuts within macadamia trees. Before sampling, each site and trees within the site should be assessed for their nut distributions.

In the 1973-74 season the nut distribution within each tree was visually assessed at each sampling. Nuts were drawn approximately in proportion to their distribution within each tree.

CHAPTER 8

MACADAMIA. II. THE DEVELOPMENT OF THE NUT AS A COMMERCIAL UNIT

The main components of nut quality which can be easily measured are nut size and nut maturity.

In Australia the minimum in shell nut size for processing is one half inch (12.70 mm) in diameter.

So far in Australian commercial processing there is no standard definition of maturity for nut kernels. Immature kernels can generally be graded out before processing begins, whilst semi-mature kernels are rejected during the processing. In either case the assessment of the suitability of a particular kernel is highly subjective.

This chapter defines the development of nut size and maturity for the orchards in which this study was conducted. These data are necessary to assess the effect of *C. ombrodelta* on the crop (Section V). In addition, the total potential crop at each site in each year of the study, is defined.

A. METHODS

1. SIZE

Nut size was recorded as equatorial diameter of the nut in husk. Measurements were taken to the nearest 0.5 mm with a CHESTERMAN (No. 550) Vernier caliper.

In husk, rather than in shell, measurements were used because of the need to handle many nuts in a short time at each sampling. Nuts which had no borer infestation would not normally be dehusked. A diameter of 20.0 mm in husk is approximately equal to the minimum processing size of 12.70 mm in shell.

1971-72

Size increase in nuts was determined by measurement of nuts on the tagged racemes. Where available, three nuts per raceme were measured at each site on each date.

1972-73

Every nut taken in destructive samples at each site and each date (except Aspley H2 29.I.73) was measured.

1973-74

Only Aspley (both varieties) was sampled. On each date, for each variety, twenty nuts from each row were selected at random, from nuts sampled from the tree, and measured.

2. MATURITY

During their development, nuts pass through three readily recognizable stages. In this study these have been called:

soft shell - the shell (testa) is white and jelly-like in consistency and quite soft;

hard sticky - the shell has hardened and cannot be cut with a knife. It is pale brown and the inside of the husk (pericarp) is sticky;

hard brown - the shell remains hard but has become dark brown. The husk when cut, comes away cleanly from the shell.

It is known that the kernel is not suitable for processing when the nuts are in the soft shell or hard sticky condition, when the nuts are hard brown they may or may not be mature.

Some Australian farmers estimate the maturity of macadamia nuts by floating them, in shell, in tap water. Nuts which float are judged mature, those that sink, immature. In Hawaii Ripperton *et al.* (1931, 1938) investigated this method and found that it was not reliable due to variation in shell thickness.

Work in Hawaii has shown that maturity can be determined by flotation of the kernels (Ripperton *et al.* 1931, 1938, Yamamoto 1967). This method relies on close correlation between the specific gravity of the kernel and its oil content (Ripperton *et al.* 1938), increasing oil content being the major factor in the development of maturity.

Yamamoto (1967) presented a method for grading kernels, before they are processed. Essentially the method requires that the nuts be dried in shell, at 60°C to a constant weight, graded for size, then cracked. Kernels are visually graded for insect damage and deformities or cracking damage, and then floated in two salt (NaCl) solutions - (1) 1.085 specific gravity (12% w/w salt in water) and (2) 1.030 specific gravity (4.5% w/w salt in water). Nuts are thus divided into:

- Rejects under size and insect damaged nuts, and those which do not float in either solution.
- Second Grade nuts with sound kernels which do float in solution (1) but not in (2).
- First Grade nuts with sound kernels which float in both solutions.

A modification of Yamamoto's method was used in the present study. All nuts taken in samples were examined for obvious *C. ombrodelta* damage - i.e. a hole in the shell. These were recorded and graded out, as were undersized nuts. A subsample was selected from the remaining hard brown nuts, and this was dried, cracked, and floated in the appropriate solutions.

Insect damage other than that caused by *C. ombrodelta* was ignored.

Sinclair P.[1] (1973 pers.comm.) took large samples of hard brown nuts and graded them by Yamamoto's technique. Extra samples, taken on the same dates, were sent for commercial processing. For several weeks after Yamamoto's method indicated the crop was approaching maximum maturity, the factory found that a higher proportion of the kernels showed signs of immaturity, and were not suitable for processing.

Ripperton *et al.* (1931, 1938) stated that nuts were suitable for commercial processing when the specific gravity of the dried kernel reached 1.00. Hamilton *et al.* (1965) used flotation in tap water to determine maturity of nut kernels - these authors noted that this method had been used in commercial factories, and was considered reliable. The reasoning behind Yamamoto's determination of grades is not clear.

Distilled water was included as a test solution with those used in Yamamoto's technique in the 1973-74 season. The other solutions were retained as they provided extra points of measurement for developing maturity. The grades available in decreasing suitability for processing were: water, 1st, 2nd, reject.

1972-73

On every sampling date at each site nuts were assessed for state of development and, if hard brown, a sample was tested by modified Yamamoto's. Nuts taken from the tree and from the ground were tested separately. Within each variety nuts sampled were pooled over rows and a maximum of 80 tree nuts and 100 fallen nuts (ground level) were tested.

---

1. Mrs P. Sinclair, Field Entomologist, CSR Ltd., Beerwah, Queensland.

1973-74

On each date nuts were assessed for state of development. A sample (maximum 50) of hard brown nuts was selected in each of the following categories (sample pooled over rows):

Tree nuts	- *C. ombrodelta* in husk
	- husk clean
Fallen nuts	- *C. ombrodelta* in husk
	- husk clean.

These were tested by modified Yamamoto's method and distilled water flotation.

B. RESULTS AND DISCUSSION

Since this chapter was included to define only approximate limits of developmental processes in the nut which may be important to *C. ombrodelta* attack, the data are presented mostly as graphs, without error estimates. Where errors have been calculated, a note to that effect is included in the appropriate place.

1. SIZE

Standard errors of the data were calculated for both seasons after 1971-72. Apart from fallen nuts during the period of minimum fall, these were almost always less than 10% of the mean. They have been included only in the figure for 1973-74 Aspley data, where they cannot be confused with data from different levels.

Figure 19 shows the size of nuts at Inala and Aspley S1 and H2 during the 1971-72 season.

At each site it can be seen that there is a decline in nut size in early October. At this time, at each site, a new series of tags was

set up. These were of newly formed nuts and consequently the mean nut size was reduced.

Figure 20 shows the mean nut size from each of the trees sampled at Beerwah in 1972-73. The means for tree nuts were estimated by pooling the data from both tree levels.

Figure 21 shows the mean nut size for tree and fallen nuts at Aspley S1 and H2 in 1972-73, and the tree nut size (with standard error) for each variety at the same site in 1973-74.

It appears that the development of nut size follows a quite regular pattern which is more or less constant between sites and years.

Fallen nuts reached the minimum acceptable size of ~20 mm diameter in mid December. Apparently tree nuts reached this size sometime in early November or October. The reason why fallen nuts are smaller than those on the tree until late December-early January has not been studied. From observations it appears to be partly due to shrinkage of the nut after falling. Shrinkage is only marked when shells are soft. In addition it appears that, at this stage, nuts which are destined to fall do not develop as rapidly as the general nut population.

The increase in diameter of tree nuts had virtually ceased by late December.

2. MATURITY

Firstly the occurrence of the three visually determined categories of nuts (soft shell, hard sticky and hard brown) is examined.

No data on these categories are available for the 1971-72 season.

Figure 22 shows the occurrence of the three categories in both Beerwah trees, combined.

The results for the Aspley varieties in the 1972-73 season and 1973-74 season are given in Figures 23 and 24.

Again the general pattern is repeated in each of these figures, although the development of maturity appears to be slower in 1973-74 than in 1972-73. This could be a manifestation of the effect of the lower temperatures experienced in 1973-74.

Nuts falling from the tree appear to reach potential maturity at a later stage than those remaining in the tree.

Kernel quality. The proportion of macadamia kernels in the various maturity classes at Beerwah 1972-73 is shown in Figure 25, at Aspley S1 1972-73, 1973-74 in Figure 26, and at Aspley H2 1972-73, 1973-74 in Figure 27.

The class reject is made up of undersized nuts, nuts destroyed by *C. ombrodelta*, and those immature by the flotation technique, or because they were seen to be soft shell or hard sticky. Obviously the reason for rejection changes throughout the season. Until December it is due both to immaturity and small size. Damage by *C. ombrodelta* may be as high as 100% of fallen nuts just after the shells harden, but at this time few nuts fall, so overall the percentage lost from this cause is generally less than 5%.

Nuts harvested from the ground appear to be of lower quality than those in the tree until late in the sampling season. Nuts in these experiments had not fallen for more than seven days before being harvested, so deterioration on the ground must be rapid, or nuts deteriorate on the tree before falling. The lower quality of ground collected nuts is also reflected in the much higher percentage of these which are 2nd grade, compared with tree nuts. The lower quality of nuts falling early in the

harvesting period has been observed in Hawaii (C.G. Cavaletto 1973 pers. comm.).

In each season, and at each site the time of change from predominantly reject to predominantly mature is consistent, and the change rapid.

3. POTENTIAL CROP

So that the amount of crop lost due to the attack of *C. ombrodelta* could be assessed, it was necessary to define the total potential crop.

During the period of natural thinning, many nuts would be lost in spite of any pest control measures taken. It was not possible to distinguish between attacked nuts, which would have fallen in any case, and those which would, in the absence of attack, have remained to mature.

Therefore it seemed that the most suitable point in the season to determine the total potential crop was after the end of natural thinning.

In the last chapter, this point was determined for Aspley varieties by an analysis of the percent likelihood of fall in 1972-73 and 1973-74, as the first week in which this value was not significantly different from the lowest recorded percent likelihood of fall.

Table 37 shows the maximum potential crop at each site in each season, and its calculated date of occurrence. For Beerwah 1972-73, Aspley 1971-72 and Inala 1971-72 the dates were subjectively assessed from the figures of percent likelihood of fall.

4. CROP CHARACTERISTICS

Table 38 gives a brief summary of the macadamia crop characteristics

---

1. Miss C.G. Cavaletto, Department of Food Science and Technology, University of Hawaii, Honolulu, Hawaii.

compiled from data in this chapter and the preceding chapter.

This characterization is important in assessing the impact of *C. ombrodelta* on the crop, both as to the type of damage and the amount of damage caused. In addition it will be helpful in assessing the impact of the crop on *C. ombrodelta* populations. These interactions are investigated further in Section V.

CHAPTER 9

ALTERNATIVE HOSTS. I. GEOGRAPHIC DISTRIBUTION OF THE SPECIES AND TEMPORAL DISTRIBUTION OF FRUITING BODIES

Alternative hosts can be an important factor in the dynamics of an agricultural pest and its potential for causing damage (Strickland 1960, p.1). For example, Cunningham (1969) stated that *Nicotiana glauca* was important in maintaining populations of *Phthorimaea operculella* (Zell.) between tobacco cropping periods. Root and Tahvanainen (1969) believed that *Barbarea vulgaris* was a critical link in maintaining insect populations attacking cruciferous crops, and Schuster *et al.* (1969) have found that overwintering by *Pseudatomoscelis seriatus* (Reuter), a pest of cotton, occurred in various weed hosts.

In the present study an attempt was made to determine the effect that the alternative host plants could have, in the seasonal population dynamics of *C. ombrodelta*.

A. METHODS

Methods used in obtaining the results in this chapter were elementary. No statistically based surveys of the type described, for example by Greig-Smith (1956) were employed.

The alternative hosts present in an area 3 km square (900 ha), with the Aspley orchard at its centre, were determined by direct observation of every part of this area. The area was observed partly on foot, partly on a bicycle, and partly with a driver and observer in a car. All of the area was rechecked once, and parts more than once.

The remaining material in this chapter resulted from general observations made throughout the course of the study.

B. RESULTS

1. GEOGRAPHIC DISTRIBUTION OF ALTERNATIVE HOSTS

(i) Around the Aspley orchard

Figure 28 is a map of the 900 ha area around the orchard. The various hosts are marked - each mark being a single host plant. It is apparent that the exotic species are the most common, and that areas of housing are rich in known host plants in comparison with farming or undeveloped land. The exotic hosts are popular garden plants in this region of Australia. The hosts observed, and their numbers in the area were: *Cassia coluteoides* (383), *Delonix regia* (95), extra orchard macadamia (82), *Bauhinia variegata,* and *B. variegata* var. *albens* (65), *B. galpinii* (38), *Cupaniopsis anacardioides* (11), *Poinciana pulcherrima* (7), *Acacia podalyriifolia* (6) and *Cassia fistula* (5).

(ii) Southeast Queensland and Northern New South Wales

In general the pattern of host distribution observed around the Aspley orchard is repeated throughout the wider region. The exotic species are common at every housing settlement. *Bauhinia* spp. and *Cupaniopsis anacardioides* are planted on the verges or median strips of streets and major roads.

It should be noted that this region of Australia is densely settled (in Australian terms) and most of the land, if not used for housing, has been cleared for agriculture or stockrearing purposes. This, combined with fairly frequent fires, has reduced the diversity of the native vegetation. Thus most of the plant species observed by Francis (1951) and Coaldrake (1961) which could be hosts for *C. ombrodelta* are not common.

2. TEMPORAL DISTRIBUTION OF FRUITING BODIES

Fruiting bodies are the most important plant parts for the maintenance of populations of *C. ombrodelta*. During the study no significant infestation of leaves or branches has been observed.

Figure 29 shows the period of fruit production of the main host plants in the Southeast Queensland, Northern New South Wales region.

C. DISCUSSION

It appears that in the closely settled areas of Southeast Queensland and Northern New South Wales there are adequate plant hosts which together provide sufficient fruiting throughout the year to maintain populations of *C. ombrodelta*. Of the known hosts exotics are the most common in number of species, number of plants, and distribution.

In more sparsely settled agricultural and pastoral land there are apparently few alternative hosts, and populations of *C. ombrodelta* are likely to be patchily distributed around housing settlements, depending on the insect's ability to disperse effectively.

In virgin bushland the diversity of plant hosts has not been established.

CHAPTER 10

ALTERNATIVE HOSTS. II. DESCRIPTIONS OF THOSE SPECIES FROM WHICH REGULAR SAMPLES WERE TAKEN

As explained in Chapter 7, when samples of a plant host are taken it is generally necessary to have some estimate of the numbers of the sample unit per unit area of the region sampled. Only in this way can budgets be constructed.

In addition it is necessary to estimate the stability of the sampling unit, and if stratified sampling is to be employed, have an estimate of the distribution of units between strata.

The alternative hosts sampled regularly at periods throughout the study were:

Acacia podalyriifolia - "Acacia Cavendish-Cooke"

Figure 30 - a single tree of this species in a private garden, approximately 270 m south of the Aspley orchard. Sampled in 1972.

Bauhinia galpinii - "Aspley *Bauhinia*"

Figure 31 - a single bush of this species in a private garden, approximately 120 m south of the Aspley orchard. Sampled in 1972.

B. variegata and *B. variegata* var. *albens* - "Grasspan Road"

Figure 31 - four trees of *B. variegata* in a stand of eight such trees, growing on the footpath in Grasspan Road, Zillmere. Approximately 1,000 m to the east of the Aspley orchard. Sampled in 1972-73.

"Cowie Road"

A single tree of *B. variegata* var. *albens* in a private garden. Approximately 250 m to the south-west of the Aspley orchard. Sampled in 1972-73.

"Bald Hills"

Three trees, two of *B. variegata*, one of *B. variegata* var. *albens*, in a stand of four trees planted on a footpath in Bald Hills, approximately 2000 m to the north-west of the Aspley orchard.

For each of the *Bauhinia* species the sample unit was a single fruit (pod). For the *Acacia* (Cavendish Cooke) the unit was one pod infested by *U. robinsoni*.

A. METHODS

Sampling in these plants was designed primarily to indicate the levels of infestation achieved by *C. ombrodelta*, and the probable importance of these hosts in providing a source of infestation for the orchard macadamia.

This aspect was assigned a lower priority than the macadamia sampling, and consequently the time available was strictly limited. The estimate of sampling units available at each sampling date gave reasonable indications of the relative numbers; the absolute estimates are very crude.

Assessment of unit numbers available was made by direct counts of the whole plants, or sections of plants, in which case the estimate was multiplied to represent the entire canopy volume. Adjustment was made on each date for the number of units sampled on the previous date, and the approximate fall of pods between dates.

The sampling stick was tested once, but was found to be impractical. In one quarter of a tree 120 samples were taken with the 50 cm sampling stick (representing 0.17% of the 1/4 tree volume). Mean pods per sample was 3.008 with standard error of 3.846. The coefficient of variation of 128% is clearly unsatisfactory, and indicates a required sample size beyond the means of the present study.

No estimates of leaf numbers or branch lengths were made.

The stability of units was approximately estimated by observation of the pod fall between each sampling date.

Assessment of the distribution of units between strata, where applicable, was by observation only.

For the *Bauhinia* species an approximate estimate of the physiological state of the fruit was made by recording the proportion of the pods sampled which were dead or alive.

B. RESULTS AND DISCUSSION

The results of the estimates are shown graphically. Figures 32 and 33. In the graphs for *Bauhinia* sp. the proportion of the crop which was alive or dead is also indicated.

In *Acacia* (Cavendish Cooke) the fall of the unit was low for most of the fruiting period but increased sharply in the last two weeks.

In *Bauhinia* fall of pods was fairly constant throughout the season with a slight peak near the mid point, when pods were beginning to die.

SECTION III

CRYPTOPHLEBIA OMBRODELTA

Identification of the Species

Larvae of the species thought to be *Cryptophlebia ombrodelta* (Lower) were collected from a variety of host plants throughout the general study area. These were reared in the laboratory and, from the adults emerging, two series of male and female moths were prepared.

The characteristics of individuals from one series were compared with the descriptions of *C. ombrodelta* given by Bradley (1953). Characteristics were as described, except for a variation in the male genitalia.

In the Queensland and New South Wales specimens studied, the valvae of the male genitalia were the same shape and had three strong setae inside the margin, as described by Bradley. However, where Bradley's Figure 1 indicates an absence of setae between the spines, those in this series had numerous smaller setae in this area.

Adults of the other series were sent to CSIRO Canberra, for identification. Common (1972 pers. comm.) also found that the small setae in this area were more obvious than indicated by Bradley. However, he stated that there was no doubt that the specimens should be known as *C. ombrodelta.*

In reply to a query on this matter, Rao (1972 pers. comm.) stated that he had also noted minute setae between the larger setae on the valvae of male genitalia in *C. ombrodelta* in India. He had also observed that on the right valva of a specimen collected on tamarind, four spines were present.

CHAPTER 11

REARING *C. OMBRODELTA*

In an ecological study, it is important to maintain a continuous supply of insects for experimental purposes, and to establish rearing methods suitable for testing the effects of various environmental factors on population regulation.

Methods for ensuring mating and oviposition of adult *C. ombrodelta* had to be devised.

To obtain a continuous supply of insects, artificial or semi-artificial diets are most suitable. Their use is less demanding of labour than the use of natural foods, which must frequently be collected and replaced - with inevitable disturbance to the insect.

The use of artificial diets is desirable in many experiments, as it allows the definition of standard and repeatable conditions of insect nutrition.

However, in other experiments the use of an artificial medium is not desirable, because it produces an unnatural environment, for instance, when testing the effects of various environmental factors (e.g. temperature, parasite attack) on population fluctuation, over several successive generations of the insect.

For this purpose it would be desirable to maintain *C. ombrodelta* on healthy plant material in controlled environment conditions.

The three aspects of rearing were examined

1. Adults : mating and oviposition
2. Immatures : artificial medium
3. Immatures : host plant material in a controlled environment.

1. ADULTS : MATING AND OVIPOSITION

(i) Mating

In the early stages of this study, attempts at achieving laboratory mating of *C. ombrodelta* were mostly unsuccessful. This is believed to have been due to a combination of the effects of unsuitable mating containers, unsuitable light conditions, and a low density of adults in each container.

For most of the early matings, adults were placed in plastic cups, with a gauze cover. Air movement through such a container was minimal. Even when using a container through which air might pass, no specific provision was made for it to be placed where there was air movement. Daterman (1968) showed that an airflow of 9.2 to 24.4 cm per second through mating cages increased the laboratory mating of an Olethreutid, *Rhyacionia buoliana* (Schiff.) from zero to a maximum of 36%. Ventilation of caged adult *Laspeyresia pomonella* (L.) (Olethreutidae) appeared to increase their egg production (Batiste and Olson 1973).

Light may also be important. Daterman (*loc. cit.*) also stated that adults of *R. buoliana* copulated only after light intensity was reduced below 10.8 lumen per square metre. Caltagirone[1] (1973 pers. comm.) found that *Paramyelois transitella* (Walker) (Phycitidae) would mate only under entirely natural lighting.

The techniques were gradually improved, until an adequate mating percentage could be achieved when required.

Two types of cages were used (Figure 34); the most common being a gauze covered aluminium frame cage 22 x 18 x 21 cm, and the other a perspex cage of 42 cm cubed with two opposing sides of gauze.

These cages were placed in natural daylight and wherever possible,

---

1. Dr L.E. Caltagirone, Div. of Biological Control, University of California, Albany, California.

where a breeze could ventilate the cage.

Unless adults were required for specific experiments, the following procedure was adopted.

Newly emerged adults of both sexes were collected from rearing containers every two days and placed together in the mating cages for two days. The females were then removed for oviposition. Males were left until they died, so that there were usually more males than females in the mating cage.

Adults were supplied with a five percent honey in water solution on a cellulose sponge (Wettex ^{R}).

(ii) Oviposition

The most suitable oviposition chamber was found to be a type of plastic cup (ADVANCE CONTAINERS PTY. LTD., Model C20) (Figure 34). Unless a specific type is referred to, "oviposition cup" will refer to the C20.

The C20 has three circular depressions in the bottom, vertical grooves 12.5 cm apart around its sides, and a pronounced lip. Ovipositing *C. ombrodelta* showed a marked preference for such irregularities (Figure 34). In other, smoother cups, eggs tended to be crowded at the junction of sides and bottom, with subsequent high egg mortality.

Up to ten females were placed in one cup, and left for a maximum of 48 hours, after which they were transferred to a fresh cup. At all times they were supplied with a five percent honey in water solution on cellulose sponge.

The cup could be cut up if specific number of eggs were required, or stored until eggs hatched, when 1st instar larvae were collected.

2. IMMATURES : ARTIFICIAL MEDIUM

(i) The Medium

The medium is an adaptation of that of Shorey and Hale (1965) for rearing Noctuid species. It is based on dried beans and yeast. Slight adaptations were made by Swaine[1] (1971 pers. comm.). The adapted recipe is shown in Appendix A.

In the early stages, when difficulty was experienced in obtaining oviposition from females reared on this medium, it was thought that it might have been lacking in a basic nutrient. Dr K. Harley[2] suggested the addition of macadamia material, and arranged the freeze drying of a quantity of macadamia husks.

Various mixtures of the diet, with from one to ten percent by weight of freeze dried macadamia husks replacing bean material were prepared. At greater than five percent macadamia material the diet became difficult to mix and later released excess moisture, drowning many larvae. Mould also developed much more frequently in medium with macadamia, than on the normal diet.

As no improvement in oviposition was observed by adults reared on the diet containing macadamia, its use was discontinued.

The normal diet could be stored at approximately 5°C for periods up to five months with no apparent reduction in its suitability or larval acceptance.

(ii) The Techniques

During the study, two main methods of rearing *C. ombrodelta* on artificial medium were devised.

---

1. Mr G. Swaine, Dept. Primary Industries, Brisbane, Queensland.
2. Dr K. Harley, CSIRO, Long Pocket Laboratories, Brisbane, Queensland.

a Wax blocks

This technique was most suitable when larvae were to be reared individually, e.g. for parasite records, or development time calculations.

Newly prepared medium was poured into flat trays to a depth of 1 to 2 cm. When cool, the medium was cut into blocks approximately 2.0 x 1.5 x 1.5 cm.

These blocks were impaled on a rod approximately 3 mm in diameter - e.g. a fine paint brush handle - and dipped into molten beeswax. When the rod was withdrawn the block of medium was covered by a layer of beeswax except for a hole in one end (Figure 35). Larvae, placed in or near the hole accepted the medium readily, and usually pupated within the block.

The temperature of the beeswax had to be close to its melting point, or cracks developed in the coating after cooling. Paraffin wax could also be used, but was less suitable, as it was much more fragile. If the wax seal were broken the block dehydrated rapidly resulting in shrinking and hardening so that larvae died of starvation and pupae were crushed.

Only one larva was placed in each block. Blocks were then placed singly in waxed paper cups (Figure 35).

The cups were HYGENIC CONTAINERS PTY.LTD., Model S51S. Each cup had a mean diameter of 7.9 cm, was 5 cm deep and could be sealed with a waxed cardboard lid.

These cups were found to be the most convenient container; they were inexpensive, disposable, and readily stacked - maximizing space usage. Their large size relative to that of the block was also advantageous as most of the adults emerged into the cup. In smaller cups a greater number of larvae chewed exit holes in the cup before pupation.

Their one disadvantage was that inspections for emergence entailed lifting and replacing the lid of each cup.

b Trays

The tray technique was suitable for rearing large numbers of insects on artificial diet with minimum effort. Plastic trays (ADVANCE CONTAINERS PTY.LTD., model T30), 18 x 12 x 6 cm proved suitable.

Newly made medium was poured into trays to a depth of 1 to 2 cm (approximately 300 gm). When it had cooled, beeswax at a temperature just greater than its melting point, was poured over the surface to form a layer approximately 1 mm thick. Hundreds of pin holes were then punched in the wax.

Oviposition cups were placed on the wax surface. Larvae on hatching, mostly found their way into the medium, although a small proportion moved off the tray and were lost.

Pupation occurred in the medium. Trays were placed in perspex cages (31 cm cubed) from which adults were collected manually (Figure 35).

The larval mortalities, production of adults, and the labour requirements, were compared for each method (Table 39). In this comparison, the waxed blocks were treated as described. Trays were suspended over a water bath so that the number of larvae leaving each tray could be detected.

Disease was apparently absent throughout the three year study period, although no special precautions were taken. Moulds, which attacked the medium, although quite common when larvae were reared in sealed plastic containers, were virtually absent after the wax block and tray methods were introduced. Mites became common in the blocks in February 1972, but did not cause difficulty in rearing and were easily controlled.

Only one colony breakdown occurred. In February 1973, muscid flies invaded uncaged trays in a constant temperature room. No *C. ombrodelta* . emerged from these trays.

Hutt and White (1972) found that *Laspeyresia pomonella* (L.) larvae had a lower survival rate in polystyrene containers than in glass

containers. Sullivan *et al.* (1970) showed that Masonite [R] could also have an adverse physiological effect on *L. pomonella*; they recommended that the materials of containers used to hold insects should be tested.

Adult emergence of *C. ombrodelta* in wax block and tray methods was adequate for this study and this effect was not investigated.

The tray rearing technique described above is similar in principle to the codling moth mass rearing techniques described by Howell (1967, 1971, 1972) and Howell and Clift (1972). It is probable that the method could be adapted to the requirements of a mass rearing programme.

3. IMMATURES : HOST PLANT MATERIAL IN A CONTROLLED ENVIRONMENT

(i) Excised Host Material

In some experiments, macadamia nuts or nut husks, were used as larval diet in the laboratory. In most cases, these were placed singly in S51S waxed paper cups. Dehydration of the material necessitated its replacement twice weekly. The disturbance to larvae caused by this frequent nut replacement was undesirable, and a method of maintaining living macadamia in the laboratory was sought.

Moore and Clark (1968) described a technique by which they were able to maintain turgidity in excised coniferous foliage for an average of five weeks.

In accordance with their procedure, nut bearing branches up to a metre long, were cut from macadamia trees, sterilized and placed in sterile 500 ml bottles of sterile distilled water. Leaves on these branches maintained turgor and were apparently healthy for at least three weeks - some for eight weeks.

However, nuts died within three weeks - too short a period for the completion of even one generation of *C. ombrodelta*.

The method was not tested for other plant hosts.

(ii) Potted Host Plants

The use of macadamia trees was not practical. They do not bear consistently for at least seven years after planting and transplantation of bearing trees is costly and unlikely to be successful. In either case, bearing trees are too large for most laboratory buildings.

Amongst the other host plants, the most suitable for potting trials seemed to be *B. galpinii*, *C. coluteoides* and cultivated bean species.

a *Bauhinia galpinii*

This is a spreading bush, growing up to four metres high with a spread of up to seven metres. However, much smaller plants carry useful numbers of pods. The fruiting period is normally December to July.

In 1971, two plants were transplanted to 70 litre plastic buckets of soil. They were fertilized and watered regularly.

By 1973, each plant had flowered twice, without setting pods. The plants were discarded.

b *Cassia coluteoides*

This bush grows to approximately two metres in height with a spread of one and a half metres. Fruits are present from February to August.

Four *C. coluteoides* were transplanted to 70 litre buckets of soil in 1971. These were also regularly watered and fertilized.

After two flowerings without pod set, the plants were discarded.

c Beans

Phaseolus spp. have been recorded as hosts of *C. ombrodelta* (Table 3). Because of their small size, relatively easy culture, and

rapid growth, they appeared likely to be suitable as laboratory host plants for this insect.

The variety tested is known as "Brown Beauty", of the species *P. vulgaris*.

Vicia faba, the common broad bean, was also tested. This species has similar growth qualities to *Phaseolus*. Its pod, being more fibrous, was thought likely to be more suitable for *C. ombrodelta*.

Bean culture

The Manager of the David North Plant Research Centre in Brisbane, offered the use of phytotron facilities.

Plants were grown in vermiculite in 15 cm diameter pots, four plants per plot. Each day they were supplied with a nutrient solution. Until fruit were set all were grown in a day temperature of 20°C and night temperature of 15°C. One third of the plants had a 16 hour light: 8 hour dark cycle, one third a 12:12 cycle, and the remainder a 8:16 cycle.

Plant growth and fruiting under the longest daylength was excellent. In the second group growth and fruiting were adequate. However, the short daylength group grew very slowly and did not flower.

Tests with *C. ombrodelta*

The following tests were carried out in the phytotron from the 18th October to 11th December 1972. Temperature fluctuated between 20°C (day) and 15°C (night) until 16th November, after which it was held at a constant 25°C; the daylength was 16 hours light with 8 hours darkness throughout the period.

Oviposition. Potted bean plants were placed singly or in groups in gauze cages, into which mated *C. ombrodelta* females were placed.

Adults oviposited satisfactorily on both species of bean. Eggs were laid on stems and leaves more frequently than on the fruit. As with all cage experiments involving *C. ombrodelta*, some eggs were laid on the cage material.

Egg hatching appeared normal.

Larval establishment. Larvae only attacked fruit. It was not possible to count eggs on these plants without seriously damaging them. To calculate establishment, larvae hatching in oviposition cups were transferred to the beans with a paintbrush.

Establishment was measured in each species for normal pods, and pods which had had small holes pierced in them. This piercing had to be carried out at least two days before each trial, so that sap exudation which followed this damage would cease.

Successful establishments were recorded as active holes (noted by frass ejection) at least 24 hours after larval introduction. The validity of this method was established by dissecting some fruit and locating the larvae.

The recorded establishment percentages were:

	P. vulgaris	*V. faba*
Pierced	35% (31)	28% (40)
Normal	28% (21)	39% (59)

The numbers in parentheses are the initial numbers of larvae introduced.

There appears to be little difference in establishment between varieties, or between pierced and unpierced pods.

Mortality of established immatures. Because the time available was

limited, and some beans did not begin fruiting until near the end of the trial period, only three adults emerged. Thus the end of the established immature stage was arbitrarily set as the final larval instar.

Mortality of larvae from establishment to final instar, prepupae or pupae was 52% for 27 established larvae in *P. vulgaris* and 53% for 34 larvae in *V. faba*.

Most of the mortality was in the first two instars, and appeared to be due to the sap exudate which followed larval feeding.

All 11 prepupae or pupae found during the trials were in pods. Two of the five pupae old enough to have emerged were crushed because of pod shrinkage. Thus the mortality of pupae which could have emerged was 40%.

Using these approximate mortalities, and the establishment percent, tentative budgets for each bean species may be constructed:

	P. vulgaris	*V. faba*
Larvae introduced	100	100
Established larvae	32	35
Pupae formed	15	17
Adults emerging	9	10

Adult fertility. Of the three adults which emerged, two were females. These were taken from the phytotron and placed in a mating cage with an excess of males. One mated and laid viable eggs - the other did not mate.

To test mating under the conditions prevailing in the phytotron 17 females and 22 males, reared on artificial medium were placed in a large gauze cage in the phytotron. Three pots of *P. vulgaris* were also placed in the cage. After ten days the plants were examined for eggs or larvae - none were found. Dissection of the 11 females still living

established that none had mated. It is probable that the lighting conditions were not suitable as dusk was of only a few minutes duration.

Plant longevity. Plants of each species stayed alive long enough after pod-set to maintain one generation of *C. ombrodelta*. Attached pods died but apparently remained nutritionally suitable for the length of the insect's larval stages.

If the problem of mating could be overcome, it is probable that successive generations of *C. ombrodelta* may be followed on these hosts. New plants would have to be supplied as each generation emerged.

During the trial, two pots of *V. faba* with pods infested with *C. ombrodelta* were caged and adult *Bracon* sp. parasites (see Section IV) (four females, one male) were introduced. After ten days the pods were dissected. No evidence of parasite activity was found. Obviously a much larger and more detailed trial would be needed to show whether this plant is suitable for use in the study of host-parasite interactions.

CHAPTER 12

IDENTIFICATION OF DEVELOPMENT STAGES OF *C. OMBRODELTA*

In a study of population processes it is important to be able to establish the age of individuals in the population at various times and thus the population age structure.

Parameters affected by population age structure include the potential for increase and the susceptibility to various controlling factors; e.g. many parasites preferentially attack individual insects of a certain age.

C. ombrodelta is a holometabolous insect and has the readily identifiable stages of egg, larva, pupa and adult. Each of these stages may be further divided into shorter age groups.

For instance, *C. ombrodelta* eggs change colour as they age and in the last two days, the larval structure, especially the head capsule, becomes visible through the chorion. *C. ombrodelta* pupae change from light to dark brown with age. Pupae of some species may be aged by dissection (Southwood 1966, p.311).

General techniques for determining adult age include dissection to determine the state of the fat body, and classifying the "wear and tear" of external structures (Southwood 1966, p.313, 315).

In this study little attention was given to dividing these stages into shorter age groupings. The egg and pupae of *C. ombrodelta* are relatively stable and mortalities may be considered to be constant throughout each stage. Female adults were taken in such low numbers during the study that division into shorter age groups was not worthwhile. It was not important to assign specific age groups to adult males, as they were sampled by pheromone, or virgin female traps, and were thus apparently

all sexually active.

The larva is the longest stage in the *C. ombrodelta* life cycle, and its mortality factors vary with age (Chapter 20). It was therefore desirable to divide the total larval period into shorter periods, each of which was subject to similar mortalities.

In past population studies of lepidopterous pests, divisions of the larval period have varied. For example, Morris and Miller (1954) divided the larval period of *Choristoneura fumiferana* (Clem.) into Instar I, Hibernacula, Instar II, and Instars III and IV. LeRoux and Reimer (1959) divided the larval instars of *Spilonota ocellana* (D.& S.) and *Coleophora serratella* (L.), into "summer larvae" - instars I to IV, "winter larvae" - instar V, and "spring larvae" - instars VI and VII. Harcourt (1961a) used only two age groups to cover the four larval instars of *Plutella maculipennis* (Curt.) - "Period 1" was from hatching to the middle of instar IV, "Period 2" from the middle of instar IV to cocoon formation.

In each case the divisions chosen were such that behaviour and mortality factors within each division were broadly similar.

The larval instars of *C. ombrodelta* may be similarly grouped. However, until its life cycle, behaviour and mortality factors were well known, it could not be predicted what grouping of instars would be most suitable. The type of grouping also depends on the purpose for which the study is being undertaken.

The present study attempted to establish a method for the identification of each instar.

A. METHODS

Because the hard parts of the insect body do not increase greatly in size within each instar, they are suitable for instar identification.

The width of the head capsule has been most frequently used; e.g. the work of Gaines and Campbell (1935) with *Heliothis obsoleta* (Fab.); Peterson and Haeussler (1928), *Laspeyresia molesta* Busck; Greene (1970), *Urbanus proteus* (L.); Smilowitz and Smith (1970), *Trichoplusia ni* Hübner; Rings (1971), *Abagrotis alternata* (Grote); Cheng (1973), *Euxoa messoria* (Harris).

However, Makiya (1969) found that the use of the siphon length of *Culex pipiens* S.1.L. was as efficient as head widths to separate its larval stages, and Lam and Webster (1972) found that the shape and size of mandibles were good characters for differentiating the larval instars of *Tipula paludosa* Meig., a Tipulid.

Some workers have found other morphological features to assist the identification of instars. In sawfly larvae, Taylor (1931) used head capsule measurement primarily but made the final distinction between instars by body size and head colour. The number of segments in the antennae was used in conjunction with head capsule measurements to identify instars in a Gryllid species (Gabbutt 1959). Allen and Grimble (1970) were able to distinguish the five larval instars of *Heterocampa guttivitta* (Walker) by a combination of head capsule size, and the colour and presence or absence of dorsal protrubences. Anderson and Mignot (1970) used a combination of head capsule widths, the crochet patterns on the planta of the prolegs, the number of lateral ocelli, and the larval length to distinguish between larvae of *Galleria mellonella* L.

Kishi (1971) determined the instars of *Pissodes nitdus* Roelofs by counting the number of cast head capsules in the galleries he sampled.

The expected size of each instar's head capsule may be determined by following larval development in the laboratory. This size may then

be used to determine the instar of field sampled insects.

Alternatively, the insect field population may be sampled over a period long enough to ensure that all stages are represented. The head capsule widths of all stages are measured and these measurements are then presented graphically in a frequency distribution. In most cases they will fall into a number of reasonably well defined groups, each representing an instar. The mean head capsule size of each instar may then be determined from the distribution.

The success of this method relies on the work of Dyar (1890) who showed that the widths of lepidopterous larval head capsules increase from instar to instar in an approximately regular geometric progression. Therefore, any marked discrepency in the ratio of increase between instars in the sample frequency distributions indicates that an instar may have been missed (Gaines and Campbell 1935).

The head capsule method has also been applied to a variety of insects other than Lepidoptera - e.g. for Coleoptera, Andrewartha (1933), Finnegan (1958), and Stevenson (1967), for Diptera by Lam and Webster (1972), and Makiya (1969), for Hymenoptera by Taylor (1931), for Hemiptera by Bliss and Beard (1954), and for Orthoptera by Gabbutt (1959).

Ghent (1956) found that the increase of head capsule width of two species of sawflies could best be described by a model of linear increase.

Richards (1949) showed that in five insects he studied, the linear measurements of sclerotized parts (including head capsule widths), increased between instars in a linear fashion (excluding the 1st instar), if account were taken of the duration of each instar. This relationship was not considered to be helpful in determining the age of field collected *C. ombrodelta* larvae. It provides a useful basis for the test of assumptions on the growth of immature stages and is examined in the next chapter.

Variations in the instar number of a species complicates the use of Dyar's method (Gaines and Campbell 1935). These authors presented data from Satterthwait (1933) on *Agrotis ypsilon* Rott. which had a variable number of instars. The frequency groups were not clearly defined. Namba (1957b) found that even though *Cryptophlebia illepida* (Butler) had a constant number of instars under laboratory rearing conditions, the frequency distribution of head capsule sizes of field collected larvae showed no definite peaks.

A satisfactory interpretation of a confused, continuous distribution of head capsule widths was made by Metcalfe (1932) for Anobiidae larvae. Her interpretation was based on a varying number of larval instars for each sex. In the sample observed the sex ratio was not unity.

C. ombrodelta larvae have either five or six instars (Ironside 1970 unpublished report). This suggested that it would be difficult to distinguish the instars on head capsule width alone. However, additional larval characters that would assist in differentiating the instars were not discovered. The difficulty of finding such a character was increased because most laboratory reared larvae had only five instars. Any such character must easily be seen because of the need to handle a large number of larvae during the sampling period. In addition, its detection should not require larvae to be killed as they are reared to maturity to detect sex ratio, and parasite attack.

It was observed that the final instars of larvae having both five and six instars had flatter and browner head capsules than those of earlier instars. Sometimes however, a larva of head capsule width corresponding to an intermediate instar exhibited this feature.

Kishi's (1971) method of counting cast head capsules is not applicable to *C. ombrodelta* larvae as they nearly always push the cast head capsule out of the feeding gallery and it falls to the ground. Less frequently the cast head capsule is chewed and incorporated into the webbing and frass plug in the hole leading to the gallery.

Thus it was decided that an analysis of a head capsule frequency graph was the most expedient solution to the problem for the present study.

This involved (1) a laboratory study of the insect to confirm the instar numbers, determine mean head capsule size of each instar, and the ratio of increase between instars and (2) a study of head capsule frequency distributions of field collected larvae so that individual sampled larvae could be assigned to a particular instar.

1. LABORATORY STUDY OF INSECT GROWTH

Upon hatching in an oviposition cup, each larva was transferred to either a nut husk (41 larvae) or a medium wax block (168 larvae). These were placed in waxed paper S51S cups.

Because the duration of each instar was also being determined (Chapter 13) the larvae had to be extracted from the medium nearly every day and sometimes twice a day to check the exact time of moulting. This largely explains the high mortality during the experiments (only 50 insects reached the prepupal stage), and also why only a relatively small number of larvae have been studied. Taylor's (1930) description of the difficulties involved in measuring the development of concealed larvae show that he experienced similar problems.

Nut husks were replaced every three days, and blocks when the wax was so damaged by inspection procedures that dehydration of the medium was rapid.

Cast head capsules were measured, except in the final instar in which the head capsule is not shed until the cocoon has been built; it is then split longitudinally. As development time was also being measured, it was not desirable to anaesthetize or kill the larvae to measure the head capsule. The final instar measurement was taken on the prepupae by opening the mouth of the cocoon; some were missed.

Head capsules were measured to the nearest half division of an ocular graticule, in several different binocular microscopes. The magnification used ranged from X24.5 to X42.0 depending on the microscope, and the graticule was calibrated against a stage micrometer for each microscope.

2. INTERPRETATION OF FIELD DATA

The data for head capsule width frequency distributions were obtained during field sampling for population purposes.

Infested fruit were opened, live larvae were anaesthetized with carbon dioxide, and the head capsules measured. Larvae collected at Beerwah were all killed before being measured. Not all first instar larvae were measured as they were easily damaged, and easily recognized.

Measurements were to the nearest half division of an ocular graticule as in (1).

It is noted that in the laboratory investigations, head capsules, apart from the final instar, were measured after they had been cast. Field measurements were all made of the head capsule on the larvae. To compare the methods, the head capsules of ten 4th instar larvae were measured before and after shedding. Mean width before shedding was 1.188 mm, after shedding 1.181 mm. A paired "t" test did not show that the measurements were significantly different (P=0.05).

The head capsule widths of field collected larvae were arranged

in frequency distributions of numbers against size. Each size increment was 0.04 mm.

These distributions were continuous and polymodal, with the peaks of the smaller sizes being more pronounced than those of the larger sizes.

To determine the number of instar groups involved in each distribution a method described by Harding (1949) seemed to be the most appropriate. Gabbutt (1959) used this method in an analysis of the head capsule widths of an Orthopteran insect. The major assumption underlying its use is that the head capsule width of each instar is normally distributed.

The data for 1971-72 were analysed manually by Harding's method.

When the total frequency distribution involves five or more instar distributions, analysis is tedious and time consuming, and subject to arithmetic errors. Although when one is familiar with the method, an analysis can be done in about five hours, considerably more time than this was spent on the 1971-72 analysis.

Since the frequency distributions for the 1972-73 season were larger, and more complicated, their analysis would have involved an enormous amount of manual manipulation. A computer programme was devised to handle the arithmetic calculations. A copy of this is presented in Appendix B, with an example of its use. A flowchart of its operation is shown in Figure 36.

By using the computer programmes an hypothesis concerning component distributions could be tested within 45 minutes. The probability of arithmetic errors was minimized.

B. RESULTS AND DISCUSSION

1. LABORATORY STUDY OF INSTAR GROWTH

Since the head capsule measurements of larvae reared on nut husks

and waxed blocks appeared similar, and total measurements were relatively few, the results of the two rearing methods were pooled.

Table 40 shows the frequency distribution of head capsule widths of laboratory reared larvae. Also shown are the mean head capsule width and standard deviation for each instar.

Only those individuals reaching at least the prepupal stage have been included, and those having five instars are shown separately from those having six. These are now referred to as the "5 instar series" and the "6 instar series". Of the 50 larvae completing their larval stages, only 6, or 12% had six instars.

Because of the low numbers of measurements available the results must be treated with some caution. The data have been interpreted with this proviso in mind.

Overlap in each series. There is overlap between the measurements of two successive instars in each series. The five instar series overlaps between the 3rd and 4th instars and the six instar series overlaps between the 4th and 5th. With more data, especially from larvae reared under varied conditions, the spread of each instar distribution would extend, aggravating the overlap.

Ratio of increase between instars. From the mean head capsule width of each instar shown in Table 40, the ratio of increase of head capsule width with each moult, and the mean ratio of increase over all moults was calculated for each series of instars. Using the mean ratio of increase, and starting from the observed first instar, the expected instar sizes were calculated. The deviation of the expected from the observed mean size was also calculated as a percentage of the observed mean. This tests the hypothesis of geometric increase - Dyar's "rule".

Similarly the hypothesis of linear increase between instars was

examined. A linear regression -

INSTAR = a (head capsule size) + b

where a and b are constants, was calculated by the method of least squares (Steel and Torrie 1960, p.163) for the observed head capsule widths. The expected mean sizes for each instar lie on this line. Their deviation from the observed instar means are also calculated as a percentage of the observed mean. These calculations are shown in Table 41.

It is clear that the hypothesis of geometric increase is more satisfactory than one of linear increase for *C. ombrodelta*.

It would appear that the increase from 1st instar to the 3rd instar inclusive is the same for both series of larvae. Some unknown factor apparently causes a decrease in growth ratio between the 3rd and the 4th instar of the 6 instar series.

To examine this further, "t" tests were used to compare the means for each instar between series - these means are shown at the foot of Table 40.

At a 5% level of significance the "t" tests did not show any difference for the 1st, 2nd, and 3rd instars between series. The 4ths of each series, and the 5ths of each series were different.

Thus the data for the head capsule sizes of larvae in the first three instars were pooled between series.

A new mean growth ratio was calculated for the 5 instar series. This was also used for the first three instars of the 6 instar series, whilst the mean ratio of increase between instars 3 to 6 was used for these remaining instars in this series. For each series, expected instar mean head capsule widths and the percentage deviation from the observed, were calculated. These calculations are shown in Table 42.

For the 5 instar series the sum of the absolute percentage deviation was reduced from 7.5% to 6.7%, for the 6 instar series from 21.9% to 13.4%.

The largest actual deviation between expected and observed in either series is 0.079 mm. Taylor (1931) pointed out that Dyar (1890) was not concerned with discrepancies between observed and calculated instar mean head widths as great as 0.2 mm; nor were Gaines and Campbell (1935) concerned with discrepancies of this order.

The laboratory work described was carried out only to aid in the interpretation of field data. It appeared reasonable to accept the interpretation that some larvae increase their head width size each moult by a factor of approximately 1.4, and these have five instars. Others, for an unknown reason, assume a lower growth ratio after the 3rd instar and have six instars.

2. INTERPRETATION OF FIELD DATA

The frequency distributions for field data are shown:

Figure 37A - 1971-72, all sites, all hosts, all dates combined

Figure 38 - 1972-73, data combined over dates.

In each distribution there are five major peaks, none of which is discrete. The general shape of the distribution suggested that there might be smaller distributions partly concealed near the major peaks.

Because considerable time and money had been expended on devising the computer programme it was decided to combine some of the distributions before attempting their analyses.

The 1971-72 data were not analysed by computer, and not combined with any other data.

The two distributions for alternative hosts data in 1972-73 (Figure 38A and B) were basically similar and were combined (Figure 39A). Similarly all the 1972-73 macadamia data (Figure 38C, D and E) were combined (Figure 39B). The combined alternative host distribution appeared to be too different from the combined macadamia distribution for these

to be pooled. Each was analysed separately.

(i) 1971-72 Data

Figure 37 shows the observed frequency distribution, the calculated frequency distribution and the component normal distributions.

The mean head capsule width, standard deviation, and population of each of the component distributions are shown in Table 43.

This interpretation provided the lowest χ^2 of two manual analyses of the data.

However, the total χ^2 of 57.56 with 30 degrees of freedom indicates a poor correspondence of expected to observed distributions.

The interpretation is untenable on biological grounds. A minimum of eight distributions would be required to account for a mixture of 5 instar series and 6 instar series individuals.

The frequency distribution for this year is broadly similar in size and shape to the macadamia data of 1972-73, and the interpretation made for this latter data will be used for 1971-72 head capsule measurements.

(ii) 1972-73 Data

a Macadamia

A reasonable solution was achieved after ten computer runs.

Figure 40 shows the observed frequency distribution, the calculated frequency distribution, and the component normal distributions.

The parameters - mean, standard deviation, and number of individuals, for each of the computed distributions are shown in Table 44.

Table 45 shows the detailed χ^2 comparison of the calculated distribution with the observed distribution. The total χ^2 of 69.94 with 30 degrees of freedom is not satisfactory mathematically. However,

this was the best χ^2 obtained in all runs; in the last three, it was very difficult to improve the fit at one point without worsening it at another point, because of the overlap of the component distributions.

Attempts to fit only five instar groups to the data were not successful.

Much of χ^2 total is contributed by the size classes of low frequency between the major groups, and a general disagreement in the region of the fourth major peak.

It is possible that some of the χ^2 total could be accounted for by irregularities in the observed data. In Figure 40A for example, the frequencies do not follow one another in a gradation of size. Although there are trends, adjacent frequency classes are often very different.

It would be difficult, if not impossible, to mimic this irregularity by using a combination of normal distributions.

Further grouping of the data into classes of 0.05, 0.06 mm etc. increments may overcome some of the difficulty. However, any further decrease in the number of classes would reduce the number of points of determination for each component distribution. This would not be acceptable in say, the first and second distribution which already only have four and six points of determination respectively.

The nine distributions shown in Table 44 are divided into the 5 instar series and the 6 instar series as follows:

No. 1 - 1st instar of both series

No. 2 - 2nd instar of both series

No. 3 and No. 4 - 3rd instar of both series

No. 5 - 4th instar of 6 instar series (designated 4A)

No. 6 - 4th instar of 5 instar series

No. 7 - 5th instar of 6 instar series (designated 5A)

No. 8 - final instar of 5 instar series

No. 9 - final instar of 6 instar series.

The inclusion of two distributions for the 3rd instar markedly improved the fit of the calculated distribution to the observed. Inspection of the Aspley macadamia distributions and the Beerwah distribution (Figure 38) indicate that the 3rd instars from each orchard did have a slightly different mean.

A weighted average of the mean head capsule width of distributions 3 and 4 was used as the estimate of 3rd instar mean head capsule size.

Evidence was not strong enough to introduce other combinations which may have further improved the fit, but at the cost of greatly increased complexity.

It is quite possible too, that a reason for poor fit was that under the variety of field conditions experienced, some larvae may have had more than six instars. For example, Satterthwait (1933) reported that *Agrotis ypsilon* was believed to have six larval instars. When he reared this species in the laboratory he found that of those reaching the adult stage 57.4% had six instars, 38.9% had seven and 3.7% had eight. *Euxoa messoria*, generally has seven instars, but a few pass through only six and occasionally there are eight (Cheng 1973).

Since the laboratory data and Ironside's (1970 unpublished report) work indicated only five or six instars for *C. ombrodelta*, and extensive studies would be required to establish the extent to which this varied in the field, no attempt to account for any such extraneous distributions has been made in the interpretation.

To test the validity of the above interpretation, the mean ratio of increase and the expected mean head capsule widths for each instar series were calculated (Table 46). The deviations of observed from expected are not inconsistent with the interpretation.

So that the calculated distributions may be used for interpreting field data it is necessary to deal with the overlap between them.

Between each instar distribution a point is discovered which has

an equal probability of belonging to either. Any particular head capsule width not corresponding to these points has a greater probability of belonging to one distribution than any other (see Appendix B for an example).

Overlap between the 4th instars of each series is too great for meaningful interpretation, as is the overlap between final instars in each series.

The divisions made for interpreting field data were:

1st instars

2nd instars

3rd instars

both 4th instars

5A

finals

It will be shown in the next chapter, that both 4th instars are the same age, so failure to differentiate between them is probably of little consequence. The two final instars differ in age, and this may be an important failure of the method.

Table 47 shows the dividing points between groups and the percentage of the data from the respective distributions which is included between these points.

Before final use, the dividing points in mm are converted to ocular units.

b Alternative hosts

After six computer runs a reasonable interpretation of the data was obtained. Figure 41 shows the observed frequency distribution, the calculated frequency distribution, and the component normal distributions used in the calculations. Table 48 shows the parameters of the component distributions.

Similar difficulties as described for the analysis of the macadamia data were encountered, and the χ^2 of 63.12 with 23 degrees of freedom is again not mathematically satisfactory. However, it was the lowest χ^2 obtained, including that for a solution attempted using only five instars.

It is noted that two 3rd instar distributions have again been used. These are combined as a weighted mean for future calculations.

The solution appears reasonable biologically.

Table 49 shows the component distribution mean head capsule sizes for each series of instars, together with the ratios of increase and the expected mean head capsule size. Deviations of expected from observed were greater than in macadamia data but were not extreme.

There appears to be an unusually low ratio of increase between the 4th and 5th instar in both series.

It is interesting to note that the mean ratios of increase of *C. ombrodelta* appear to be lower on alternative hosts than on macadamia.

The overlap is less pronounced between the two final instars than in the macadamia data, although it is still considerable. The distribution representing the 5th instar of 6 (i.e. 5A) is considerably overlapped with the 4th of 5 instars. Because of this, the division into age classes is rather difficult. The divisions made are shown in Table 50, together with the division points in mm between the groups and the percentage of the data contained between these points. The method for obtaining these values has been described previously.

The main difficulty with the grouping of the 5th instar of 6 with the 4th instar is that the two instars are of different ages. It has been considered a smaller error to include them as one group than to try to separate the instars from the considerable overlap. A study of the mortality factors in these age groups will determine whether further division is necessary.

In summary: Figure 42 shows the interpretation of the macadamia field date and alternative host data compared with the laboratory data interpretation. Each of the field interpretations, made with the aid of the computer analysis, appear to be in agreement with the hypothesis of geometric increase proposed for laboratory data.

Further study of the pest's life cycle and age specific mortality factors may show that a division of individuals to instars is not necessary, and groupings of instars will render the present interpretation adequate. On the other hand, additional identifying characters may be found which will allow for the more complete division of the larval period.

CHAPTER 13

RATE OF DEVELOPMENT OF IMMATURE *C. OMBRODELTA*

Various extrinsic factors affect the rate at which insects develop. Variations in light (Imms 1964, p.245), nutritional or host plant factors (van Emden and Way 1973, p.196) and temperature. Temperature is of over-riding importance as the rate of an insect's physiological processes vary directly with temperature (Clark *et al.* 1967, p.7) except in the extremes of the range to which it is normally accustomed (Bodenheimer and Swirski 1957, p.119). The amount of water vapour in the atmosphere, usually expressed as the percent relative humidity, can modify the effect of a particular temperature on an organism (e.g. Bengston 1969, Hughes *et al.* 1972).

The first part of this chapter describes the work undertaken to determine the rate of development of the different immature stages of *C. ombrodelta*. These estimates were required to facilitate the interpretation of field population change, and for use in the construction of pest-crop simulation models.

The second part describes some variations observed in the expected development rates.

I. DEVELOPMENT RATE

A. METHODS

Watt (1968, p.274) believed that despite the large amount of work done on the effects that variations of temperature and humidity have on organisms, no completely satisfactory model of the process had yet been devised.

However, some authors have devised models which in practice

adequately described the effect of temperature on the organism they were studying, e.g. Davidson (1944) found the logistic curve of rate of development against temperature useful. Hughes (1963) and Greenham (1972) used the central portion of the logistic curve as an approximation to a straight line. Bodenheimer and Swirski (1957) and Helgesen and Haynes (1972) used the inverse of the logistic curve - i.e. development time against temperature, which is a hyperbola over its central region.

Each of the methods quoted measured development at a number of constant temperatures, although Greenham (1972) also assessed the effect of fluctuations in temperature. Some authors have pointed out that the development time (or its inverse - development rate) calculated under constant temperature, will be at variance to that calculated for temperatures fluctuating about a mean of that constant temperature (Odum 1959, p.105, Messenger 1964).

However, Watt (1968, p.284) stated that the effect of fluctuations can be understood by summing the effects at each temperature experienced, so that development times calculated at constant temperatures are adequate for practical purposes. Greenham (1972) reached a similar conclusion. Watt (*loc. cit.*) noted however, that a short exposure to a temperature extreme may be beneficial, although that temperature would be lethal under constant conditions.

The way in which humidity variations affected development at each of the temperatures studied has generally not been assessed. Humidity was not discussed by Bodenheimer and Swirski (1957), or Hughes (1963), whilst Helgesen and Haynes (1972) maintained a humidity between 60-80% R.H. Greenham (1972) was working with larvae of *Musca vetustissima* Walk. - the Australian Bushfly - so the humidity was conditioned by the cattle dung in which it was reared.

The method of Hughes (1963) and Greenham (1972) appeared to be most suitable to determine the rates of development in response to temp-

erature variation of the life stages of *C. ombrodelta*.

This method requires the assessment of development rate at a number of non-extreme constant temperatures. These rates, plotted against temperature approximate to a straight line.

A linear regression fitted to these points may be extrapolated to the temperature axis. The point at which it crosses the axis is the Threshold of Development (k), the assumption being that development ceases at this temperature. The difference between k and any temperature θ, greater than k, is called the Effective Temperature (θ-k).

The product of Development Time (D) at temperature θ and the effective temperature is a constant K - the Thermal Constant.

Therefore $D(\theta-k) = K$

K is expressed in time-temperature units, e.g. hour degrees, day degrees, and is the number of such units which must be accumulated before development is complete.

(i) The Equipment

a Constant temperature room

This room was approximately 3 x 3 x 4 metres - situated in the Entomology Department, at the University of Queensland. It was lit by natural daylight from a window in the western wall. It was normally maintained at 25 ± 2°C and a relative humidity between 60% and 85%.

The room was used for the two preliminary larval development experiments.

b Multitemperature cabinets

This was used for the major experiments on immature stage development. It was owned by, and located in the offices of the Department of Primary Industries, Brisbane. (It was built by Linder and May Pty. Ltd.,

Brisbane, to a Department of Primary Industries design.)

It had ten chambers. Temperatures were maintained by water circulation. At one end there was a refrigeration unit, and at the other end a heating unit. The chambers were 18 x 24 x 30 cm in size and insulated with felt. Each was equipped with a thermometer which could be read without opening the chamber. Periodically during the experiments, the temperatures were checked using a "Grant" multi-probe temperature recorder. Table 51 shows the temperatures recorded during these experiments. When closed, the chambers were in constant darkness.

c Humidity control

Humidity was controlled by the use of saturated salt solutions. Winston and Bates (1960) published an extensive list of salt solutions which yield known relative humidities in a closed atmosphere. From their lists the following saturated salt solutions were prepared:

Lithium chloride	$LiCl.H_2O$	10-20% R.H.
Magnesium chloride	$MgCl_2.6H_2O$	30-40% R.H.
Magnesium nitrate	$Mg(NO_3)_2.6H_2O$	50-60% R.H.
Sodium chloride	$NaCl$	70-80% R.H.
Potassium sulphate	K_2SO_4	90-100% R.H.

Figure 43 shows the estimated percent relative humidity for each of these solutions, over the range of temperatures used. This figure was compiled from data supplied by Winston and Bates.

Approximately 1.5 cm depth of saturated solution was placed, with its excess salt, in 2 oz (57 ml) Pomade jars. These are glass jars 6 cm high, and approximately 4 cm internal diameter. The jars were prepared at least 48 hours before the experiment began, to allow the air to come to equilibrium with the solution. However, this was no doubt disturbed when the study material was introduced.

(ii) The Experiments

a Eggs

Because eggs in the field are exposed to variations of humidity it was considered desirable to investigate how these variations could affect rate of development at different temperatures.

The effects of five relative humidities at eight constant temperatures were tested. For each temperature-humidity combination, two replicates (Pomade jars), each of five eggs were used.

Eggs to be used in the experiment were laid on plastic oviposition dishes by adults which had been reared as larvae on artificial medium. The dishes were cut into pieces, each containing five eggs or less. Five eggs were placed in each treatment jar - at random with respect to parent moths - and within one hour of being laid.

The eggs rested in an open glass vial, 1.5 cm high and 2 cm in diameter, suspended above the liquid in a fibre glass sling (Figure 44).

The jars were sealed with Gladwrap ^{R} - a very fine transparent plastic sheet. This allowed inspection without disturbance to the humidity equilibrium.

Development was assessed every 12 hours.

b Larvae, prepupae and pupae

The immature stages of *C. ombrodelta* are normally concealed within plant material. Therefore the effect of humidity variation on their development rate at various temperatures was not evaluated.

Two preliminary experiments were performed to establish the approximate duration of the different stages. These were carried out at 25 ± 1^{o}C with humidity between 60% and 85% R.H. In the first experiment 41 larvae were reared on nut husks and the duration of each stadium was estimated, in the second, 45 larvae were reared in waxed medium

blocks - only the prepupae and pupal stage durations were estimated.

In the main experiment it was planned to test seven temperatures. At each temperature, there were to be eight larvae, placed singly in waxed medium blocks; two blocks to a waxed paper cup; a total of 56 larvae.

Unfortunately, mortality of the larvae was so high that maintenance of the main experimental design was not possible. A variable number of larvae were reared in each of the seven temperatures.

Larvae used in all experiments were the progeny of adults reared on artificial medium. Upon hatching larvae were transferred to waxed medium blocks or nut husks with a camel hair brush.

The blocks or husks were allocated to treatment cups at random, within three hours of larval hatching. This time at ambient temperature has not been considered different from test temperatures in subsequent calculations.

It should be noted that larvae were left at the one temperature for the duration of their life.

In the preliminary experiments, inspections were made every twenty-four hours. After these had furnished some information on the relative length of the different stadia it was possible to rationalize the inspection periods.

Thus after initial transfer the larvae were left undisturbed for two days, and then examined every twelve hours until they moulted. They were then left undisturbed for at least one day and were then examined every 24 hours until a moult seemed imminent, when examination was every 12 hours. Few moults were missed.

"Inspection" consisted of removing each block or husk from its cup, placing it on a binocular microscope stage and (with magnification X8.6) dissecting it with a pair of forceps. When the larva was located its head capsule width was checked approximately (without anaesthesia)

unless a cast head capsule was obvious. It was then returned to the treatment. Food was replaced as required.

The high mortality associated with all three experiments was largely due to accidents during inspection. Of a total of 254 larvae at the start of the experiments, only 76 completed their development.

Initially when a larva was killed, it was replaced. Had time been unlimited this process could have been continued until the required number reached maturity. However, the experiment had to be finished when the intensive 1972-73 sampling programme began.

B. RESULTS AND DISCUSSION

(i) Development Time

a . Eggs

Table 52 shows the length of development in hours, and the number of eggs hatching in each temperature-humidity combination, pooled over replicates (jars).

The variate analysed was mean development time per replicate, transformed to log (x). The analysis of variance was of the form of a randomized complete block with two observations per experimental unit (Steel and Torrie 1960, p.143).

All humidities were included in the main analysis, but only five temperatures - from 15.0°C to 29.0°C inclusive. An examination of Table 52 shows that mortality increased sharply at each end of the temperature range examined. It was thought undesirable to include these extreme constant temperatures in a consideration of normal development rate.

The main analysis showed that development time was statistically different (P=0.05) for each temperature. Development times for 10-20% and 30-40% R.H. were not significantly different (P=0.05) but both were significantly longer than those for the three higher humidities - which

were not statistically different from one another. The interaction was not significant.

This experiment indicated how temperature, humidity combinations can affect the development of *C. ombrodelta* eggs.

Under field conditions the extremes of temperature and humidity used in the experiment are rarely encountered for more than six hours at most, before a return to more normal conditions. It is therefore, difficult to interpret field data from the evidence of this experiment. The development time at each temperature, averaged over all humidities, is considered the most realistic measure of development time available at present.

b Larvae, prepupae and pupae

From the larvae examined, a small number (7.9%) of those completing larval development passed through six larval instars. The remaining larvae had only five instars.

Table 53 shows the mean development time in hours, for the instars reaching the pupal stages in both the five and six instar series at the constant temperatures tested for all experiments. The number of individuals for each mean is given in parentheses.

In addition, nine replicates of two larvae each were reared at 11.0^{o}C, in the multitemperature cabinet. The results have not been included in the table. Of the six larvae which could be accounted for at the end of the experiment, three had died as first instars, but all had lived for 21 to 28 days. One was still living as a first instar after 45 days. The remaining two had changed to second instar, after a period of 28 days. Presumably the 12 lost larvae died as first or second instars which are difficult to find in the medium, which became very wet at this temperature.

(ii) Threshold Temperatures and Thermal Constants

For the egg stage, the mean development time at each temperature tested (Table 52) provided the basic data. The average percent hourly development of eggs, and standard errors, at each temperature is shown in Table 54, together with number of eggs developing at each temperature where

$$\text{Average \% hourly development, } \frac{100}{D} = \frac{1}{\text{average total devel. time in hours}} \times \frac{100}{1} \%$$

In the remaining immature stages, the number of readings for stadia in each instar series was very low (Table 53). To improve this, the results from the experiments in the constant temperature room and in the multi-temperature cabinets were pooled.

A further improvement could be achieved if results obtained for young larvae which were killed before pupation, could be included. A comparison of the development time between corresponding stadia within each instar series was required. Since there were never more than two larvae of the six instar series at any one temperature, a statistical test was not satisfactory. Graphs of average % hourly development against temperature were prepared for each instar, with the mean rates for larvae of each series distinctly marked. These did not show a marked difference between development time of larvae of each series for the 1st, 2nd, 3rd and 4th instars or for prepupae and pupae. Therefore the extra data were included.

Table 54 shows the average % hourly development of immatures, with the standard error, and number of individuals for each average after all the data were included.

The means in Table 54 were used in graphing the rate of development against temperature (Figure 45). The approximate shape of the logistic curve can be seen in most of these figures.

Only the points between 17.0°C and 30.0°C were used in fitting a weighted linear regression to the data. Temperatures greater or less than this range apparently had a detrimental effect on the rate of development of most stages.

The weighted regression, fitted by the method of least squares is seen in Figure 45 as a solid line. The equations and the threshold temperatures are shown in Table 55. The weighted mean threshold temperature was 10.43°C. For some stages insufficient data were available to plot a meaningful regression; these are discussed below.

In the case of prepupae the calculated regression coefficient was negative, which is not consistent with this model of development. The difficulty arises because the 46 records of prepupal development from the constant temperature room indicate a more rapid development compared with those in the multitemperature cabinet.

No reason for this substantial variation could be discovered, so that it was felt best at this stage, to use all the data to obtain a general result. A weighted regression of the data was obtained which passed through the point (Y = 0, X = 10.43). This regression is shown in Figure 45 - prepupa as a dotted line.

Data available for the 5th and 6th instars of the 6 instar series were inadequate to allow the calculation of a regression line. To overcome this a weighted linear regression of the data which passed through (Y = 0, X = 10.43) was obtained. These lines are also shown in Figure 45 - 5th instar of 6, and 6th instar as dotted lines.

So that all thermal constants could be calculated on a common basis, the regressions obtained originally were all recalculated as weighted regressions through the common threshold temperature 10.43°C. The recalculated regressions are shown in Figure 45 as dotted lines. In the case of eggs, the recalculated line was so close to the original that it could not be shown. Table 56 shows the regression equations of all

immature stages calculated on this common basis, and the thermal constants (K) for each stadium calculated from these regressions.

The time from oviposition to adult emergence for *C. ombrodelta* having five larval instars is 13,340 hour degrees; for those having six instars the period is 15,097 hour degrees. If the temperature after oviposition were a constant 25°C the total duration of immature stages would be 38.1 days and 43.2 days respectively.

II. TEST OF LINEAR INCREASE OF HEAD CAPSULE WIDTH

Richards (1949) showed that in some insects head capsule widths of immatures increased linearly between moults (excluding the first moult) if account were taken of the duration of each instar period, i.e. the growth increment per day is constant.

In accordance with Richard' work, the mean head capsule width of each instar of the 5 and 6 instar series of *C. ombrodelta* were plotted against accumulated days development to that instar. The means plotted were those of Table 40, for laboratory reared larvae. Accumulated development time in days was calculated from accumulated hour degrees of development at 25°C - e.g. from Table 56 the hour degrees accumulated to the period where the head capsule has the size of a 3rd instar is 2,113 hour degrees or 6 days at 25°C. The points are plotted in Figure 46.

Weighted linear regressions for each series (excluding the 1st instar, in accordance with Richards' method) were calculated by the method of Sokal and Rohlf (1969, p.430-432). The analyses of variance of regression for both instar series are shown in Table 57.

These analyses show that in each series, the deviations about the linear regression are significant (P=0.01). This means that either the relationship is curvilinear, or that there is random heterogeneity around the regression line, or that both factors are present. Examination of

Figure 46 indicates that the relationship may be weakly curvilinear (especially if the position of the point for the 1st instar were included). However, since the linear relationship of head capsule width and accumulated development time is highly significant (P=0.01) the relationship explains much of the variation of head capsule width between instars.

The linear regression for each instar series is:

5 instar series

head capsule width = 0.136 days development - 0.013

6 instar series

head capsule width = 0.099 days development + 0.150

The regression coefficients are significantly different ($0.05 < P < 0.01$) (test method of Steel and Torrie (1960, p.173)).

To uphold Richards' supposition this difference in regression coefficients must indicate that the assumption made concerning the equivalence of development time and head capsule measurements of the 2nd and 3rd instars of each series is wrong. In the 6 instar series, the 2nd and 3rd instar head capsule measurements, and consequently the development time of each instar, would have to be slightly less than the corresponding value in the 5 instar series. Unfortunately, too few data for larvae in the 6 instar series are available to statistically test such differences. As the assumption of equivalence provides a practical solution to the determination of instars, and the calculation of their development times, it will continue to be held by the present author, with the proviso that future experiments may necessitate its alteration.

On the other hand, the relationship between head capsule size and accumulated development time may be curvilinear, as indicated by the significance of the deviations about regression (Table 57). For each instar series, a curve of the form

$$\text{Head width} = \text{Days}^{a} + c$$

may be appropriate, variations in "a" would account for the divergence of

the lines as Days increased, whilst points for each instar series at low Days may be so close as to be indistinguishable from each other. This treatment could also include the 1st instar, and thus be more complete than that of Richards. It is not pursued in this study because of the paucity of data for the 6 instar series.

In conclusion. The assumption of equivalence of head capsule width and development time of *C. ombrodelta* 1st, 2nd, and 3rd instars of the 5 and 6 instar series is suitable for the present study. However, if more detailed, and accurate descriptions of either head capsule determination, or development time calculations are required, more extensive experimentation to determine the exact mode of growth should be undertaken.

III. VARIATIONS IN THE EXPECTED DEVELOPMENT TIME

Larvae collected during the regular destructive macadamia samples were transferred to waxed medium blocks and placed in the constant temperature room, which is exposed to natural daylight.

In the last months (February, March) of each sampling season it appeared that larvae developed more slowly than those collected earlier in the season. Rearing methods had not been changed and the room temperature remained constant. This apparent decrease in development rate was examined in the 1973-74 season.

In addition *C. ombrodelta* larvae were reared on nuts in different stages of development to determine whether these became less suitable as larval food as nut development progressed.

A. METHODS

(i) Larval Development in Response to Daylength

On three dates: 14th November 1973, 12th January 1974, and 11th March 1974, newly hatched larvae were transferred singly to a waxed medium block in a waxed paper cup, and placed beside the window in the constant temperature room. On each date 30 larvae were randomly allocated to three groups of ten cups.

The cups were inspected after 20 days, and then periodically until it was seen that pupation was occurring. Inspection was then carried out daily until the adult emerged.

Development time was recorded as the total period from hatching to adult emergence.

(ii) Larval Development in Nuts of Different Stages of Development

On three dates: 1st November 1973, 21st December 1973, 1st March 1974, newly hatched larvae were transferred singly to 30 freshly picked nuts of S1 and H2 varieties. Each nut was placed in a waxed paper cup in the constant temperature room.

A V-shaped cut was made in each nut before the larva was transferred to it. For the first series (beginning 1st November) this cut extended to the kernel; for the next two series the nut shell had hardened, and only the husk was cut. Each larva was transferred to a fresh nut twice a week. When it was apparent that larvae were approaching maturity, daily inspections were made.

Development time was recorded as the total period from hatching to pupation.

B. RESULTS AND DISCUSSION

(i) Larval Development in Response to Daylength

The recorded development times in each series are shown in Figure 47. It is apparent that as the daylength shortened the development period of an increasing proportion of larvae lengthened. Although this increased the mean development time, it had a greater effect in increasing the variance of development time (see below).

Within each date, "t" tests of the mean development time showed that there was no difference between sexes for the first or last date, but for the second date males had a longer development time ($0.05 < P < 0.01$) than females.

The mean development times recorded, with the variance (σ^2), of each population were:

Commenced		Mean (days)	Variance
14.XI.73		30.00	1.70
12.I.74	females	31.73	1.50
	males	36.08	28.63
11.III.74		49.43	222.53

"t" tests show that each of the above means is significantly different from the others (between dates P=0.01, within 12.I.74 P=0.05).

Using the thermal constants calculated in the first part of this chapter, the expected development time from hatching to adult emergence is 35 days at 25°C. During the period when daylength was increasing the development time was shorter than expected, just after daylength began to decrease it was similar to that expected, and in the later period development time in most immature *C. ombrodelta* was much greater.

In individuals with a development period longer than that expected, the final larval instar and prepupal stages appear to be responsible for the increase. The final larval instar accumulates a very large fat body.

When feeding ceases, the prepupa constructs a silken cocoon, remaining in this for a considerable period before pupating. During this period it remains visually in the larval form, and if removed from the cocoon is able to construct another.

When *C. ombrodelta* field collections were made in the winter months, these large bodied final instar larvae were the most common form found.

It appears therefore that the development period of immature *C. ombrodelta* at a constant temperature varies with the seasonally changing daylength. The shorter development period in early summer probably helps the insect rapidly to increase its population after winter. The longer and more variable development period as daylength shortens in autumn probably increases the insect's chances of survival during winter when host plants are less plentiful.

There appears to be no ecological advantage for the sexes to vary in development time - as recorded for the second date in this experiment. The recorded difference may have been due to chance in the relatively small test population.

J. Munro[1] (1974 pers. comm.) believed that the pattern of emergence shown in Figure 47 may indicate that the constant temperature conditions of this experiment were interfering with the expression of diapause. Munro suggested that had the temperature decreased, as would be expected at this time of year under natural conditions, the mean development time in the last period would probably have been greater and the variance (σ^2) of development time less.

Further experimentation would be required to confirm the presence of a true diapause. If diapause were present, this would have important implications in the study of population fluctuation.

---

1. Dr J. Munro, Senior Lecturer, Department of Biology and Environmental Sciences, Queensland Institute of Technology, Brisbane.

(ii) Larval Development Time in Nuts of Different Stages of Development

The development time of larvae on nuts varied in a similar way to that described for larvae on medium. The results are not directly comparable as the development time in this case excluded the pupal period. Mean development times and their variances (σ^2) were:

Date commenced	S1		H2	
	Mean (days)	Variance	Mean (days)	Variance
I.XI.73	16.09	3.90	15.74	2.54
21.XII.73	31.64	27.79	29.89	8.86
I.III.74	43.00	28.25	42.92	41.24

A series of "t" tests were performed on these data.

For 21.XII. and I.III. the development time of the sexes was determined separately. No significant difference between sexes was found (P=0.05).

For no date was there a significant difference between the development time on either variety (P=0.05). The development time for each date was significantly different from that for the other dates (P=0.01).

The expected development time from hatching to pupation at 25°C is 20 days. The times recorded for the first date are shorter than expected; those for the other two dates are longer than expected. A comparison of the variation with expectation for this experiment and the previous one is:

Larval response to daylength	14.XI.	-14.3%	12.I.	-2.5%	11.III.	+44.2%
Larval response to nut development	1.XI.	-20.5%	21.XII.	+54.0%	I.III.	+117.5%

It may be suggested from the above, that when nut shells harden (between I.XI. and 21.XII.) the nuts become less suitable as a larval food, and this increases the development time. Such a view is supported by

the fact that a significant decrease (P=0.01) in pupal weights of nut reared *C. ombrodelta* occurred between the first and second dates. Mean pupal weights for the three dates (± standard errors (σ)) were:

I.XI.	21.XII.	I.III.
0.0436±0.0071	0.0311±0.0078	0.0288±0.0053 gm

Although pupal weights for the medium reared larvae were not obtained, the emerging adults remained of normal size for each date.

The reason for the poorer growth on nuts may be due to a deficiency in experimental technique rather than to a deficiency in the nuts. Pupae collected from S1 and H2 nuts in the field in February had a mean weight of 0.0539±0.0130 gm. This is significantly (P=0.05) heavier than any of the weights recorded in the laboratory.

There is therefore no real evidence that nuts become less suitable for *C. ombrodelta* development as they mature.

CHAPTER 14

SAMPLING I. IMMATURES

Sampling is an essential procedure in any study of a natural insect population. A suitable sampling technique provides the basic data for the estimation of pest impact, e.g. LeRoux (1961); the discovery of behaviour patterns, e.g. Harcourt (1960); and the formulation of theories of population regulation (Harcourt 1969).

Before any sampling programme can be initiated its objectives should be clearly defined, because these will determine the way in which the information is collected (Morris 1960, Southwood 1966, p.1).

In the present study it was decided that sampling of field populations should provide information on immature *C. ombrodelta* of the following type:

- the presence of *C. ombrodelta* in various areas
- the occurrence of its natural enemies in various areas
- its numerical fluctuations with time in specified areas
- its population age structure at various times in specified areas
- the occurrence and magnitude of effect of its various mortality factors in specified areas.

It was obvious that the same time devoted to establishing say, population age structure could not be devoted to the examination of a wide area to determine *C. ombrodelta* presence.

Morris (1960) considered that sampling plans could be usefully divided into the "intensive", and the "extensive". - terms which are indicative of the type of sample obtained. He stated however, that both types need the same basic data on frequency distributions of the insect, major sources of variance, and optimum sample unit size.

In this study it was planned that the more detailed samples should

provide this type of information, but others would basically indicate presence or absence of the larva with its enemies.

Therefore the terms "intensive samples" and "survey samples" have been used.

A. METHODS

1. INTENSIVE SAMPLES

Before an intensive sampling plan can be fully prepared one should have certain basic data on the species to be studied and its host material. The most important data are:

1. Numerical characteristics and the stability of the host material (Morris 1955).
2. Life cycle and behavioural characteristics of the subject species (Stark 1952).
3. Details of the statistical distribution of the subject species in space and time (Stark 1952, Harcourt 1969).

Such data on *C. ombrodelta* populations were not available at the commencement of the study. However, there is an extensive literature on sampling theory and practice, which assisted in the planning of a sound sampling programme. A review of this literature concentrated on that dealing with pests of fruit and forest trees.

The details of the sampling programme follow.

(i) Objectives

The intensive samples were planned to provide information on the fluctuations over time of the magnitude and age structure of populations of *C. ombrodelta*. In addition, it was desired to establish the occurrence and magnitude of effect of the main mortality factors of these *C. ombrodelta* populations.

At the same time the results should continually provide statistical data which would enable efficient allocation of sampling resources.

(ii) Population Expression

The expression of population used depends on the objectives of the study (Southwood 1966, p.2-3).

Population intensity: numbers of pests per sampling unit will be the first estimate obtained. The mean intensity of the various immature stages, together with the standard errors for these means, is required for estimating absolute populations, and altering the sampling design.

Absolute population: the number of pests per unit area. This can usually be obtained by multiplying population intensity by the number of sample units in the desired unit area on each sampling date. As this unit accounts for numerical changes in sample unit population (e.g. fruits per tree), and allows the integration of population estimates from different types of sample units, it is essential to the construction of life tables, budgets etc., on which analysis of population change depends.

The use of absolute population is particularly important because of the instability of the host plant fruits.

At Aspley S1 and H2 and Inala, absolute population was expressed as numbers per one half hectare of orchard. Adjustment to this area did not seriously distort the density basis of populations as the area of each site was close to 0.5 hectare.

At Beerwah, where only two trees were sampled intensively, the basic unit chosen was a tree - this is termed the "within tree" population, as used by Berryman (1968); to convert figures to a unit of ground surface would be highly artificial and it would be out of the question to

increase it to 0.5 ha as a density within a tree could not be expected to be maintained with 50-60 trees.

Populations in the alternative hosts were similarly estimated on a "within tree" population. Where more than one tree was sampled at each site, the "within tree" population is a mean of the number of trees sampled.

(iii) Definition of the Sampling Universe

Morris (1955) emphasized that this definition is important, so that one's conclusions closely refer to that universe, and are not applied to a broader or more heterogeneous universe.

Morris (1955, 1960) also believed that it is sensible to specifically select the universe, and restrict it, to obtain homogeneity. He believed, when sampling trees, that it is best to restrict successive samples to the same trees.

Harcourt (1961b, 1969) recommended that samples be not taken from outside rows of the crop under study, as infestation is generally higher in these rows than in the remainder of the crop.

The following sampling universes were defined:

Macadamia

Inala	-	complete Armanasco orchard	1971-72
Aspley	-	all H2 variety)	1971-72
		all S1 variety)	1972-73
			1973-74
Beerwah	-	Tree 194)	1972-73
		Tree 146)	

Bauhinia galpinii

Aspley *Bauhinia*	-	one bush	1972

Bauhinia variegata

Grasspan Road	-	four trees	1972-73

Cowie Road	- one tree	1972-73
Bald Hills	- three trees	1972-73
Acacia podalyriifolia		
Cavendish Cooke	- one tree	1972

In the orchard situations outside rows were sampled as they constituted quite a large proportion of the crop and there was interest in detecting a border effect.

Also, at Aspley and Inala, the same trees were not used on successive dates as there was a real possibility of exhausting the nut supply.

In most studies of insects on trees, it has been found that between tree variance is greater than within tree variance. Thus the universe should be treated as a universe of trees, rather than a universe of fruit, leaves etc. (Morris 1955). Until evidence is gathered to the contrary it is desirable to treat the macadamia orchards and alternative hosts as universes of trees.

(iv) Timing of Sampling

Richards (1961) and Southwood (1966, p.6) pointed out that sampling will be determined by the life cycle of the insect. The *C. ombrodelta* life cycle was not well known so sampling was planned to coincide with the fruiting period of the host. In macadamia, sampling was terminated in late March or early April, when harvesting is normally begun. In the alternative hosts sampling finished when all fruit had died and there was a corresponding decrease in the insect population intensity.

Within this period of fruit availability sampling should be restricted to times when populations are relatively stable (Morris 1959), and preferably confined to non cryptic stages (Harcourt 1969). Southwood (1966, p.23) stated that a series of regular samples is required for life table (or similar budget) preparation and Richards (1961) pointed out

that regular samples were essential when dealing with an insect with overlapping stages so that each stage is sampled in proportion to its abundance.

Sampling should be frequent enough to provide continuity from sample to sample.

From the work of Ironside (1970 unpublished report) it was estimated that up to four generations of *C. ombrodelta* would occur during one macadamia season. With this rapid generation time, considerable overlap in generations was expected. A sampling at least once a month was considered desirable initially. This period was shortened in each subsequent season. In 1973-74 samples were taken weekly.

(v) Habitats to be Sampled

Harcourt (1969) believed that it is preferable to sample only one habitat, but indicated that this is not always possible. As *C. ombrodelta* damage is restricted to the fruit (Ironside 1970 unpublished report), the fruit is the obvious habitat to sample.

Geier (1963) found that the eggs of codling moth (another Tortricid) were laid on leaves as well as fruit. He also established that pupation occurred in branch junctions. MacLellan (1962) found that codling moth eggs were also laid on branches.

It was decided that the habitat of fruit was of overriding importance, and the main sampling effort should be devoted to this. Samples of leaves and branches should also be taken to establish the use of these habitats by *C. ombrodelta* populations. This is an approach similar to that used by Morris and Reeks (1954) who studied *Operophtera brumata* (L.), different stages of which could be found on bark, foliage and forest floor; studies were concentrated on the foliage initially.

Samples of soil from under the tree to detect *C. ombrodelta* were not taken. The effort involved seemed too great for the low probability

of success. The proportion of population, if any, using this habitat was to be determined by experiment.

(vi) Sample Units

Sample units used in past insect field studies have varied with the host and the insect's behaviour, and to a lesser extent the resources of the researchers. LeRoux and Reimer (1959) used 25 apple leaf clusters; Harcourt (1961b) used a crown quadrant of cabbage; MacLellan (1962) used an entire apple tree; Berryman (1968) used a 6 x 12 inch (15.2 x 30.5 cm) area of bark; Mason (1970) used whole branches of Douglas fir. The choice of unit depends largely on the type of habitat being studied.

As a general rule a small unit is more likely to give the best estimate of variance components associated with the mean under study (Morris 1960, Harcourt 1969).

For the various habitats to be studied the following units were selected:

Fruit - a single fruit

Canopy - a single leaf (1971-72)

- a group of 10 leaves (1972-73, 1973-74)

plus

20 cm of branch (1972-73, 1973-74)

plus

1 rachis in macadamia (1972-73, 1973-74)

Morris (1955) proposed six characteristics of a suitable sampling unit. These are (as stated by Southwood 1966, p.18):

(1) It must be such that all units of the universe have an equal chance of selection.

(2) It must have stability (or if not its changes should be easily and continuously measured).

(3) The proportion of the insect population using the sample unit as a habitat must remain constant.

(4) The sampling unit must lend itself to conversion to unit areas.

(5) The sampling unit must be easily delineated in the field.

(6) The sampling unit should be of such a size as to provide a reasonable balance between the variance and the cost.

It was believed that the canopy sampling units chosen would meet these six requirements. Leaves and branch measurements can be considered stable during one fruiting season, at least for the accuracy needed for these habitats.

Before sampling has been carried out it is difficult to say if the last criterion will be met.

The single fruit also was believed to fulfil the criteria adequately. It is not stable - but lack of stability can be measured (Section II, Chapter 7).

The use of the "sampling stick", as described in Chapter 7 would have overcome the problem of lack of stability of the fruit. The volume taken would be constant at each date, and self correcting for nuts which had fallen. However, as noted in that chapter, the variability of nut numbers per sample is large, and an adequate number of samples would have required an impractical amount of time. In addition, its use would have to some extent ignored the role of *C. ombrodelta* in causing the fruit to fall.

(vii) Stratification of the Sample

Ives (1955) showed that stratification increased the efficiency of sampling; i.e. it decreased the standard error of the mean and thus the sample size for a desired precision. Watt (1968, p.198) explained

that the population should be divided into several internally homogeneous and non-overlapping subpopulations. Because of the homogeneity within strata, a small sample from each can be used to obtain a precise estimate of the mean for the stratum.

Examples of stratification which may be considered are: direction - MacLellan (1962) found that in Nova Scotia codling moth eggs were laid mostly in the southeast quadrant of apple trees early in the season; tree size - Lyons (1964) found that egg cluster density of *Neodiprion* sp. was strongly correlated with tree size; tree levels - Berryman (1968) showed attack of *Scolytus ventralis* LeConte on fir was correlated with height above the ground, Mason (1970) found the density of *Hemerocampa pseudotsugata* McDunnough was similarly correlated with the crown level.

To estimate the number of samples to be taken from each stratum, so that the resultant mean has the minimum variance for a given effort, one needs estimates of the within and between strata variances to use in various formulae, e.g. Cochran (1963, p.97).

If these variances are not known it is best to take samples from each stratum in proportion to the number of units available for sampling (Sampford 1962, p.77).

The strata recognized in this study were:

level (in most sites) - upper tree, lower tree and ground where applicable (i.e. fruits which fell to the ground)

quadrants (at some sites) - north, east, south and west

lateral directions (at some sites) - inside crown and outside crown.

In the first season samples were drawn approximately in proportion to the number of units thought to be present in each stratum. Subsequently, equal numbers of units were taken from each stratum, so that adequate estimates of strata variances could be made. After the first season the

ground stratum was considered as a separate population.

Although these strata were recognized in each host, and samples taken accordingly, it was proposed that only in macadamia (this being the main host of the study), would an attempt be made to process the data from each stratum separately. In the alternative hosts strata were to be used to ensure that sampling was representative of the whole tree. LeRoux (1961) believed that samples should be taken throughout the tree canopy of apple trees even if stratum differences were not detected. In this study no differences between strata in alternative hosts were investigated.

Harcourt (1969) points out that because of the "spotty nature" of insect infestation many plants must be sampled. Thus it was decided to draw a small number of sample units from a large number of trees - in accord with the strata mentioned above.

(viii) Sample Size

The size of the sample taken depends on the required precision, the density of the population, and the time available for examination of the samples (Morris 1955, Southwood 1966, p.19).

No estimate of sample size in relation to the required precision can be made until some idea is obtained of the variance of the estimates involved. Preliminary sampling is required for this.

In some cases of sampling from macadamia, there was risk of depleting the crop by sampling over a whole season, at least in some strata.

Examination time was thought to be the main restriction. This was confirmed in each season.

Description of the sample sizes taken is given in the results section.

(ix) The Mechanics of Sampling

a Delineating sampling subdivisions

Rows. No delineation of rows was made in the 1971-72 season. The entire area of the universe was sampled randomly. In the 1972-73, and 1973-74 season the Aspley varieties were divided into rows - outside, inside, and border.

Trees. When the tree selection was random, this was done by drawing the required numbers from a random numbers table. To assist identification of trees in the 1972-73 and 1973-74 season numbers were painted on the tree trunks.

Levels. Sample units on the ground were easily defined. Upper tree crown was defined as being a certain height above the top of the 2.43 metre ladder used - the actual distance depending on the tree size, which was judged approximately before sampling commenced.

Lateral crown within levels. Where applicable this was assessed visually.

b Drawing sample units from within strata

In theory it would be possible to devise a truly random procedure for drawing samples of fruit etc., from within the trees studied. However, it would not be practical. Morris (1960) pointed out that very little insect sampling is truly random, as even if one knows how to draw such a sample, its cost is usually prohibitive.

Southwood (1966, p.21-22) also discussed this problem. The main consideration should be that samples are drawn so that the pattern of units chosen does not coincide with some systematic distribution pattern

of the insect.

Where samples were being drawn from large trees, a system similar to that of Anscombe (1948) was used: starting from some random point, every nth unit was selected, the spacing of samples (size of n) depending on the approximate number of units available within the strata. Counting was up and down the branches. If the limit of the strata was reached before the required number of units was selected, counting continued back towards the start.

For smaller trees, where many trees were being sampled, this method was attempted but was too time consuming. The final method was to approach a tree, and walk around it, thrusting a hand in after a certain number of paces and taking the first unit encountered. An adequate distribution of units seemed to be obtained this way. For the upper strata it involved moving the ladder (use of the ladder was found to be quicker than the use of a pole to pull units down, unless the tree was very high).

It was very important not to look before picking, as *C. ombrodelta* larval damage is visible.

In selecting the fruit from ground strata a system such as that of Anscombe's (1948) was used if fruit were plentiful. However, if fruit were scarce or ground cover dense, when the required number of nuts was located these could be considered a random sample.

If the unit were to be examined in the laboratory it was labelled (using an oil pen) and stored with the other units from the same stratum.

If examination were delayed the nuts were stored in a refrigerator at near freezing temperatures (Morris 1955, Harcourt 1969).

c Examination of the sample unit

Strickland (1961) stated that a direct assessment of insects on

host plants should be the goal; although he also believed that any method which reduced field counting particularly in adverse weather was useful.

The examination of plant material *in situ* is not common. The method of Morris (1955), LeRoux and Reimer (1959), Harcourt (1960), Geier (1963), Berryman (1968), and Mason (1970), all involved extracting tissue from the plant, usually followed by dissection and microscopic examination. Geier (1963) pointed out that this method is onerous, and damaging to the crop. MacLellan (1973) mainly used field examination.

Because immature stages of *C. ombrodelta*, other than the egg, are cryptic it was necessary to remove fruit from the host and examine it in the laboratory with dissection. An unsuccessful attempt was made to develop a non-destructive sampling method. Details of this can be seen in Appendix C.

Fruit. All fruit was examined externally for the presence of eggs under a binocular microscope at 8.6 magnification. In most cases from 1971 to 1973, unhatched eggs were cut from the fruit with a small sliver of its surface. This was placed on a 1% agar surface and examined periodically until hatching.

All damaged fruit was then dissected and examined in detail for any signs of borer. If a living borer were found it was anaesthetized with carbon dioxide, its head capsule width was measured, using an ocular micrometer, and it was placed in a waxed medium block.

If the larva were dead, the head capsule width was measured, and the probable cause of death noted.

If larvae had penetrated the hard shell and were in the kernel, the shell had to be cracked during examination. The Crackerjack^{R} (Figure 48) was found to be the most suitable instrument. It allowed cracking with minimum damage to the kernel and larva.

Table 58 shows the characteristics recorded for each nut.

Leaves. Originally samples of leaves were taken from the tree and examined in the laboratory under magnification. However, it was later found that field examination with magnification was less time consuming, although still onerous.

Branches. The collection and transport of branches was considered to be impractical; in addition, no grower would agree to the removal of branch material. The branches were examined in the field, using magnification.

Rachides. Each rachis was examined *in situ*, with magnification.

Field magnification was obtained by the use of a GOWLANDS head loupe of X3 magnification.

A description of the sampling design of each universe studied will be found in the results section. This course is followed because the methods used evolved during the study.

2. SURVEY SAMPLES

The objective of these was to detect the presence of parasites of *C. ombrodelta* in areas not being sampled regularly.

Periodic casual surveys were made for host plants in different areas; when located, these were examined for external evidence of *C. ombrodelta* infestation. No samples were taken unless this examination indicated that the insect was present. Only in one site, Collins, were fruit selected randomly as described in the intensive sample section.

At all other sites, quantities of infested fruit (manifest by

frass ejection) were collected. Larvae were removed and placed in waxed medium blocks. The emergence of parasites or *C. ombrodelta* was assessed frequently.

These samples will be discussed in Section IV - The Natural Enemies.

B. RESULTS AND DISCUSSION

These results are concerned with the estimation of populations of living immature stages of *C. ombrodelta*.

The main interpretation of these population figures and the implication of certain sampling results will be discussed in appropriate following chapters. Mortality is considered in Section V.

1. INTENSIVE SAMPLES - MACADAMIA

(i) Nuts

Table 59 gives a brief summary of the results of the major samples taken in macadamia during the study.

Table 60 shows the major sampling design at each site in 1971-72. The actual number of nuts taken on each date for each stratum summed over trees is also shown. There were some anomalies e.g. Inala 27.I.72, and throughout Aspley, as variations in the method were tested. On many occasions the full number of nuts per stratum could not be found. In general, there is a very great imbalance in the data.

Normal practice is to analyse the data by an analysis of variance to obtain error estimates for the means of each stage, and to obtain between, and within strata variances (e.g. Morris 1955, LeRoux and Reimer 1959, Harcourt 1961a). This allows the precision of absolute population estimates to be defined, and enables the sampling plan to be improved.

After consultation with a statistician[1] it was thought that no meaningful analysis could be performed, because of the imbalance, and the low population intensities.

It was obvious that the numbers taken per sample had to be increased, and an attempt made to reduce the imbalance in the data.

Absolute populations were estimated (this will be discussed in detail later) for each site, and these are presented in Figures 49 and 50. From these graphs it was obvious that the time between samples was too long to provide continuity of population estimates. The overall sampling period appeared to be appropriate, in that the initiation of infestation was detected. Although there were still insects present when sampling was terminated, its extension was not considered worthwhile, as nut numbers are low after March and harvesting has begun.

Improvements in the sampling techniques for 1972-73 are shown in the sampling plans in Table 61. Numbers taken per stratum were greatly increased. The populations present in fallen nuts were estimated from the regular sample, and also from those nuts falling in the "Fallen Nut Count" experiment. The time between samples was reduced to a maximum of two weeks, and sampling occurred rigidly on the due date so that stages could be sampled in proportion to their abundance (Richards 1961).

Unfortunately, there was still imbalance in the data. In the tree, this is particularly evident for the upper level in Aspley S1 outside row; many trees did not have sufficient nuts in their upper level. On the ground, nuts were very hard to find in all varieties during December-January.

At Beerwah, on the 13.XII.72, a small sample was taken to conserve nuts as no infestation was evident to that date.

A computer programme was available to analyse these data, despite

---

1. Mr A.W. Beatty, Senior Lecturer in Biometrics, Department of Animal Husbandry, University of Queensland.

the imbalance. However, mean infestation was very low and R. Sandland[1] (pers. comm.) and D.R. Strong (pers. comm.) after studying the data, suggested that no analysis was worthwhile. Mr Strong expressed the opinion that as the results were so disappointing despite the large number of nuts taken, field sampling would be unlikely to be satisfactory, unless vast numbers of nuts were taken.

To sample the number of nuts shown in Table 61 was a major undertaking, and occupied nearly the entire season.

If the sampling unit were to be increased, to say 50 nuts, means per sample of each immature stage would usually fall in the range of five to ten. If a large workforce were available to examine an adequate number of such samples, good estimates of error would be expected. However, such a procedure would disguise the fact that a nut is a discrete unit, and it is doubtful if this adequate variance could be achieved at an acceptable cost.

It is likely that the precise determination of population processes will require the use of set experimental populations (Morris 1960) in which sampling error may be eliminated. Such experiments, to be realistic, require a large labour input and could not be used in this study.

However, sampling is still required, as it is necessary to know levels of attack, damage levels, and to have estimates of orchard populations by which to test models.

In 1973-74 only the two Aspley varieties were sampled. It had been planned to repeat the Beerwah sampling of the previous year, but *C. ombrodelta* populations remained very low at Beerwah and the plan was dropped.

At Aspley, sample sizes were increased again so that even though

---

1. Mr R. Sandland, Statistician at CSIRO Cunningham Laboratories, Mill Road, St Lucia, Queensland.

the precision of the sample estimates was expected to be low, there was a greater probability that these would be accurate. So that the increased numbers could be dealt with, the head capsule widths of larvae were not recorded; a subjective assessment was made of each stage.

The sampling plan and the nuts taken at Aspley are shown in Table 62. Nuts were taken from the entire tree canopy approximately in proportion to their within tree distribution, which to a large extent overcame the imbalance due to low cropping in the upper level. S1 outside rows again had too few nuts to sustain the intensity of sampling. On the 25.I.74 only half the normal H2 sample was taken because rising flood waters meant that it was necessary to spend as little time as possible in the orchard.

It was again difficult to find fruit on the ground during the December-January period.

The sampling results for each season will now be examined in more detail.

a Strata differences

Since analyses of variance were not suitable, Mr Strong (pers. comm.) suggested the use of a chi-square test to examine strata differences within sites and years. A suitable test of this type is explained by Brownlee (1949, p.46-47).

The criteria of test were: nuts with living *C. ombrodelta* signs ("with *C. ombrodelta*") and nuts without signs ("without *C. ombrodelta*"). Only tree nuts were tested, and the strata tested were Rows and Levels (where appropriate); i.e. results had already been pooled over trees and each entire season. The tests are shown in Table 63 and a summary of the results in Table 64.

The tests are crude, in that the summation over the entire sampling

period masks variation between weeks. However, general differences are revealed.

Rows were significantly different in two of the four cases where a row test was possible. In each - Aspley S1 1972-73, and H2 1973-74 - the inside rows had significantly fewer affected nuts than expected. The outside and border rows had approximately equal proportions of nuts affected. Thus there is some suggestion of outside row effect - as usually recorded (e.g. Geier 1963, Harcourt 1961b, 1969); it is interesting that the border rows within the orchard exhibit a similar effect.

Levels were significantly different in four of the seven level tests. In each case the upper level had a significantly lower proportion of affected nuts than the lower level.

b Absolute populations

With one exception, in each year means per nut were calculated for each immature stage on each sampling date, for the results pooled over strata found to be non significant by the above chi-square test. The exception was Inala. Here levels were found to be significantly different (P=0.05). However, as the estimate of nuts within each level was not at all accurate for this site, the results were pooled over levels as well. This was believed to have minimized error.

All means were then multiplied by the appropriate number of nuts to give strata absolute populations, and these were summed and adjusted to a 0.5 hectare orchard or "within tree" absolute population.

The absolute population estimates are shown in Figures 49 to 53.

c Error estimates

To obtain error estimates of these calculated absolute populations, it was necessary to determine the model of mathematical distribution, to

which they conformed (Richards 1961,Green 1966), or to which they could be fitted most conveniently.

A plot of variance (s^2) against the mean ($\bar{x}$) of samples pooled over non-significant strata for each site, year, and date, was prepared for each of the immature stages for tree, and fallen nuts. These are shown in Figures 54 to 57. Inspection of the data during plotting did not reveal any consistent differences between sites and years. Thus all points are represented by a single symbol.

In both graphs for each stage, most of the points are concentrated in the bottom left hand corner, approximately along the line variance= mean, which characterizes a Poisson distribution. As the mean increases, there is no clear trend away from this line, except for unhatched eggs, which usually lie above the line, and total living immatures where the points are below it. This will be discussed below.

In view of these plots, it was thought that the error limits could be defined as those of a Poisson variable. This is not strictly accurate but H.M. Finucan[1] (pers. comm.) agreed that it would be the most practical course and justifiable on the grounds that most of the means are very low and fall in the region where it is unlikely that the distribution could be distinguished from that of a Poisson variable. Richards (1961) pointed out that as a species becomes more rare its distribution is very difficult to distinguish from a Poisson type.

Following this assumption, the error estimate for absolute population calculations may be obtained from tables (Pearson and Hartley 1966, Table 40, p.227). The limits to absolute population estimates for S1 1973-74 tree and fallen nuts are shown in Tables 65 and 66 respectively. Also shown is the mean length of the limit as a percentage of the non zero

---

1. Mr H.M. Finucan, Reader, Department of Mathematics, University of Queensland.

estimates, and the range in lengths of each non zero estimate as a percentage of that estimate.

Table 65 also shows the error estimates for eggs, obtained by transforming the data to $\sqrt{x+\frac{1}{2}}$ (the most suitable for data consisting mainly of 0's, 1's, and 2's (Steel and Torrie 1960, p.157)), calculating the confidence interval of the mean eggs/nut,retransforming its limits, and multiplying these by the appropriate nut numbers.

Many of the other absolute population estimates were a sum of two or more single estimates (e.g. rows summed, or levels summed). There is no method for calculating an accurate error estimate for the sum of estimates (D.R. Strong, H.M. Finucan pers. comm.). The error estimate for the population calculations for lower tree in Beerwah Tree 194 are shown in Table 67. This stratum was thought likely to yield the most precise population estimates as it had the highest population intensity. The table shows that precision is still very low.

No more error estimates were calculated as there was no reason to suppose that the data from any other site would be more or less accurate than those shown in Tables 65 to 67. Thus it appears that, at best, the absolute population estimate may have a 95% confidence interval length of 40% of the estimate, at worst 600%. Clearly this is unsatisfactory, and emphasizes the difficulties experienced in sampling for this insect. A large increase in nut numbers sampled would be required to reduce this confidence interval length in an acceptable length (e.g. 10% or 20% of the mean).

As these results are the best available they must be accepted, with reservation, as being a fair record of population fluctuations of *C. ombrodelta* in the sites studied.

d Indices of dispersion

Green (1966) and Southwood (1966, p.23) pointed out that consideration of changes in the indices of dispersion of populations were important in interpreting population size. A paper by Harcourt (1960) is an excellent example of the efficacy of this approach.

Green (1966), Lefkovitch (1966), and Southwood (1966, p.34-43) each reviewed a variety of indices of dispersion. These are values calculated from sample data which give some quantitative measure of the type of distribution to which the population conforms. Each author pointed out that none of the indices is ideal. Green and Lefkovitch each presented a new index which they claimed overcame some of the difficulties encountered with others. These difficulties include awkward calculation, influence on the distribution of sample size, and total number of individuals sampled.

The "b" of Taylor's Power Law ($s^2 = a\bar{x}^b$) (Southwood 1966, p.9) was described by Lefkovitch (1966) as the most universal index yet proposed. Taylor (1961) believed that the relationship held for very low means, a characteristic which is doubtful for many other relationships on which indices are based. This would be an advantage for the data collected during this study. "b"s obtained from different populations may be tested for differences between them (if they were derived from $\log s^2 = \log a + b \log \bar{x}$, the test is one of homogeneity between linear regression coefficients), or for their difference from 1.0, which would be their value if the random Poisson distribution held (if derived as above a "t" test is appropriate).

"b"s have not been tested mathematically here, because the lengthy calculations necessary for their derivation and testing of differences from each other would not be justified considering the present state of knowledge of *C. ombrodelta* population processes.

However, it is of interest to subjectively assess the shape of the plots of variance against mean in Figures 54 to 57.

The distribution of unhatched eggs appears to be weakly contagious. As egg density increases, the variance apparently increases to a greater degree. This indicates that at high egg populations the proportion of nuts carrying more than one egg increases, compared to that at low egg populations i.e. clumping occurs.

The distribution of each of the instars 1 to 4 appears to be random over the whole range of densities encountered. This indicates that between hatching and establishment some factor reducing population numbers acts most strongly on the larger clusters of eggs, or newly hatched larvae. Any factor reducing numbers between establishment and 4th instar apparently acts equally on all densities.

In the remainder of the stages, there is some suggestion that the distribution is more regular, i.e. individuals are spaced more evenly through nuts than would occur under random distribution. Therefore it again appears as if some factor reducing numbers between the 4th and 5A, or Final instars acts most severely on those with highest clumping.

If all living larvae, prepupae and pupae are considered together, their distribution in the tree appears to be random. However, in the fallen nuts the population is quite strongly regular. This is believed to be due to the sharp reduction in the proportion of nuts with no larvae, taken in fallen nut samples.

e General discussion

The within tree populations at Beerwah, in 1972-73, represent very high density conditions for *C. ombrodelta*. If the peak egg laying of 1,343 unhatched eggs in Tree 194 were converted to a 0.5 ha basis (with tree planting distances the same as those at Aspley), the peak would

be 104,266 eggs. This may be compared to the actual peaks in 1972-73 in Aspley S1's of 7,166 eggs, and H2's of 9,011 eggs.

From the Figures 49-53 it is apparent that most of the population of living immature stages is found in tree nuts. Only for the older larvae and prepupae and pupae does the proportion of the population in fallen nuts become appreciable.

The figures also indicate that a period between samplings of one week is not short enough to detect all population changes. This is especially evident in the case of unhatched eggs. As the period between samples was shortened during the course of the study, more fluctuations in the oviposition rates became apparent.

With the temperature range commonly experienced in Southeast Queensland during the macadamia fruiting season, *C. ombrodelta* eggs hatch in less than seven days. Therefore none of the eggs present on one sampling day are present on the next. This, and the apparently large fluctuations in recorded oviposition makes estimation of total natality within any period difficult.

Similar problems arise with young larvae and prepupae, where the duration of the stage is considerably shorter than one week (at the temperatures prevailing). For instance, any 1st instars present on one sampling day will be detected as 3rds one week later.

On the other hand, many final larval instars present on one sampling day will still be present as final larval instars a week later.

Partly for this reason, the peaks of successive instars do not show constant succession with each other, and some of the older instars have peaks higher than those of earlier instars. Sampling error undoubtedly also contributes to some of the observed variation.

On nearly every date every age group is represented in a single sample. This indicates an extreme overlap of generations. Indeed it

is doubtful if any generations in the usual sense of the word were present.

There appears to be continual and wide fluctuation in population age structure and growth rate of population size.

These features of *C. ombrodelta* populations in macadamia suggest that it will be difficult to analyse the various population processes involved (Varley *et al.* 1973, p.9).

Certainly conventional life tables (Southwood 1966, p.277, Harcourt 1969, and Luck 1971) will not be suitable, as they can only accommodate a slight degree of overlap of generations. Population tables, derived by Beaver (1966) to deal with a greater degree of overlap, are also unsuitable for the extreme overlap exhibited in these *C. ombrodelta* populations (Beaver 1972 pers. comm.).

The assumptions of constant population size, time specific survival, stable age distributions, or constant rates of population growth and decline, required for the four methods reviewed by Southwood (1966, p.316-19) for interpreting change in populations which overlap between stages cannot be fully met.

There have been methods derived to deal with various degrees of overlap, which may be suitable for *C. ombrodelta* populations (e.g. Dempster 1956, Richards 1961, Kiritani and Nakasuji 1967). However, their derivation and testing required a reasonably stable and controlled population (usually in cages).

Many of the concepts and techniques used in these methods will prove of value in analysing *C. ombrodelta* population processes, especially in experiments where sampling error is minimized.

However, the limitations of the present data are too great for these mathematical methods to be used with any confidence.

Although precise mathematical description of population processes must be regarded as the aim of population studies, there should also be room in such studies for a certain amount of subjective assessment of

relationships, and of hypotheses of cause and effect. These assessments are based on the worker's observation and experience of the subject insect.

The population samples described in this chapter, form a basis for certain deductions as to the processes involved. These deductions, combined with mathematical descriptions where possible, will be tested for veracity in the construction of a population simulation model in later chapters.

Precise estimates of *C. ombrodelta* parameters are likely to be achieved if more workers are employed to solve the problem. In the meantime, and also if this occurs, the construction and use of computer simulation models will greatly increase the appreciation of the processes involved.

(ii) Other Canopy Parts

The results of the leaf samples taken during the 1971-72 season are shown in Table 68. This shows that eggs are laid on the leaves, although a large sample would be required to precisely estimate the numbers involved. Only eggs were found.

In the subsequent seasons, canopy samples were taken only in those sites of high *C. ombrodelta* infestation. They were taken on the same dates as nut samples, so that egg intensity and calculated absolute populations on nuts could be compared to those for the remainder of the canopy. The comparisons are shown in Table 69.

Although the estimations of populations of total eggs are only approximate, they do indicate that about one quarter of the eggs are not detected if sampling is confined to fruit only. The importance of this population of eggs, not laid on the nuts, is discussed in the next chapter - it is thought that only those eggs laid on the rachides could contribute

appreciably to larval populations.

However, it would be desirable to detect these eggs during the sampling programme. The only way of doing this would be to use a system involving whole tree examination *in situ* such as that described by MacLellan (1973), or modifying this to part tree examination. In either case a large number of workers would need to be involved in the sampling.

2. INTENSIVE SAMPLES - ALTERNATIVE HOSTS

A brief summary of the results of the alternative host samples taken during the study is shown in Table 70.

There was variation in the sampling at different sites. At Cowie Road and Grasspan Road numbers of pods sampled were increased early in the season; at some sites some strata were depleted earlier than others and at Grasspan Road and Cowie Road it was often difficult to find sufficient pods on the ground because local residents considered fallen pods untidy and removed them.

In Table 71 the sampling designs used for most of the sampling period in each host are shown.

The object of these alternative host samples was to gain some idea of the probable importance of these plants in the life system of *C. ombrodelta*. Examination of strata differences and statistical analysis of the data was minimal.

The results of the examination of samples taken on each date were recorded under their separate strata. However, to estimate the absolute within tree populations for each site and date, means for each immature stage were calculated per fruit for all fruit pooled over strata - except that means for the tree were estimated separately to those in fallen fruit. These means were then multiplied by the appropriate

number of fruit available.

Undoubtedly this method inflated the variance of the means. It is not thought to have seriously biased the estimates as it is believed that there were approximately equal numbers of fruit per tree stratum.

The absolute estimates for each site are shown in Figures 58 and 59.

The confidence intervals for these estimates are again disappointingly large in relation to the estimate, even allowing for the inflation of the variance by the pooling of strata.

A sample of the data from Cowie Road, shown in Table 72, illustrates the general level of imprecision. Also shown are the number of pods which would have had to be taken on these dates to reduce the length of the confidence interval to 10% and 20% of its estimate.

In general, the trends of the absolute populations are similar to those in macadamia. There are fluctuations in the oviposition rates, and a decline in numbers occurs with progression through the instars. The populations have a shorter duration than those in macadamia. In *Acacia* (Cavendish Cooke) there was apparently only one, quite well defined generation.

On most sampling dates all stages were represented in the samples. Difficulties of population process analyses, similar to those in macadamia, would be expected.

The populations are very high, compared to those of macadamia. The peak within tree egg and 3rd instar larval populations recorded at each site are compared with the Beerwah within tree populations in Table 73.

The probable importance of populations of *C. ombrodelta* in its alternative hosts is discussed in Chapter 19.

CHAPTER 15

SAMPLING. II. ADULTS

A method of monitoring the adult *C. ombrodelta* population was required in the present study.

It was visualized that a suitable method would provide an estimate of the within study site population (e.g. Steiner 1969, Phillips and Dustan 1970, Proverbs 1970) which could be compared with the adult population estimated from the sampling of immatures.

Suitable trapping techniques may also be used to obtain direct estimates of immigration and emigration with respect to a study site (e.g. Hopkins *et al.* 1971) and information on the behaviour patterns of adults may be obtained (Batiste *et al.* 1973).

Examination of collections may also provide the basis for estimating field adult population age structures so that oviposition expectations may be estimated (Geier 1960).

A. METHODS

Various traps were tested. These may be classified as non-attractive and attractive traps, although as Southwood (1966, p.191) points out such division usually cannot be rigid.

1. NON-ATTRACTIVE TRAPS

(i) Malaise Traps

Two Malaise traps of the Gressitt type (Southwood 1966, p.192) were used. One was 4 m wide and 2.5 m high, the other 3 m wide and 2 m high. The killing agent used in the collecting jars was dichlorvos

impregnated plastic strips (Shelltox Pest Strip ^{R}).

Traps were suspended between macadamia trees in the inside rows of both the Aspley and Armanasco orchards in the 1971-72 season.

(ii) Flight Traps

In 1971-72, a number of traps were prepared to a design used by Elder (1969). Two slotted perspex sheets (0.32 cm thick) were fitted together at right angles to form baffles and placed in a shallow metal tray (Figure 60). The trays were filled with water and a little detergent added. A small overflow hole near the top of the tray allowed rain water to escape while the insects were retained.

Eight such traps were placed at regular intervals through both Inala orchards. Two traps had baffles 91.5 cm square, two 61 cm square, two 30.5 cm square, and two 15 cm square. Each trap was placed on a wooden platform at a height of 100 cm.

Sixteen traps, all of 30.5 cm square were used at Aspley in 1971-72. Six were spaced evenly through the orchard at 100 cm height. The remainder were attached to poles placed in the centre of rows 3 and 9. The five traps on each pole were at heights of 30, 152, 274, 396, 518 cm (Figure 60).

In the 1972-73 season the flight traps used were built to a design modified from that of Graham (1970); Graham's traps were a heavy sheet of celluloid rolled into a half completed cone with an open end and a killing bottle at the apex of the cone, which was hung apex down. In this study, sheets of clear plastic (0.10 cm thick) were shaped to form opposing cones with an entrance hole at one side. The lower cone was filled with water plus detergent; the upper cone led to a killing bottle in which a small piece of dichlorvos plastic strip was placed. From cone tip to cone tip the trap was 61 cm. The entrance hole was 30 cm

long and 20 cm wide.

Four traps were placed at each of four heights on a pole, so that at each height entrance holes were facing north, east, south and west. The poles were placed at the edge of the tree canopy (Figure 60). A total of 64 traps were used at Aspley.

(iii) Sticky Traps

Metal cylinders 6.5 cm in diameter and 11 cm long were painted either white, black, yellow or green, coated with a sticky substance, and hung within the tree canopies.

The catching agent was either Stickem Special [R], Tree Tanglefoot [R], or Bird Tanglefoot [R]. It was applied evenly to the metal surface with a fine toothed spreader, such as that described by Maxwell (1969).

At least once a week the surface was "freshened" (Holbrook *et al.* 1960) by scraping it with the spreader, and the traps were periodically replaced.

Twenty traps were placed in the Aspley orchard and twenty at Armanasco in 1971-72; 21 were placed at Aspley in 1972-73.

(iv) Suction Trap

One nine inch (22.9 cm) Johnson-Taylor suction trap was used at Beerwah in 1972 and 1973. A twelve inch (30.5 cm) trap of the same design was used at Beerwah in 1974.

The trap was placed under the tree canopy. It was not possible for the author to attend the trap daily. A technical assistant from the Beerwah orchard collected the catch daily and it was inspected weekly by the author.

(v) Emergence Traps

These consisted of a square (30 cm) metal base, roofed with a dark cloth pyramid on a wire frame. The apex of the pyramid held a clear collecting bottle with a small piece of dichlorvos plastic strip as a killing agent.

In use, the base was buried to a depth of several centimetres in the soil under host trees. Catch was checked every week, when the traps were moved to a new position.

Two traps were used for a three week period under the Cavendish Cooke *Acacia* in August 1971. Eight traps were used for six weeks under one tree at Beerwah in January to March 1973.

2. ATTRACTIVE TRAPS

(i) Bait Traps

Bait traps have been used successfully for trapping Tortricid adults (e.g. Nel 1940, Van Leeuwen 1943, Phillips and Dustan 1970).

Solutions of 10% molasses and yeast (7 gm to 9 l) were poured into plastic dishes 25 cm in diameter and 12.5 cm high. A small vial was embedded in cork and floated on the surface of the solution. In the control traps the vial was empty. Other vials had either Terpinyl acetate, Citral, or Safrole in them. Van Leeuwen (*loc. cit.*) found that these compounds were highly attractive to codling moth.

An overflow device was fitted to the dishes, which were then placed in trees in the Aspley (4 traps) and Beerwah (8 traps) orchards in the 1972-73 season - at Aspley one trap of each type, at Beerwah two of each type.

(ii) Light Traps

Sinclair P. (1973 pers. comm.) has shown a correspondence of light trap catches of *C. ombrodelta* and damage by this insect in the Beerwah orchard.

A number of light traps were tested briefly. Their constant use would have been difficult at Aspley, as there was no power source within reasonable distance of this orchard. Traps tested were:

New Jersey (a) five miniature traps operated by a six volt battery, with a 3 watt tungsten bulb light source. Tested at Aspley, Inala 1971.

(b) standard trap with a 240 volt, 150 watt mercury vapour light source; the power source was a Honda ^{R} petrol driven portable generator. Operated at Aspley 1971-72.

Rothampsted. One trap with a 240 volt, 150 watt mercury vapour light source; powered by the Honda generator. Aspley 1971-72.

Black light. A 122 cm black light fluorescent tube powered by the Honda generator was tested at Aspley 1971-72. A white sheet was spread before the light and this was inspected every five minutes for *C. ombrodelta.*

(iii) Pheromone Traps

In October 1972, Professor W.C. Mitchell[1] of the University of Hawaii, forwarded six different types of pheromone lures for testing in Australian macadamia orchards. They were:

---

1. Professor W.C. Mitchell, Department of Entomology, College of Tropical Agriculture, University of Hawaii, Honolulu, Hawaii.

Lure	Number supplied	Basic chemical	Lure designed for:
Orfamone	6)		
Orfamone II	7)	Cis-8-dodecenyl acetate and dodecyl alcohol	*Grapholitha molesta* (Busck)
Orfamone III	13)		
Grapemone I	6	Cis-9-dodecenyl acetate	*Paralobesia viteana* (Clemens)
Cablemone II	6	Cis-7-dodecenyl acetate	*Trichoplusia ni* (Hübner)

These lures are manufactured by the Zoecon Corporation of California. They are impregnated in small rubber caps.

Also supplied were a number of 3M Sectar [R], and Zoecon Phero-traps I [R]. These were white cardboard traps with internal surfaces coated with Tanglefoot.

The following trials were carried out:

a Suitability of each lure for attracting *C. ombrodelta*

At Aspley 1972-73: One lure of each type was placed in a Sectar trap and hung in the positions - Row 3 tree 5 (SE), Row 3 tree 15 (SW), Row 6 tree 10 (centre), Row 9 tree 15 (NW), Row 9 tree 5 (NE). A control consisting of a Sectar trap without a lure was included for most of the experiments.

Catch was checked each week, when the traps were rotated around the orchard one position. Lures were first replaced after 7 weeks and then after 11 weeks. The last set of lures was exposed for six weeks.

At Beerwah 1972: One lure of each type was placed in a Phero-trap I trap which was hung in macadamia trees in one of five positions in a straight line running east-west through the orchard. Positions were

at least 45 metres apart.

Catch was checked each week and the traps were moved forward one position. Lures were exposed for 52 days.

In each orchard the traps were hung in the tree canopy at a height of 150 to 180 cm.

b Comparison of lure catch with virgin female catch

A small trial was conducted in the Aspley orchard in 1973 to compare Orfamone, Orfamone III and virgin female *C. ombrodelta*. Traps were Pherotrap I type.

Single lures or a number of females were placed in metal gauze cages 4 cm in diameter and 5 cm long. One cage was suspended within each trap.

Females had been reared on artificial medium. The number of females per trap varied between three and five, depending on the numbers emerging in the laboratory. They were segregated by age - either 24-48 hours old, 48-72 hours old, or 72-96 hours old. Traps were checked daily.

A larger trial, conducted in 1974 in the Aspley suburban area, tested virgin female catch against Orfamone II catch. The traps were based on a USDA design, used by Professor W.C. Mitchell. They consisted of a triangular cardboard cover with a detachable cardboard bottom, on which Stickem Special was spread (Figure 61).

One lure or one virgin female was placed in a gauze cage as described above, and this was suspended within the trap (Figure 61).

There were four treatments: one Orfamone II lure; a single virgin female 0-24 hours old; a single virgin female 24-48 hours old; a single virgin female 48-72 hours old. These treatments were tested at five positions, on the circumference of a circle approximately 300 metres

in diameter. Each treatment position combination was replicated three times.

c Height of trap for best catch

Sharma *et al.* (1971) found that the height of lure traps had a significant effect on the catch of *Pectinophora gossypiella* (Saunders). A similar effect was noted by Ladd and Jurimas (1972) for lures attracting *Popillia japonica* Newman.

To test the effect for *C. ombrodelta*, a trial was conducted at Beerwah in January, February 1973, using Orfamone III lures in Pherotrap I traps.

Heights tested were 45-60 cm, 150-180 cm, and 300-360 cm. The orchard was divided into three areas - eastern, central and western, in each of which a set of treatments was placed.

In the first week each level was tested in separate trees. In the subsequent three weeks all levels were represented in a single tree. Test trees were at least 50 metres apart.

Catch was assessed once a week.

d Lure trap catch in macadamia trees against lure trap catch on poles

Daterman and McComb (1970) found that the catch of male *Rhyacionia buoliana* (Schiff.) was greatest for lures placed in host trees. These caught more males than lures in non host trees, and both were more attractive than lures placed on poles away from trees. They concluded that the host foliage had some supplementary attraction for the insect.

A small trial using Orfamone III lures in Pherotrap I traps was carried out at Beerwah from 21.II.73 to 7.III.73. Traps were placed in pairs in eastern, central, western orchard areas with at least 50 metres

between each test position.

Within each test position one trap was hung in macadamia foliage, and one on a pole five metres from macadamia foliage. The distance between each trap was at least 30 metres. Trap height was 300-360 cm.

Catch was checked each week, when the position of traps within positions was reversed; that on the pole being put in the nearest tree, that in the tree being moved to a pole near that tree.

B. RESULTS

(i) Non Pheromone Traps

The results of the trials for the malaise traps, flight traps, sticky traps, suction traps, bait traps and light traps are shown in Table 74.

None of these traps could be considered effective enough to be used as a general survey tool. The suction trap, however, may be useful for specific tree studies if power outlets were available.

To illustrate the relative effectiveness of light, flight, and suction traps under conditions of high population density, data were provided by P. Sinclair (pers. comm.) on catches in the Beerwah orchard for a light trap (240 volt, 150 watt mercury vapour modified Robinson type), and flight traps (rigid baffle 30.5 cm sq.) in operation at the same period in 1972 that the suction trap was being used. In this period, the catches in each type of trap were:

Light trap - 41.17 *C. ombrodelta* per trap night
Flight trap - 0.10 *C. ombrodelta* per trap night
Suction trap (22.9 cm) - 0.48 *C. ombrodelta* per trap night.

Under these conditions the light trap was overwhelmingly superior to the other types of trap.

(ii) Pheromone Traps

a Suitability of each lure for attracting *C. ombrodelta*

Only male *C. ombrodelta* were attracted to these lures.

The results of the two trials are shown in Table 75. It is quite clear that the Orfamone group were the only lures effective for *C. ombrodelta*. Orfamone II appears slightly better than Orfamone III, and both are markedly better than Orfamone.

b Comparison of Orfamone lures to virgin *C. ombrodelta* females

In the 1973 trial, to overcome the varying number of virgin females used, the catch of males was reduced to a per female or per lure basis. During the trial, recorded catch was:

per Orfamone lure	1.083	males per trap night (6 nights)
per Orfamone III lure	1.833	males per trap night (6 nights)
per female 24-48 hours old	1.165	males per trap night (4 nights)
per female 48-72 hours old	1.478	males per trap night (4 nights)
per female 72-96 hours old	0.875	males per trap night (2 nights)

The lure catches appear comparable to those traps with virgin females.

The results of the 1974 trial are shown in Table 76. The F values of the analysis of variance of the data, transformed to log (x+1) are also shown. There was no significant difference between treatments (P=0.05).

It therefore appears that one Orfamone II lure was as attractive to male *C. ombrodelta* as one virgin female of this species.

c Height of trap for best catch

The results for this trial are shown in Table 77.

The data were transformed to log (x+1) and examined by an analysis of variance. F values are shown. As there was no replication, all effects mean squares were tested against the second order interaction mean square.

This analysis showed that the catch in traps at 300-360 cm was significantly higher (P=0.01) than at either of the two other heights which were not significantly different to each other.

d Lure trap catch in macadamia tree against lure trap catch on poles

The results of this trial, and the F values of its analysis are shown in Table 78.

Although the mean catch for traps in the tree was higher than that for traps on the pole, an analysis of variance of the trap data, transformed to log (x+1), did not show these were significantly different (P=0.10). This trial was unreplicated and the third order interaction term was used as an error term.

The trial was small and a larger experiment, with replication and yielding more degrees of freedom for an analysis, would be needed to obtain a conclusive result.

However, until such a trial is conducted, the possible difference should be kept in mind.

C. DISCUSSION

Some of the trials described were insufficiently detailed to be conclusive. However, if a trap is to be effective in monitoring an adult

insect population, it should record adults over a wide range of population densities. The malaise, flight, sticky, and bait traps clearly did not fulfil this requirement as the recorded population of immature stages (Figures 51, 52) indicated that populations of adults were present during the trial periods.

The Orfamone lure traps were effective in trapping male *C. ombrodelta* in Aspley in October 1972, before damage to the crop was evident.

The failure of the light traps at Aspley and Inala was probably due to the low populations and insufficient perseverance, since a light trap has been shown to be effective at Beerwah. The use of these traps was not pursued because of the lack of a power outlet within reasonable distance of the Aspley orchard.

An attempt was made to obtain the lure cis-5-tetradecenyl acetate which Mitchell (1972 unpublished report) reported attracted a female *C. ombrodelta*. C.M. Olsen[1] (1973 pers. comm.) stated that it was not currently available from the Zoecon Corporation. He could not suggest an alternative source of supply.

Orfamone II, providing the most effective and practical trapping method was used to monitor adult *C. ombrodelta* populations within and around the Aspley orchard in 1973-74. The experiment will be described in Section V.

The use of a trap attractive to males only, should allow the source of a population to be discovered and should record population fluctuations arising from breeding within an area. However, it precludes the estimation of female sexual development, which is important in estimating expected population fluctuations.

More importantly it severely restricts any study of migration leading to new colonization. Johnson (1969, p.9) stated that the females

---

1. Dr C.M. Olsen, Director of Marketing, Zoecon Corporation, Palo Alto California, U.S.A.

of a species are of greatest importance in the study of migration. Therefore, the search for an effective female *C. ombrodelta* trap should be continued.

CHAPTER 16

BIOLOGY AND BEHAVIOUR. I. ADULT AND EGG

This and the next chapter describe the biology and behaviour of *C. ombrodelta* which has been observed and determined by experiment during the course of the study. Whilst most of the material recorded is of relevance to the model building within this study, some does not have immediate relevance.

Most work was carried out in macadamia. Where differences and variations have been observed in other hosts this will be noted.

It has not been possible to discuss these aspects of *C. ombrodelta* without assuming elements of interaction - in this case between different stages of the insect and between the insect and its host. These elements have been kept to a minimum. Mortality in the insect is assumed to be predominantly due to interaction of it with other elements in the environment, and this aspect will therefore be discussed in Section V.

This chapter, dealing with the adult, and the egg, is arranged in parts which discuss aspects of the biology and behaviour. The sources of the data are recorded, and the experimental methods will be explained within each part.

1. ADULT

(i) Emergence

C. ombrodelta may emerge from the pupal stage at any hour, although there is a peak of emergence before sunset. Figure 62 shows the recorded emergence times, over a 14 day period, for a series of rearing trays observed hourly from 0600 to 2400 hours in the laboratory under ambient conditions.

After emergence, the moth rests near the pupal case during wing expansion, which usually takes 15 to 20 minutes. Wings are expanded initially in a loosely folded position; towards the end of the process they are held vertically for two to five minutes before being folded normally.

When wing expansion is complete the moths are able to fly, although they commonly rest in the same position for a longer period.

(ii) Activity

Observations of laboratory caged adults indicate that activity is mostly restricted to several hours before and after sunset. During this time adults flutter continuously within the cage. The activity in the laboratory is associated with oviposition and possibly mating.

The small amount of data on field activity also indicates this restricted activity period for female *C. ombrodelta*; males appear to have a longer active period. Figure 63 shows the hourly distribution of *C. ombrodelta* catch recorded in the Johnson-Taylor suction traps at Beerwah in 1972 and 1973.

Apart from those collected in lure or suction traps only eleven adults were observed in the field during the study.

Of the seven males four had obviously just emerged, and three of these were observed between 1700 hours and 1900 hours, the other at 1000 hours. Of the remaining three, one was caught in a flight trap between 2130 and 0230 hours. The other male was seen fluttering from leaf to leaf in a macadamia tree at 1030 hours.

One of the four females seen had just emerged, between 1700 and 1800 hours; the others were resting on macadamia foliage during the daylight hours.

If resting moths are disturbed during the active period they

usually fly. At other times they are more likely to feign death, falling from their resting place and lying on their sides with their wings folded. Females more commonly take this action than males. If disturbed further, the moth wriggles, almost imperceptively, just away from danger and lies still again.

(iii) Sex Ratio

Of 3,404 adult *C. ombrodelta* which emerged in the laboratory from larvae collected during sampling, 1,737 were males and 1,667 females. A chi-square test did not show that the ratio of 1.000:0.960 was significantly different from 1:1 ($P>0.1$).

(iv) Mating

No specific study of mating was undertaken. Observations were made during the course of rearing and various experiments.

Time. Females are able to mate within 12 hours of their emergence. Virgin females remain attractive to the male for at least three days (Table 76). Successful mating was also observed in one five day old female, previously caged without males.

In one experiment, 23 newly emerged female *C. ombrodelta* were placed in a mating cage with an excess of males, and removed within 24 hours of their emergence; 18 had mated. On another occasion seven newly emerged females, caged for 48 hours with an excess of males had all mated within this period.

Mating has been observed in the laboratory at all times of the day and night, although most frequently at night. It is probable that mating is usually associated with the active period.

Frequency. Daterman (1968) believed that *Rhyacionia buoliana* females mated only once, both because he had only observed single matings in the laboratory and because of the large size of the spermatophore in relation to the bursa copulatrix.

The spermatophore of *C. ombrodelta* is also large compared to the bursa copulatrix. In approximately 90 dissections of field collected and laboratory reared females (ratio *ca.* 1:2), all except one had no more than one spermataphore. In the exception there were three; this female had been caged for several days with an excess of males. It is possible that a small percentage of females do mate more than once, (e.g. Geier 1963, *Cydia pomonella;* Dustan 1964, *Grapholitha molesta*).

The spermatophores break down and are very difficult to find in old, mated females.

It is probable that a single mating is adequate for the field life span of female *C. ombrodelta*. In a laboratory experiment involving 20 females which had mated only once, their ovaries appeared near exhaustion at death. The mean age of these females when egg laying ceased was 11.35 days, in a mean laboratory life span of 14.50 days.

(v) Oviposition

a Fecundity and oviposition rate

To determine the oviposition rates of *C. ombrodelta*, twenty mated females were placed singly in oviposition cups within 24 hours of emergence, under natural lighting conditions at 25±2°C. At all times females were supplied with a 5% honey in water solution.

These were inspected daily, and each female was moved to a new cup. The eggs laid in the previous 24 hours were counted.

The recorded daily oviposition figures are shown in Table 79. The arithmetric mean eggs/female was 107.2 and standard error(s) 78.34.

Most females began laying on the second night after emergence (mean 2.95 days) and the mean oviposition period was 9.40 days. Figure 64 shows the mean accumulated percentage of total egg laying per day for these 20 females.

Oviposition is apparently restricted to the few hours before and after sunset each day.

The probability of a correlation between female pupal weight or size and fecundity (e.g. Schmiege 1965, Southwood 1966, p.241) was not investigated.

The data presented are a reasonable first estimate of the potential fecundity of *C. ombrodelta*. Geier (1963) stated that it is very difficult to determine accurately the number of eggs laid per female under natural conditions; under controlled conditions the estimate is likely to be biased by experimental artifacts. Schmiege (1965) found that the number of eggs laid by *Acleris varianna* (Fern.) (Tortricidae) in the laboratory was significantly less than the numbers laid in the field. Although Southwood (1966, p.241) and Wearing and Ferguson (1971) explained that the variations about expected oviposition rates may be important in interpreting field population changes, it was considered that the more sophisticated experiments required to fully measure and explain variations in *C. ombrodelta* fecundity would not be profitable until the life system has been more adequately defined.

b Placement of eggs

There appear to be stimuli acting on the female so that eggs are not placed at random on any available surface.

In the laboratory oviposition cups, nearly all eggs are laid on the side of the cup nearest to the fading twilight. The presence of a tactile stimulus is indicated by the preferential placement of eggs in

the grooves of oviposition cups, as mentioned previously.

Such a preference has also been observed on the host plant *B. galpinii*. The small depressions near either extremity of the pod make up only 1% of the pod surface area. Of 513 eggs recorded on 150 pods, 30.5% were laid in these regions. The ridged edge of the pod, which is 10% of the surface area, carried 61% of the eggs. The remaining 89% of the area is mainly flat and carried only 8.5% of the eggs.

The eggs observed on the leaves of macadamia and *Bauhinia* were invariably against the mid-rib or prominent veins. Eggs on branches or rachides were usually in rough patches, especially old leaf or nut scars. No pattern of egg laying was evident on the surface of the macadamia nut itself.

Fallen fruit. It is believed that eggs are not laid on fruit which has fallen.

At Beerwah in 1973, a total of 395 nuts were placed under Tree 194 during the period from 31st January to 28th February; 229 of these were exposed for periods of one week, the remaining 166 nuts were exposed for periods of two weeks. No unhatched eggs were detected on these nuts when they were inspected under magnification at the end of the exposure period. In this period the mean expectation of unhatched eggs on 395 tree nuts was 140.

The unhatched eggs found on fallen nuts are mostly on *C. ombrodelta* damaged nuts: e.g. in 1972-73 during the period of low nut fall, 37 unhatched eggs were recorded on undamaged nuts and 186 on damaged nuts.

It is explained below, that *C. ombrodelta* females exhibit a preference for oviposition on damaged nuts. In Section V it will be shown that damaged nuts are more likely to fall from the tree than undamaged nuts. These two factors explain why unhatched eggs are found on fallen nuts.

c Varieties and damage preference

A cage experiment was carried out to test a preference for oviposition on certain varieties of nut, and damaged nuts against undamaged nuts.

Sixteen nuts were hung in a random pattern from the top of a large gauze cage (59 x 59 x 88 cm). The nuts were: 4 damaged S1, 4 "clean" S1, 4 damaged H2, and 4 "clean" H2. Various numbers of mated female *C. ombrodelta* were placed in the cage for 24 hours; the eggs laid on each nut were then counted. The cage was exposed to ambient weather conditions. The experiment was replicated six times. The results and their analysis, is shown in Table 80.

The mean eggs/nut on H2's was higher than that on S1's but only significantly different at the 10% level. Such a preference is unlikely to be of consequence in the field, as tree and variety spacing is probably too great for a female to exercise a preference.

The preference for damaged nuts against undamaged nuts was significant at P=0.05, and was consistent over both varieties, and a wide range of egg laying densities.

Field data were examined to determine whether such a preference existed under natural conditions.

From the tree nut samples taken in 1972-73, and 1973-74 the following variables were calculated:

$$\frac{\text{mean unhatched eggs/damaged nut}}{\text{mean unhatched eggs/undamaged nut}} = \text{Egg Ratio} \quad \ldots\ldots(1)$$

percent of crop damaged ..... (2)

overall mean unhatched egg density ..... (3)

Those samples in which either or both eggs/damaged nut, or eggs/undamaged nut was zero, were discarded.

Because only the nuts in the tree were considered there may be a bias in the results, as some eggs probably fell to the ground on damaged nuts; the proportion is not large (see Figures 51 and 52).

The egg ratio (1) was plotted as the dependent variable, against percent crop damaged (2). This is shown in Figure 65. There appears to be a relationship between the size of the ratio and the percent of damaged crop; *C. ombrodelta* apparently preferentially oviposits on damaged nuts; this preference appears greatest at low levels of damage and appears to decrease as damage increases.

An examination of the plotted points suggested that a curve of the type $Y = aX^b$ (where b is negative) would describe the relationship. Each variate was converted to common logarithms, and a linear regression of the type

$$\log Y = b \log X + \log a$$

for each site and each year was calculated by the method of Steel and Torrie (1960, p.163).

The regressions for Beerwah, and S1 1972-73 were both highly significant (P=0.01) (Table 81). A test of the difference between their regression coefficients and adjusted means (by analysis of covariance, Snedecor 1956, p.395) did not show that they were different from each other. When combined, the regression coefficient was highly significantly different from zero (Table 82). The regression explained 53.7% of the total variation of the observations.

The regressions for S1 1973-74, and H2 1972-73 and 1973-74 were not significant (Table 81). These data cover only the low percent damage range (Figure 65). Relatively few of the points for Beerwah and S1 1972-73 lie within this range.

It was considered most useful to combine all the data for a gen-

eral expression. The failure of three sites to provide significant regressions has been noted, and may be investigated at a future date if the proposed relationship proves useful. The linear regression equation for the combined data is:

$$\log (\text{egg ratio}) = -0.7092 \log (\% \text{ damage}) + 1.4198$$

The regression is highly significant (P=0.01), with a linear correlation coefficient of r = -0.6938 with 76 degrees of freedom. The relationship explains 48.14% of the total variation of the observations. Using antilogs the relationship becomes:

$$\text{egg ratio} = \frac{26.29}{(\% \text{ damage})^{0.7092}}$$

If the egg ratio (1) is plotted against density of unhatched eggs (3), a graph almost identical to that in Figure 65 results.

The general linear regression (all sites and years combined) line for this is:

$$\log (\text{egg ratio}) = -0.7230 \log (\text{unhatched egg density}) - 0.0458$$

This regression is also highly significant (P=0.01) with a linear correlation coefficient of r = -0.5701. The relationship explains 32.5% of the total variation of the observations.

Following these calculations, it was thought that the amount of unexplained variance might be reduced by combining the two expressions in a multiple regression using the method described by Little (1966, p.53-58). The resulting espression was:

$$\log (\text{egg ratio}) = 1.0877 - 0.5869 \log (\% \text{ damage}) - 0.2193 \log (\text{unhatched egg density})$$

or

$$\text{egg ratio} = \frac{12.24}{(\% \text{ damage})^{0.5869} (\text{unhatched egg density})^{0.2193}}$$

This expression explained only 49.7% of the total variation. The addition of the unhatched egg density factor to the regression of egg ratio on % damage did not significantly decrease the unexplained variation about

regression (Table 83).

It is therefore apparent that in the data used to obtain these expressions, egg ratio can be predicted equally well by percent damage or unhatched egg density. This may not always be the case. Situations where there is a high percentage of damage and a low egg laying, or *vice versa*, can be visualized.

Therefore although the expressions may describe what occurred in this study, careful consideration should be given to accepting their generality. More precise experimentation is indicated.

The use of these relationships will be discussed in Section VI.

The distributions of unhatched eggs on damaged nuts and on undamaged nuts were investigated further.

Figure 66 shows the relationship of variance to mean of unhatched eggs per nut for both damaged and undamaged nuts taken in samples of tree nuts for 1972-73 and 1973-74.

Examination of these plotted points suggested that a relationship of the type $s^2 = a \bar{x}^b$ may hold (this is the relationship of Taylor's power law (Southwood 1966, p.9)).

Logarithms were taken for the mean and variance in each of the 10 site-year combinations of data (e.g. S1 1972-73 damaged, S1 1972-73 undamaged, Beerwah 1972-73 damaged, Beerwah 1972-73 undamaged etc.) and linear regressions of the type $\log (s^2) = \log a + b \log \bar{x}$ were determined.

Within each class - damaged, and undamaged - the regressions at each site and year were significant (P=0.01). They were tested for homogeneity by the analysis of covariance (Snedecor 1956, p.395). All were homogeneous (P=0.05) in damaged nuts. In undamaged nuts all the regression coefficients (b) were homogeneous, but the adjusted mean of H2

1973-74, was just significantly different from the mean of the other pooled regressions (computed F (1,62) = 4.01, tabular F 0.05 (1,60) = 4.00). This difference was marginal, and under the circumstances not considered great enough to justify the exclusion of these data.

Pooled regressions for each of damaged, and undamaged nuts were then calculated and tested for homogeneity by the same covariance test. These results (in Table 84) showed that although the regression coefficients were not different, the adjusted means were ($0.05 < P < 0.01$). The two lines are therefore not the same. They are:

(1) Damaged

$$\log (s^2) = 1.1543 \log (\bar{x}) + 0.1325$$

or

$$s^2 = 1.357\ \bar{x}^{1.154}$$

(2) Undamaged

$$\log (s^2) = 1.0431 \log (\bar{x}) + 0.1289$$

or

$$s^2 = 1.346\ \bar{x}^{1.043}$$

These are plotted in Figure 66.

The curve describing the variance relationship with mean eggs for undamaged nuts seems flatter than that for damaged nuts; the rate of clumping or contagion of eggs seems to increase in damaged nuts as the mean increases, but not to the same degree as in undamaged nuts. There could be a variety of reasons for this. One possible explanation is:

If, during periods of oviposition activity, the female *C. ombrodelta* lays one egg and then moves on before laying another, at a low rate of egg laying few nuts would be visited more than once and the distribution of eggs would tend to be random. At higher rates of egg laying, damaged nuts (usually a small percentage of total nuts) would be relatively scarce, and would be revisited frequently; this would increase

the contagion of eggs on these nuts. Undamaged nuts being plentiful, would receive fewer visits per nut, and thus the distribution of eggs on these would be less contagious.

2. EGGS

Hatched and dead *C. ombrodelta* eggs remain on the plant surface for a considerable though undetermined period. Their stability seems to depend to some extent on the weather, and to some extent on characteristics of the host plant.

Wet weather appears to dislodge hatched eggs, and break up dead eggs, making them difficult to distinguish from those which hatched normally. van Emden and Way (1973, p.188) noted that some plants dislodge or suffocate eggs by producing callus tissue. This reaction was observed in *B. galpinii* in relation to *C. ombrodelta* eggs. However, the eggs are not affected until after they have hatched.

If these various effects were estimated, the counting of hatched eggs could be a useful means of estimating total natality, and its rate over a period, as discussed by Morris (1955) for *Choristoneura fumiferana*.

CHAPTER 17

BIOLOGY AND BEHAVIOUR. II. LARVAE, PREPUPAE, AND PUPAE

In this chapter the prepupal stage is divided into two parts. The first is the mobile prepupa which is defined as being that stage after larval development is complete, and before the pupal cocoon is spun. This period is visually indistinguishable from the mature larva. The remaining prepupal period is functionally indistinguishable from the pupa, as both are immobile, and relatively insulated from the active forces of their environment.

Observation and study of larvae and prepupae was difficult because of the concealed habit of larvae and the impracticality of maintaining constant watch for prepupal movement. Some experiments were performed in macadamia, in an attempt to elucidate behaviour patterns and mortality factors which were suggested by observation and the sampling results. These were only partly successful but have given some indication of the processes involved. Emphasis is given here to the behaviour patterns; mortality factors will be discussed in Section V.

The experimental methods will be described first, and their results shown. These will then be discussed in the appropriate part of the description of developmental periods.

A. METHODS

(i) General

Experimental study populations in the field were obtained by caging mated female *C. ombrodelta* on racemes for 24 hours. This method usually provided very high density populations of young larvae for study. Alternatively, known numbers of newly hatched larvae were transferred to

racemes in the field. A small hole made in the surface of the nut encouraged establishment.

(ii) Sticky Cones

Nine groups of racemes carrying 2-12 nuts each were selected in Aspley S1 in 1973-74. There was a total of 50 nuts.

Mated adult females were caged on the racemes for 24 hours. Eggs were counted, and plastic cones, coated with Stickem Special, were suspended in the tree so that each cone enclosed one of the groups of racemes (Figure 67).

Branches leading from these racemes to other parts of the tree were banded with Stickem Special at a point within the cone. Inside the Stickem a band of artificial medium in an open ended plastic bag, was tied to the branch and inside this a strip of corrugated cardboard was placed to detect mature larvae moving out of the nuts to pupate.

A week after oviposition the nuts were examined, and dead eggs and active holes estimated. Active holes are manifest by the frass ejected from them. In macadamia the number of active holes is not a good indicator of larval numbers, as several larvae may use one hole.

The cones were removed and examined with the aid of a Gowlands head loupe and any larvae on the sheets were counted and removed, after which the cones were replaced. The artificial medium was removed and examined under magnification to detect larvae. The cardboard strips were also examined. This inspection procedure was repeated every week for six weeks.

The racemes were checked daily, and fallen nuts removed intact to field trays (to be explained below).

(iii) Pupal Bands

Geier (1963) found that strips of corrugated cardboard, tied round the trunks and branches of apple trees, were used as pupation sites by mature codling moth larvae.

Strips of corrugated cardboard, approximately 5 cm wide, were tied round the branches and trunks of macadamia trees.

On Tree 194 at Beerwah, 30 bands were placed so that movement within at least half the tree was covered, and all mature larvae moving down the main trunk to the ground, or up from the ground would have had to pass through the bands.

At Aspley in 1972-73 five bands were placed in each of six trees in the inside rows of each variety from 2.I.73 to 2.II.73. On the latter date five bands were also placed in each of six trees in the outside rows of each variety. Thus from 2.II.73 to 23.III.73 there were 120 bands in position. In each tree one was around the base of the main trunk and the other four detected movement on two major branches which together were estimated to total one third of the canopy.

Bands were checked each week.

Ants were present, especially in wet weather when they built extensive nests in the bands. This may have reduced the probability of pupal formation in the band.

It was assumed that pupal bands were efficient traps for mobile prepupae. To test this assumption mature larvae were released on the trees with bands; it was found that larvae did not leave a band after they had entered it.

The numbers of prepupae and pupae found in the bands are accepted as an estimate of those mobile prepupae which left tree nuts. For the time being no assumption is made of their fate if the bands had not been present.

(iv) Fallen Nuts

a Beerwah barriers

During the period of highest nut fall at Beerwah in 1972-73, not all nuts falling from Tree 194 were examined in the week of fall. Those not examined were divided into four groups and placed in a restricted area under this tree. Each group was surrounded by a ring of corrugated cardboard approximately 10 cm high and 40 cm in diameter. The bottom edge of the cardboard was buried in the ground to a depth of 1 cm, and the outside surface coated with Stickem Special to discourage entry or exit of larvae with respect to the enclosed area.

Conditions within the barrier were expected to be similar to those outside. However, ants were more numerous within it. Rainfall run off was also restricted and in periods of heavy rain, water partly submerged the nuts.

Two of the four groups were examined after one week, the remaining two after two weeks. Each nut was dissected and examined under the binocular microscope as described in Chapter 14; larval head capsules were measured. The cardboard barrier was pulled apart and examined for prepupae and pupae. The soil within the barrier, to a depth of 1 cm, was collected and subjected to both wet and dry sieving to detect larval remains, or prepupae and pupae.

In an attempt to define the movement of larvae from fallen nuts more precisely further series of experiments were prepared in 1973-74. A major aim was to restrict more closely the experimental area, so that escape from it by any larvae could be considered very unlikely.

b Plastic trays

Plastic T20 trays had numerous drainage holes punched in the bottom which was then covered with a single piece of cotton gauze. Each tray was filled to a depth of 2 cm with sieved soil and the sides were lined with strips of corrugated cardboard. A maximum of five nuts was placed in each tray (Figure 68). The tray was then placed on supports over a shallow dish of water and placed in a large cage (120 x 180 x 304 cm) in the author's garden. A clear plastic cover was placed over the cage, so that different water regimes could be artificially maintained in each tray.

c Cups

S51S cups were prepared as above except that they were not placed over water. A maximum of five cups were placed on a 30 cm square metal tray covered with Stickem. Holes were bored in the corner of the tray to allow for drainage. Cups were held under roofed ambient conditions and watered lightly every two days. One nut was placed in each cup.

d Field cups

Waxed S51S cups were pierced for drainage, fitted with a gauze bottom and filled to a depth of 1 cm with sieved soil. A corrugated cardboard strip was placed around the inside wall of each cup. One nut was placed in each. Each cup was then placed inside a C20 plastic cup with drainage holes and which was coated inside with Stickem. The whole was covered with cotton gauze (Figure 68). Nineteen such cups were placed under trees in the Aspley orchard in 1974.

All the dishes described above (b, c, and d) were protected completely from predators.

e Field trays

These were metal trays, 30 cm square and 5 cm deep, welded to a cross piece of 2.5 cm diameter pipe, which held them off the ground. Their bottoms were pierced to provide numerous drainage holes. A single piece of cotton gauze was placed in the bottom, and sieved soil added to a depth of approximately 2 cm. Corrugated cardboard was placed vertically inside the perimeter and the outside edge was liberally covered with Stickem Special to prevent larval escape. Two such trays were placed under macadamia trees in Aspley S1. Each tray held 16 nuts (Figure 68).

Ants nested in the trays, gaining access through the drainage holes. Winged parasites and predators would have had relatively uninterrupted access to the nuts.

The nuts used in each of these experiments came from source (i) or (ii) on page 171-2. These nuts had been examined daily in the tree and, when one fell, it was transferred to one of the types of trays within 24 hours. It was not possible to determine the number of larvae being introduced to each tray as this could only have been done by dissecting the nuts.

It was hoped, however, that if the barriers to larval escape were secure all living and dead insects could be found and counted at the conclusion of each experiment, thus allowing a budget to be compiled.

All trays except the field cups were examined at least once every two days to detect escapes or adult emergence. After a period of not less than 60 days, when it was considered that all possible emergences would have occurred, a final examination was conducted.

This consisted of dissecting all nuts and examining them (X3 magnification) for larval remains or dead pupae, opening the cardboard barrier and examining it for insect pupation, and dry sieving all soil to detect dead larvae or pupae.

B. RESULTS

(i) Sticky Cones

With the exception of the mature drowned larvae in the 4th and 5th week of inspection, the only larvae detected in the various barriers were first instars in the first and second weeks after oviposition, and two second instars in the medium bands in the second week (Table 85); it is considered that these probably entered the medium as 1st instars and moulted within it.

A very large number of larvae, 247 in a total of 390, were not accounted for. This is disappointing and severely hinders interpretation of the results.

The only likely explanation for the loss of larvae is that it occurred in the period soon after hatching. When newly emerged larvae were being transferred to nuts in the field, it was noted that only a slight wind was required to blow them away from the nuts, horizontally, or even upwards. Such a loss could have occurred in the experiment; older larvae falling from nuts are thought to have been too heavy to have been blown out of the cones.

(ii) Pupal Bands

The results of the pupal band trials are given in Table 86.

The comparison between estimated numbers of prepupae moving out of nuts at each site, with the estimated number of prepupae and pupae in nuts of similar dates, is only approximate. It has previously been explained (Chapter 14) that the estimates of stages within the nuts have a very low precision. The estimates of stages in the bands are also imprecise in that they are subject to error in the estimate of the proportion of the tree the bands cover, and sampling error is again high - the 95% confidence interval length being of the order of 200% of that estimate.

However, the comparison suggests that a substantial proportion of the prepupae present in nuts on the tree leave these in search of pupation sites.

(iii) Fallen Nuts

a Beerwah barriers

Figure 69 shows the population change with time for each of the three series of nuts examined; these estimates are expressed on a per 100 nuts basis.

The length of the 95% confidence interval for each week and series estimate averaged over all non zero estimates in the week-series is shown in Table 87.

Because there were only three series covering three weeks each, and the graphs of population change shown did not exhibit any marked differences, the series were pooled (Table 87).

These pooled results reveal a steady decrease in living immatures in fallen nuts over a three week period. The number of deserted holes increased sharply in the period between the first and second weeks, followed by a further increase in the next week. The proportion of mature larvae moving out of nuts to pupate appears substantial, approximately 70%.

The larvae recorded in nuts in week three were assigned to the instars shown on their head capsule measurements. It could be expected from the development time data and the mean temperature of 25.3^{o}C at Beerwah during the experiment that no larvae younger than finals would be found. The apparently younger larvae are probably the result of adverse conditions and poor nutrition. Nuts collected and held in the laboratory frequently gave rise to many very small adults after several weeks.

The decline in numbers of young larvae during the three week

period was too great to be accounted for by the formation of new pupae. This experiment did not establish whether this decline was due to mortality in the nut or after emigration.

b Cups and trays 1973-74

The results for all experiments are shown in Table 88. Although all the nuts showed signs of larval damage when examined, in 47 of the total 146, no signs of larvae or pupae, dead or alive, could be found; nor were there sufficient numbers of dead larvae or living or dead pupae outside the nuts to be assigned to these 47 nuts. Considering the precautions taken it is unlikely that such large numbers of larvae could have been missed; they are assumed to have died within the nut either from a variety of causes before the nut fell, or from cannibalism after the nut fell.

Because of this uncertainty and because initial larval numbers were unknown, all results are examined as a percentage of pupae found in the nuts. Statistical comparisons were not made.

Because of the extremely wet weather in the field during early 1974, the conditions in the field cups and trays may be considered comparable, or even wetter than those which were watered every second day.

Temperature in fallen nuts. Temperatures in the husk of fallen nuts, were compared to that in nuts on the tree. Records were taken at Beerwah, in 1972-73. The equipment used was a Thermocouple Potentiometer, type D.R.P. 3 No. 1354/23 (CSIRO patent 2180/61). The results are shown in Figure 70.

C. DISCUSSION

The information available for the period between egg and established prepupae will now be given. The results of the above experiments and their implications will be discussed in the appropriate place.

The period is divided into:

(1) Pre-establishment larvae - between hatching, and tunnelling to a secure depth in the host.

(2) Established larvae - from establishment to the onset of the prepupal stage.

(3) Mobile prepupae - as described previously - from the completion of larval development to establishment in a pupal cocoon.

1. PRE-ESTABLISHMENT LARVAE

Upon hatching, the larva moves away from the egg shell and begins an apparently random search of the nut surface which may be continued for as long as 24 hours. Its movements are rapid at first, with frequent changes in direction. It frequently raises its head, moving it from side to side. Its behaviour appears very similar to that described by Hall (1934) for newly hatched codling moth larvae.

During this period, if the larva finds a hole - usually caused by a previously established larva - it will almost invariably enter and become established in the side of the existing tunnel. If such a hole is not found, the larva often begins tunnelling in the surface but frequently

begins to wander again before establishment. Larvae which do not succeed in establishing either die on the surface or, more frequently, fall from the nut with or without a silken thread attached to the nut surface.

In successful establishment, the larva chews into the fruit, covering itself with a light silken net, into which chewed pieces of fruit are incorporated. The results of the sticky cone experiment indicate that only a small percentage of total larvae are successful in establishment on undamaged nuts.

It is unlikely that an appreciable number of larvae falling from the nut on which they hatched would land on another nut. If they landed on a leaf or branch there would be a low probability that they could negotiate the numerous junctions to reach a nut.

For a similar reason, it is believed that many of the eggs (approximately 25% of total, Chapter 14) laid on canopy parts other than the nut, do not become established. However, those on the rachides probably would. In the laboratory, larvae could find nuts as far as 50 cm away from the point of hatching on a straight macadamia branch.

Establishment in parts other than fruit: In the sticky cone experiment none of the 380 pre-establishment larvae attacked parts other than the nut. In another experiment inspected one week after oviposition, only four of 228 established larvae were in rachides.

During the canopy inspections of macadamia trees no signs of *C. ombrodelta* larval activity were observed in any part other than the nut. On racemes on which adults had been caged, resulting in very high densities of pre-establishment larvae, only eight cases of establishment in rachides were observed; four of these were left undisturbed and larval

activity appeared to cease after 7-10 days; no adults emerged.

In *Bauhinia*, infestation of the peduncle appears to be quite common and successful. As the peduncle is taken with each fruit sampled this does not constitute a sampling error.

Table 3 shows that *C. ombrodelta* attacks the terminal branches of many of its hosts.

2. ESTABLISHED LARVAE

Very little is known of the details of larval activity within the fruit.

In macadamia, when the shell is soft, larvae tunnel through to the kernel which they eat preferentially. When the kernel is consumed (approximately 4 days for 4th or older instars) they then attack the inside of the husk. The shell is usually not completely eaten. When infestation occurs after the shell has hardened, tunnelling is confined to the husk; the inner portion against the shell is preferred. Sometimes small depressions are chewed in the hard shell, but only in thin shelled varieties or in nuts severely damaged by other insects (mostly *Amblypelta nitida* (Coreidae)) do larvae penetrate to the kernel. In hard shelled nuts, a single husk appears to provide sufficient food for complete larval development.

In *Bauhinia* fruit, larvae tunnel through the husk to the seeds, which are found along one margin. They appear to eat the seed preferentially and, having consumed one, tunnel inside the margin to the next.. In dead pods with a hard dry husk, larvae are most frequently found within the seeds which remain soft and apparently palatable for a much longer time.

In both hosts the tunnel always extends to the outside of the fruit; the opening is usually sealed by a plug of frass. Frass and exuviae are regularly ejected from these holes, keeping the tunnels clear.

(i) Multiple Infestations

In view of the preference of the female *C. ombrodelta* to oviposit on previously damaged nuts, and the apparently easier establishment of larvae in these, it is not surprising to find multiple infestations in some nuts. Table 59 shows the total recorded occurrence of macadamia nuts taken in samples which had one or more living immature stages (excluding eggs). 75.38% of infested nuts had only one living larva, 18.50% two, 4.63% three, 1.17% four and 0.32% five.

Table 89 gives a summary of multiple infestation of immatures found in samples taken from both Aspley varieties in 1972-73 and one of the Beerwah trees in 1972-73. Only those nuts having two or three living stages were considered for this summary.

It is apparent that a mixture of ages is most common. This would be expected from the oviposition habits of the adult.

In alternative host fruit samples 69.16% of infested fruit had one living larva, 21.14% two, 5.97% three, 2.37% four, 1.01% five, 0.28% six and 0.07% seven (Table 70). There were slightly more multiple infestations in alternative hosts - possibly a reflection of their larger fruit size.

(ii) Movement of Larvae and Prepupae from the Fruit

a In the tree

In the sticky cone experiment no larvae were detected in the various barriers, after the pre-establishment period (excluding the five

mature larvae which drowned in the cones).

Tree inspection at Beerwah, where the trees are large and infestation is heavy, usually revealed some empty pupal cases in the junctions of branches where debris had collected. Pupal cases were also present, although infrequently, in the rough areas where branches had broken off. One *C. ombrodelta* pupa was observed between two leaves which touched. No pupae were found in the Aspley trees.

Considerable numbers of pupae were found outside the fruit in the Aspley *B. galpinii*. This plant has a dense network of branches which die and rot inside the canopy, apparently becoming suitable for pupal shelters.

The results of the pupal band experiments indicate that a large proportion of mobile prepupae leave the tree nuts in search of pupation sites (Table 86). How long they search and how far they travel in this search is unknown. It is thought that pupation sites are relatively scarce in macadamia trees.

Several mature larvae were released on macadamia trees and their actions observed. Each moved along the branches, rapidly at first, pausing frequently to examine irregularities in the surface. During this period they invariably ignored junctions of twigs and leaves and remained on large branches. After approximately 30 minutes their movements slowed, and they began searching leaves and twigs. They generally moved back and forth along only a few branches. After 83 minutes one fell 1.8 metres to the ground. It was attached to a leaf by a silken thread and immediately began climbing this and regained the leaf after 12 minutes. It then began searching the branches again.

Searching was terminated in each case by the placement of pupal bands in front of each larva. This searching behaviour of mobile *C. ombrodelta* prepupae is similar to that described by Geier (1963) for mat-

ure codling moth larvae.

The pupal bands did not detect the proportion, if any, of young larvae moving in the tree.

b From fallen nuts

Only on one occasion has a *C. ombrodelta* larva been observed free on the ground under natural conditions. This was a 4th instar at Beerwah, which was attempting to establish itself in an undamaged fallen nut. It was being attacked by ants.

The Beerwah barrier experiment (Table 87), whilst indicating that a substantial proportion of mature larvae in fallen nuts leave these in search of pupation sites, does not indicate the amount of movement from fallen nuts by younger larvae.

In the cups and trays experiments (Table 88), 43 larvae were detected leaving the nuts. All but one were mature; the exception was a 4th instar.

Ten of the mature larvae died within the trays or cups; seven of these were observed during the process of dying. These all moved out of the nuts in hot sunny weather, apparently in distress, and moved under the shadow of the nut. Five, all in unwatered trays, died within six hours of their emerging from the nuts. The other two, in field trays, remained alive but moribund for two days, during which time they were not attacked by ants within the tray. They disappeared within 48 hours of their apparent death.

Larvae in fallen nuts probably frequently suffer severe heat stress. Figure 70 shows temperatures recorded in nuts on several occasions. Even in cloudy weather temperatures in fallen nuts are higher than those in nuts on the tree, although not to an extent likely to produce stress. On sunny days temperatures become extreme; in one fallen

nut the temperature was greater than 40°C for three hours, with a peak of 49.9°C.

Nine of the 43 mature larvae leaving nuts pupated in the cardboard barrier. For these experiments, the figure of:

$$\frac{\text{pupae in cardboard}}{\text{pupae in nuts + pupae in cardboard}} \times 100 = \frac{9}{70+9} \times 100 = 11.4\%$$

can be compared with the result of 71.4% for the Beerwah barrier experiment. The greater movement out of Beerwah nuts was probably due to their being partly submerged during heavy rain. To test the effect of submergence a number of infested nuts were dropped into water. Most larvae left the nut after a short period.

The remaining 24 larvae which moved out of tray and cup nuts (Table 88) did not establish themselves in the cardboard barriers but fell into the water or Stickem surrounding the cups and trays. They may have been searching for a new feeding site as the nuts in the trays deteriorated or may have been searching further for a pupation site.

These results indicate that $\frac{43}{70} \times 100 = 61.4\%$ more mature larvae than are found in the nuts on the ground may have moved out.

Young larvae released on the ground usually showed some signs of distress and were quickly attacked by ants.

Mature larvae, however, were less troubled by ants unless they were injured. The movements of seven mature larvae released under Tree 194 at Beerwah were recorded. The ground had been raked the previous week, so few leaves were present; nuts had been collected that day. The soil is sandy loam and was moist on the day of the observations. The observations are summarized in Table 90.

It seems that mature larvae or mobile prepupae are able to pupate on the ground although such pupation was not detected by emergence traps.

The mobile prepupal phase is terminated when the pupal cocoon is completed. In this process a tight silken cocoon is spun, the exit hole of which is closed by two flaps folded together. The outside of the pupal cocoon has pieces of frass and plant tissue incorporated into it. Approximately one quarter of the way down the cocoon the prepupa finally constructs a light silken barrier behind which it pupates.

3. IMMOBILE PREPUPAE AND PUPAE

The head of the prepupa changes from a prognathous to a hypognathous position and within the larval skin the external pupal case is formed. The larval skin is split longitudinally from the anterior end and discarded at the base of the pupal cocoon. The newly formed pupa is white, changing rapidly to a light brown, and more slowly to a dark brown.

When ready to emerge the pupa, by wriggling and using the rows of spines on its dorsal surface, moves forward in the cocoon until it is about half way out of the exit. The forward part of the pupal case splits off and the moth emerges.

4. OVERWINTERING

Froggatt (1897) described larval populations of *C. ombrodelta* infesting *Acacia farnesiana* in northern New South Wales during the winter months, and Ironside (1970 unpublished report) reported that in Southeast Queensland, if macadamia nuts are available throughout the year, larvae may be found in these in every month (see p.14). The author has found all immature stages of the insect present in various host plants throughout the year.

It was shown in Chapter 13, p.114 that development time of immature *C. ombrodelta* is extended with the onset of decreasing daylength in autumn. These winter larvae require a suitable food supply.

In the new varieties of orchard macadamia it is expected that there could be a nut free period within the orchard between July and October. With suitable crop hygiene measures during this period, the probability of a carry over of within orchard populations of *C. ombrodelta* should be low.

SECTION IV

NATURAL ENEMIES

CHAPTER 18

THE NATURAL ENEMIES

The present investigation of the *C. ombrodelta* life system did not include a detailed study of the natural enemies of the subject species. However, some information was obtained during the course of the sampling programme.

Natural enemies are discussed in their traditional divisions of parasites, predators, and pathogens.

1. PARASITES

A. METHODS

(i) Egg Parasites

All eggs sampled, either hatched, dead, or unhatched, were examined under magnification for parasite activity.

In addition, more than 700 unhatched eggs from the alternative hosts sampled in 1972-73 were maintained in the laboratory on a surface of agar plus Nipagin and formaldehyde. These eggs were examined frequently for signs of egg parasite development.

(ii) Larval or Pupal Parasites

In both the intensive and survey samples, immature *C. ombrodelta* were extracted from the plant host material, examined for signs of external parasite attack and, if alive, placed in waxed medium blocks. The emergence of *C. ombrodelta* or parasites was then checked periodically.

The survey samples were mostly taken from the towns marked on Figure 1, to the south and west of Brisbane. Several samples of

Cupaniopsis anacardioides were taken in the Brisbane area. Collins - two backyard macadamia trees in suburban Brisbane - was sampled four times in 1971-72.

a Identification

Identification of the parasites is not yet complete. Mr I.D. Galloway[1] and Dr E.F. Riek[2] have assisted; some parasites have been sent to the British Museum (Natural History) for identification.

b Apparent percent parasitism

Apparent percent parasitism, although clearly an interaction of the parasite with its host, has been described in this chapter as a property of the parasite. It was calculated in the following way:

Ectoparasites. The number of hosts parasitised was expressed as a percentage of the total living hosts (1st instar to prepupae) plus the number parasitised:

$$\frac{\text{total parasitised}}{\text{total living + total parasitised}} \times \frac{100}{1} \%$$

Endoparasites. As the identification of endoparasitism relied on the emergence of a parasite in the laboratory, those hosts which died before emergence in the laboratory, and those which had died due to the ectoparasite (on the assumption that multiple parasitism occurred) were excluded from the totals. Therefore the figure was obtained from:

$$\frac{\text{parasite adults emerged}}{\textit{C. ombrodelta} \text{ adults emerged + parasite adults emerged}} \times \frac{100}{1} \%$$

---

1. Mr I.D. Galloway, Department of Primary Industries, Brisbane.
2. Dr E.F. Riek, Division of Entomology, CSIRO, Canberra.

To estimate the standard errors of these apparent percent parasitism rates the data are assumed to be consistent with the binomial distribution (the host either is parasitised - or not), and the approximation to the normal distribution (Steel and Torrie 1960, p.353) has been used. Thus the variance is: p (1-p)/n where p is the proportion of individuals with parasites, n is the total number of individuals emerging. The standard error of a percentage is $(\sqrt{\frac{p(1-p)}{n}}.(\frac{N-n}{N-1})).\frac{100}{1}$; N is the total larvae in each sample.

B. RESULTS AND DISCUSSION

(i) Egg Parasites

No signs of parasite attack were discovered. Of the eggs maintained on agar, some were killed accidentally during inspection, or eaten by newly hatched larvae. Of the 699 which had the opportunity to hatch normally, 659 hatched and 40 died without signs of parasite activity.

(ii) Larval or Pupal Parasites

Six primary parasites of *C. ombrodelta* were recorded during the study. Five were endoparasites, the other an ectoparasite. One apparent hyperparasite was recorded. These are shown in Table 91.

Tables 92 and 93 give a summary of the occurrence of each of the parasites. More detailed descriptions are given below.

a Primary parasites

Tachinidae. The highest apparent parasitism recorded for this unidentified species was 22.22% (± standard error(s) 13.86%) in Aspley H2 during the 1972-73 season.

It is not known when or how the parasite attacks *C. ombrodelta*.

The parasite pupates inside the host pupal integument. On emergence, the fly pushes through this integument and through the exit of the *C. ombrodelta* cocoon.

Chalcididae *Brachymeria pomonae* (Cameron). 6.67 ± 6.44% is the highest intensity of attack recorded for this parasite. This was in the Aspley *Bauhinia (B. galpinii)* in 1972.

Like the Tachinid it pupates within the *C. ombrodelta* pupal integument, and emerges in a similar manner. It is not known how host infestation occurs.

Riek (1970, p.918) stated that *B. pomonae* is a parasite of codling moth.

Eulophidae *Euderus (Neoeuderus)* sp. Only one specimen of this parasite was recorded. The host was collected on *B. galpinii* at Boonah, Queensland.

It emerged from a 2nd instar larva, which was left as an empty integument. No cocoon was visible.

Ichneumonidae *Gotra bimaculata* Cheeseman. The highest rate of parasitism recorded was 10.0 ± 9.49% in Aspley S1, 1973-74.

There is no information available on the initiation of infestation. When the host has completed larval development and spun a cocoon, the large apodous parasite larva emerges from the host, and constructs a black papery cocoon inside that of *C. ombrodelta*. It emerges through the *C. ombrodelta* exit hole.

For the two most common parasites described below, the apparent percent parasitism recorded during the seasons at the main sites is shown

in Figures 71 to 74.

Braconidae *Apanteles briareus* Nixon. The time or manner of infestation by this parasite in *C. ombrodelta* is unknown. It is probable that infestation occurs early in the immature stage of the host. None of these parasites emerged from host larvae which were older than 4th instar (estimated by head capsule width) when collected (Figure 75). It is possible that the development of the parasite retards development of the host, so that a head capsule width equivalent to that of a normal fourth, may in fact represent an older stage.

When the infested host larva has a head capsule width equivalent to that of a 4th instar, it spins a pupal cocoon in the normal manner. At this stage the parasite larva leaves the host, discarding the host body near the opening of the cocoon, and spins a white papery coccon about 6 mm long in the lower part of the host cocoon. This is sealed with a flat circular white barrier. On emerging as an adult, the parasite pushes aside the barrier and leaves the host cocoon by the prepared exit hole.

Braconidae *Bracon* sp. This species is an ectoparasite.

In the field, attack by the *Bracon* sp. has been observed several times, both in macadamia and the alternative hosts. One such attack was observed from initiation to completion.

The plant host was *B. galpinii*. The parasite female moved slowly over the pod surface in the vicinity of borer holes, brushing the surface with its antennae. After about three minutes, it moved to the edge of the pod, and taking up a position along the pod axis began probing into the husk with its ovipositor. Within eight minutes, three probes each lasting from 30 seconds to 2 minutes 35 seconds were made. Each probe was accompanied by lateral, sometimes violent movements of the ovipositor.

Between each probe, the female moved forward several millimetres.

These movements were followed by a final probe which lasted 35 minutes. On six occasions the ovipositor was almost withdrawn, and then re-inserted. Periodically the female would sweep her antennae along the edges of the pod.

When the ovipositor was finally withdrawn, the female remained in position for approximately one minute, and then flew to a different pod, where she remained motionless for 10 minutes, at which point observation was terminated.

The fruit was dissected. The attacked larva (a 5A instar) was immobile, though still respiring; the heart was pulsating at approximately 60 beats per minute.

Three parasite eggs, translucent white, elongate, cylindrical (about 1 mm long and 0.2 mm diameter) were attached to the ventral surface of the first thoracic segment. During sampling eggs have been observed on most parts of the larval body.

The parasite larvae are apodous, 2-5 mm long. They feed externally and two or three larvae usually develop on each host larva. When their development is complete each constructs a white rectangular cocoon near the host body. Adults usually emerge through the host exit hole.

Figure 75 shows the frequency of attack in *C. ombrodelta* larvae of various head capsule widths. Apparently, older larvae are preferred. In addition, five prepupae were found to be attacked.

One of the prepupae had a head capsule width equivalent to a 4th instar, and an apodous larva was within its body. Presumably this was *A. briareus*. This is the only evidence available for multiple parasitism.

Bracon sp. is the only parasite recorded in this study in which more than one adult emerged per parasitised larva.

Occasionally during the sampling, moribund *C. ombrodelta* larvae were found. Some showed no signs of body movement, others "quivered". No evidence of parasites were found on these; they died in the laboratory. It is possible that this was the result of unsuccessful *Bracon* sp. attacks. Campbell (1963) reported that certain Ichneumonid parasites sting and kill up to 200 times more hosts than they successfully parasitise.

b Hyperparasite

Encyrtidae *Eupelmus* sp. Only four of these parasites emerged from *C. ombrodelta* collected in samples. All were from *B. variegata*, three from Cowie Road and one from Bald Hills.

The author was unable to identify the remains from which these parasites emerged. However, the *Cryptophlebia* larval body and its cocoon, and a papery white parasite cocoon with a white circular barrier, built inside the *Cryptophlebia* cocoon, suggested that *A. briareus* was the primary parasite.

The circular barrier was not pushed aside as usual. Instead there was a circular hole, approximately 1 mm in diameter, chewed in it.

2. PREDATORS

A. METHODS

The comparison of emergence from field trays and from laboratory trays and cups (Chapter 17) did not provide information on the effect of predators.

Consequently, the data available have been gathered by observation only.

B. DESCRIPTIONS

Ants (Formicidae). It was noted in Chapter 17 that ants have been observed attacking larval *C. ombrodelta*. However, during wet weather, ants' nests are sometimes found in nuts infested with living larvae, so their role as predators is not clear. There may be different species involved.

Pristhesancus papuensis Stål (Reduviidae). On four occasions during the study *P. papuensis* nymphs have been observed in the field (Aspley) preying on concealed *C. ombrodelta* larvae. One nymph was reared to an adult in the laboratory on *C. ombrodelta* larvae.

It is not known how important *P. papuensis* is as a control agent.

None of the sampled eggs showed signs of predator activity.

Probably, the frogs, spiders, and birds common in macadamia orchards also contribute to some extent to the natural control of *C. ombrodelta*.

3. PATHOGENS

A. METHODS

During sampling, a number of dead *C. ombrodelta* immatures were observed in various stages of breakdown, but with no visible signs of external damage. The number of such larvae was usually only a small proportion of the total in the sample.

Some of these dead larvae were taken to an insect pathologist[1]

---

1. Mr R. Teakle, Department of Primary Industries, Long Pocket Laboratories, Brisbane.

in an attempt to discover if a pathogenic agent was responsible for the death.

Two tests were conducted, at which the author assisted. In brief these were:

(1) The predominant bacterium present in the larval bodies was isolated, painted onto medium blocks and nut husks, on which a series of laboratory reared larvae were placed.

(2) A suspension of the dead larvae was prepared and painted onto medium blocks and nut husks and fed to young laboratory reared larave.

The rearing medium was prepared without the addition of formaldehyde, sorbic acid, or Nipagin.

B. RESULTS

In neither case was mortality in the test larvae greater than in control groups. It was thus concluded that infectious disease organisms were not responsible for the death of these sampled larvae.

The pathologist believed that it was unlikely that disease did not exist in field populations of *C. ombrodelta*, however it was apparently of little importance in the populations examined during this study.

SECTION V

INTERACTIONS IN THE *CRYPTOPHLEBIA OMBRODELTA* LIFE SYSTEM

In this section, the data available on each of the subsystems of the *C. ombrodelta* life system, are examined in their various interactions. Some new experiments are described and discussed. The interactions involved are summarized in Figure 76.

Two major subsystems, ALTERNATIVE HOSTS and MACADAMIA, are linked by migrating adults. The population processes involved in MACADAMIA have been summarized and shown in boxed areas, linked by unidirectional arrows. The arrows represent population changes with passing time.

The effect of *C. ombrodelta* infestation on crop quality is also shown. Those states of the insect which cause crop loss are linked to the CROP LOSS area with broken lines.

This interpretation of the life-system will be discussed further in the chapters on modelling.

The chapters in this section deal with:

(1) The alternative hosts as a reservoir for *C. ombrodelta*.

(2) Within macadamia interactions of the insect and its environment, with an emphasis on mortality factors.

(3) The effect of *C. ombrodelta* infestation on crop quality.

CHAPTER 19

ALTERNATIVE HOSTS AS RESERVOIRS OF INFESTATION FOR ORCHARD MACADAMIA

Full comprehension of the importance of alternative hosts of *C. ombrodelta* in providing a source of infestation for macadamia orchards will be possible only when a suitable technique for trapping the female moths has been developed. Extensive adult female trapping, detailed field observation of the adults, and laboratory experiments - e.g. flight mill studies - will provide information on which hypotheses of the insect's migration may be based.

Before such studies are carried out, however, it is important to survey the area around a study orchard, to estimate the size of a potential migrant population.

Such a survey was carried out in the area surrounding the Aspley orchard. This has been described in part, in terms of species present, sampling techniques, and sampling results in Chapters 9 and 10.

In 1973-74 one other experiment was performed to estimate qualitatively, the production of adults from areas around the orchard in comparison to the production of adults within the orchard. This experiment is now described.

A. METHODS

Orfamone II lure traps as described in Chapter 15 were used. Thus only males were caught. This is believed to have indicated sources of breeding, but yielded no data on the migration of insects.

One Orfamone II trap was hung in each of the 41 numbered positions shown in Figure 28. Five were in the orchard itself, eight in a square

0.2 km from the orchard boundary, 12 in a square 0.4 km from the first square, and 16 in a square 0.8 km outside the second.

Thus, the area trapped was approximately 3 km square, or 900 hectares. The traps may be considered non-competitive, as the manufacturers recommend their placement at one trap per 1-2 acres (0.4-0.8 ha) (Zoecon 1972). Trap density was as high as this only in the orchard.

The traps were hung in trees of various species, at a height above the ground of 300-360 cm. Traps were in position, with some exceptions, for 30 weeks, from 21st August 1973 to 19th March 1974. The exceptions were as follows:

1st week 21-28.VIII.	- 8 traps	- 5 not yet placed, 3 blown down.
16th week 4-11.XII.	- 1 trap	- lost without trace.
23rd week 22-29.I.	- 36 traps	- blown down by cyclone 'Wanda'.
24th week 29-5.II.	- 1 trap	- lost without trace.
25th week 5-12.II.	- 1 trap	- blown down
30th week 12-19.III.	- 12 traps	- blown down by cyclone 'Zoë'.

Lures were replaced every eight weeks. Dr Olsen (1973 pers. comm.) stated that tests by Zoecon had shown no appreciable decline in lure attractiveness over six weeks in normal field conditions, and only slight declines after this. Traps were replaced as required by their weathering.

B. RESULTS

The total catch of male *C. ombrodelta* in all traps is shown in Figure 77. For those weeks in which traps were missing, their catch was estimated from their catch in other weeks. These estimates are indicated in the figure by a distinct symbol.

Mean catch per trap per week for the different squares of traps,

and the orchard traps are shown in Figure 78. No adjustment for missing traps was made in this case.

Finally the catch for each trap, each week is shown as a percentage of the total catch that week in Figure 79.

C. GENERAL DISCUSSION

(i) Species Distribution

The distribution of alternative hosts in Southeast Queensland was discussed in Chapter 9. The distribution of hosts in the 900 ha square ("lure trap area") around the Aspley orchard was examined in more detail (Figure 28). In this area there were:

383 *Cassia coluteoides*

95 *Delonix regia*

82 extra-orchard macadamia

65 *Bauhinia variegata* (and *B. variegata* var. *albens*)

38 *B. galpinii*

11 *Cupaniopsis anacardioides*

7 *Poinciana pulcherrima*

6 *Acacia podalyriifolia*

5 *Cassia fistula*

It is apparent that certain traps (Figure 79) had a consistently low catch, in other traps a consistently high percentage of the weekly total catch was recorded. A comparison of the trap numbers in Figure 79 and the host distribution (Figure 28) shows that, with the exception of trap 6, high catch coincided with dense host distribution. Figure 80 shows the different types of vegetation in different trapping areas.

Figure 78 shows that the outermost square of traps consistently caught the highest number of males per trap. In general, mean catch per trap decreased in squares successively closer to the orchard. There is

a high concentration of hosts around the perimeter of the lure trap area, but catch in the outermost square is undoubtedly influenced by conditions outside the area mapped (Figure 28). In the region to the north of this area, housing settlement becomes less dense and the number of alternative hosts is also low. To the south and east, housing is more dense with gardens rich in alternative hosts (this includes the area used in the lure trap trial described in Table 76 where average catch was approximately four males per trap night). To the west, although housing was sparse, gardens were extensive and had many alternative hosts.

(ii) Temporal Distribution

The periods when the common alternative hosts may be expected to be suitable for carrying populations of *C. ombrodelta* are illustrated in Figure 29. The host availability can be broadly classified as follows:

Overwintering	*Acacia farnesiana*
	B. galpinii
	Cassia coluteoides
	Cupaniopsis anacardioides
	Delonix regia
	some macadamia
Immediately prior to orchard infestation	*Acacia podalyriifolia*
	B. variegata (and var. *albens*)
	Cupaniopsis anacardioides
	some macadamia
During orchard infestation	*B. galpinii*
	B. variegata (and var. *albens*)
	Cassia coluteoides
	Delonix regia
	Poinciana pulcherrima
	macadamia

The period immediately before orchard macadamia infestations may be expected, has the lowest number of the host species listed. Only the *B. variegata* provides large sources of infestation early in the macadamia season. By the end of December the number of hosts available increases, and large populations of adults may be expected.

(iii) Relative Population Size in the Alternative Hosts

Data are not available on which accurate comparisons of the number of adult *C. ombrodelta* produced from each of the alternative host species can be made.

Very approximate comparisons can be made between orchard macadamia, and those alternative hosts from which samples were taken: e.g. the mean weekly estimate of third instar larvae was:

Host	Mean weekly 3rd instar population per tree
Aspley orchard macadamia H2 and S1, 1972-73, 1973-74	5.9
Acacia podalyriifolia	36.4
B. galpinii	291.0
B. variegata (all sites)	202.9

A subjective assessment of the other hosts indicates that *Cassia coleutioides*, and *Poinsiana pulcherrima* would support a slightly lower population than macadamia, say 5 on the above scale; *Cupaniopsis anacardioides*, *Cassia fistula* and *Delonix regia* probably are somewhat better hosts, say 15.

Thus it is expected, that in the lure trap area there would always be migrant adults present, building up to a peak in summer, during the macadamia fruiting period.

The lure trap catches (Figures 77 to 79) confirm this expectation.

The very high catches in the first three weeks apparently are the result of emergence of adults from winter hosts. The two smaller peaks correspond to the late spring period of lower host availability, and the final peak to the summer abundance of hosts.

It is interesting to note that the insect appears to maintain generations over a fairly wide and diverse area although in any host, breeding may be considered to be continuous with all stages represented in any sample (Figures 49 to 53, 58 and 59). Synchronization is imperfect. The average generation time is 14,218 hour degrees (egg to adult) plus 1,014 hour degrees (time for egg maturation) equalling 15,232 hour degrees.

At the temperatures prevailing from August 1973 to March 1974 the periods between the peaks were as follows:

1st peak to 2nd	1.3 generation periods
2nd peak to 3rd	0.8 generation periods
3rd peak to 4th	1.1 generation periods
4th peak to week 30	0.9 generation periods.

Taking account of the inaccuracies in the calculations, it seems that the period between peaks, up to the 4th (week 24) was that taken by one generation. Some variation may have been due to changes in the suitability of the weather for trapping.

The failure of the trap catch to approach a peak again between week 24 and 30 may be due to a high mortality incurred by the cyclones and heavy rain, or due to the lengthening of the generation time due to shortening day length (Chapter 13).

The plot of estimated total eggs laid per week in the Aspley orchard (Figure 77) shows an approximate correspondence with the total adult catch, indicating that male catch has some relationship to female activity. The fact that egg numbers did not fall in December-January, and in March, as sharply as the total adult catch, may be explained by local variation in the emergence of adults compared with that in the entire

area (e.g. from the Aspley *Bauhinia* (*B. galpinii*)), or by some breeding and emergence of adults within the orchard itself. The reason for the sharp decline in egg laying on 1.II. is not clear.

Breeding and emergence of *C. ombrodelta* in the Aspley orchard was apparently much less in 1973-74 than in 1972-73. Four Orfamone II traps hung in the orchard in 1973 for a period of six weeks (31.I.73-13.III.73) caught an average of 22.33 males per trap per week. The five traps in 1974 over the six weeks from 30.I.74-12.III.74 caught an average of only 2.27 males per trap per week. This difference was confirmed by the sampling data (Figures 51 and 52).

(iv) Migration between Hosts

As the *C. ombrodelta* hosts listed are suitable for infestation by this insect for only two or three consecutive generations each season, it is likely that adults are adapted to migration from the breeding area, seeking new hosts. Southwood (1962) discussed this concept. It is similar to Johnson's (1969, p.20) Class I migration.

Examination of the population graphs for *C. ombrodelta* on *B. variegata*, and *B. galpinii* confirm this view (Figures 58 and 59). In each of these hosts, it seems that adults continue to emerge for a longer period than eggs are deposited on that host. In each host, the sharp decline in oviposition on the host corresponded with host pod death (Figures 32 and 33).

The sudden decline in oviposition suggests that the adults emerging after pod death move rapidly out of the area, and are not merely carried on the wind by accident as they search the emergence area for suitable oviposition sites. Accidental wind borne migration appears to occur in *Choristoneura fumiferana* (Clem.) (Johnson 1969, p.447). (Southwood (1962) described this insect as a permanent habitat species.)

There is therefore some suggestion of ontogenetic development of migrating *C. ombrodelta* adults, with host fruit physiological development.

CHAPTER 20

WITHIN MACADAMIA INTERACTIONS. I. MORTALITY FACTORS OF IMMATURE *C. OMBRODELTA*

Bess (1945), Simmonds (1948), Morris (1957, 1965) and Southwood (1966), discuss the difficulty of measuring and interpreting the importance of insect mortality factors. From such discussions, it is clear that even with accurate measurements of apparent field mortalities, the interpretations of their effect on populations is difficult. The difficulties are increased if mortalities act contemporaneously, if generations overlap, and if there are irregular fluctuations in the rates of population growth and decline.

Where measurements are associated with very large sampling errors, as in this study, interpretation is severely hindered.

The data collected during this study and the observations made, have given some indication of the mortality factors and their effect on the populations of *C. ombrodelta* in macadamia.

In this discussion, most of the mortalities given are an average over all sites and seasons. Where data, or observation, indicated variation in different periods of a season, or at different sites, such variation is described.

Ideally, estimates of each mortality should be obtained for a large number of short periods during the season, so that within each period the probability of a particular mortality may be considered homogeneous. These homogeneous estimates could then be integrated to give an estimate of the total field population mortality.

A. METHODS

1. SAMPLING

Despite the limitations of the sampling data (high standard errors of estimates, and relatively long periods between samples) its examination gives an indication of the extent and role of mortality in *C. ombrodelta* populations.

(i) Partial Budgets

Southwood (1966, p.306, 1967) described a method which provides an estimate of the relative importance of natality and mortality in population fluctuations. The method makes use of a number of incomplete budgets for part of the insect life cycle, e.g. egg to late larval stage.

As seen from the samples, *C. ombrodelta* breeds continuously without discrete generations. This complicates the application of this method. However, an approximate succession of stages may be deduced. At the temperatures prevailing during the summer months in Southeast Queensland, eggs present on one sampling date would be expected to be detected as 4th instars two weeks (4,900 hour degrees) later, or as Final instars three weeks (7,300 hour degrees) later. This does not allow for variation in development rate, weather, or other factors, such as food supply and daylength effect. It is a reasonable preliminary approximation.

Southwood *et al.* (1972) devised a computer programme to calculate from observed oviposition rates, the expected number of insects of any stage on a given day, in a multi-age, multi-cohort population of *Aedes aegypti* (L.). Although it appears that this programme could be adapted to suit *C. ombrodelta* populations, to justify its use the collection of data for its input would have to be much more comprehensive than it was in this study.

In the approximation, the estimate of eggs per variety on each sampling date was paired with the estimate of 4th instars on the sampling date two weeks later for Aspley 1972-73, and the estimate of final instar numbers three weeks later for Beerwah 1972-73, and Aspley 1973-74. Each estimate was then converted to logarithms (base 10) and the larval figure subtracted from the egg figure. Thus:

$$\log P_E - \log P_R = \kappa$$

where P_E is the population of eggs

P_R is the resultant population of 4th instars (P_4), or finals (P_F) respectively.

κ is the total mortality over the period under consideration.

Each value ($\log P_E$, $\log P_R$, κ) was then graphed against date of egg population record. The population values were graphed normally on the vertical axis, but κ was on an inverted axis so that peaks of P_R corresponding to regions of low mortality would coincide with a "peak" in the mortality graph.

The correspondence between plots then indicated the importance of P_E, and κ, in the resultant larval populations.

(ii) Direct Examination

Although it was not known how long dead *C. ombrodelta* immatures remained recognizable as such, it was assumed that if mortality were high in any one period, sampling would record more dead *C. ombrodelta* in this period than in others. The regular samples from each site in 1972-73 and 1973-74 were therefore examined for evidence of *C. ombrodelta* mortality, other than that caused by parasites, and the results expressed as an apparent percent mortality.

(iii) Deserted Holes

Deserted holes are feeding galleries not occupied by a larva of size appropriate to the gallery size or, if so occupied with gallery surfaces of a state indicating that the gallery had been present longer than the current larval occupant. There is no firm evidence that the larva which formed the gallery emerged from it as an adult (i.e. no cocoon is present).

Deserted holes are believed to indicate the past occurrence of either a direct larval mortality - and subsequent breakdown of larval body, or conditions severe enough to cause the larva to move out of the nut prematurely, or movement out of the nut in search of a pupation site - in either case death is likely.

It is apparent that the assessment of deserted holes and their importance as an indicator of population pressures is very subjective. However, a consideration of their numbers throughout the sampling seasons is believed to give some indication of the loss of insects from the *C. ombrodelta* populations.

2. EXPERIMENTAL POPULATIONS

Data on mortalities was also obtained from the following sources:

(i) Egg Development Time Experiment

The mortality of eggs at eight constant temperatures and five relative humidity levels in combination was measured (Chapter 13). In each temperature-humidity combination there were two replicates, each of five eggs.

(ii) Cohort Nuts

In 1973, 75 S1 nuts on 20 racemes, and 130 H2 nuts on 20 racemes, were caged for 24 hours - each raceme singly - with mated female *C. ombrodelta*. Random samples of the nuts were taken after 9 days, and then every seven days until nuts were exhausted; in each variety samples consisted of 16 nuts from the tree if available, and all nuts which had fallen. These nuts were examined under magnification and the number of larvae present on each date estimated.

(iii) Sticky Cones

50 S1 nuts on nine racemes were caged with adult female *C. ombrodelta* for 24 hours in December 1973 (Chapter 17). Cones of perspex coated with Stickem Special were suspended around each raceme, and Stickem, cardboard, and artificial medium barriers were placed on the branches leading away from each raceme. Each raceme was examined daily and the various barriers were examined in detail once a week. Fallen nuts were placed in field trays (Chapter 17).

(iv) Varietal Establishment

In 1972, adult females were caged for 24 hours on five racemes of the varieties - 246, 508 (at Beerwah), S1, H2 (at Aspley). These racemes were picked after one week and examined in detail, to estimate the rate of establishment of young larvae in the different varieties.

(v) Multiples

A known number of newly hatched *C. ombrodelta* larvae were placed in artificially prepared holes on S1 tree nuts in the Aspley orchard, during 1973-74, as follows:

Series 1, using a total of 20 racemes each with two nuts

5 racemes, each nut with 1 larva

5 " " " " 2 larvae

5 " " " " 4 larvae

5 " " " " 8 larvae

and Series II, using a total of 15 racemes each with two nuts

5 racemes, each nut with 1 larva

5 " " " " 2 larvae

5 " " " " 4 larvae.

The nuts were observed daily, and within 24 hours of falling, were transferred to either field cups or laboratory trays as described in Chapter 17.

B. RESULTS

The mortalities are described for stages of *C. ombrodelta* in order from egg to pupa.

1. EGGS

Dead eggs were present on nearly every sampling date at each site; as a percentage of total eggs they varied from zero to 12.5%. There were no marked differences between sites, or years, or any trends within particular seasons. The results were therefore pooled over all samples to give:

Dead eggs as a percentage of total eggs (± standard error)

Tree nuts 3.44 ± 0.19%

Fallen nuts 3.77 ± 0.35%

The remaining field results for egg mortalities are for eggs on tree nuts.

In the Sticky Cones experiment 2.56% of eggs died, whilst in the Varietal Establishment experiment, and Cohort Nut experiment the mortality was 6.79%, and 5.56% respectively.

The very high densities of eggs (up to 32 eggs per nut) in the last two experiments mentioned, probably increased egg mortality, in that eggs were laid in overlapping groups. Under these conditions, common in the laboratory, the eggs which are covered by others usually do not hatch. Such high densities do not occur normally in the field.

Apart from this unusual cause, no reason for egg deaths in the field can be suggested. Eggs are found dead in all stages of development, usually without external damage.

The analysis of mortality of eggs recorded under various constant temperature and humidity conditions in the Egg Development Time experiment is summarized in Table 94. It is apparent that *C. ombrodelta* eggs are sensitive to low humidities and temperature extremes.

The temperature-humidity combinations which caused significant mortality in this experiment are unlikely to be encountered in the field, except for very short periods. Therefore, the estimates of mortalities under these conditions do not have relevance to an interpretation of field mortalities.

The means marked "f" in the table are all for conditions that may be expected in the field. The treatments apparently had no effect on egg survival, and the recorded mortality may be conceived as a base level for *C. ombrodelta* eggs. When all these means are pooled, the base mortality is 1.36 ± 0.78%.

Little confidence may be placed in the estimate from this small experiment. However, if it were repeated for adults raised under varying conditions, the concept could be useful. The difference between such a basic mortality and that recorded in the field would reflect the environmental stresses in a particular situation.

2. PRE-ESTABLISHMENT LARVAE

The Varietal Establishment experiment results are shown in Table 95. For the analysis of variance, the data were transformed to arcsin $\sqrt{x}$.

It is apparent that nut variety has a substantial bearing on the percentage of larvae which can successfully establish. The two Hawaiian varieties and S1 (overall mean establishment 50.6%) are much more suitable for *C. ombrodelta* establishment than H2 (establishment 3.25%). This is reflected in the sampled population figures (Figures 51 and 52).

It is assumed (Chapter 17) that those larvae not establishing on the nut, or raceme of nuts, on which they hatch have a very low probability of establishing elsewhere. Therefore, the complement of the establishment figure may be assumed to be a mortality. These mortalities (H2 96.75%, S1 34.11%, 246 69.66%, 508 44.44%) represent a substantial loss to the population.

The very low rate of establishment on H2 appears to be due to properties of the nut surface. Larvae on H2 chew numerous small holes, in an attempt to enter - in this experiment 38.3 per established larva, compared with 0.8 per established larva for the other varieties. The discussion on p.116 (Chapter 13), shows that larval growth in S1 and H2 is comparable if larvae do not have to make their own way through the nut surface.

The order of magnitude of this pre-establishment mortality is repeated in other experiments.

In the Cohort Nuts (Aspley S1 and H2), this mortality in S1 was 46.8% and in H2 90.9%.

The above discussion was concerned with establishment on nuts previously uninfested by *C. ombrodelta*. The establishment of larvae on infested nuts has not been measured. It is considered that it would be

higher than that measured above because of the readiness of young larvae to enter existing holes (Chapter 17).

High rainfall apparently can increase this pre-establishment mortality. In the samples from S1 1973-74 (Figure 51), peaks of egg laying usually coincided with, or were closely followed by peaks of established 1st instar larvae. However, whilst the sample on 25.I.74 showed very high egg populations, the 1st instar larval population declined, and did not recover until 8.II.74. Cyclone "Wanda" passed over Brisbane during this period, with flood rains. As egg mortality in samples after 25.I.74 did not increase young larvae were presumably washed from the nut surface.

3. ESTABLISHED LARVAE, PREPUPAE, AND PUPAE

(Prepupae, unless otherwise stated refers to the immobile stage.)

(i) Sampling

a Partial budgets

The plots of log egg population (log P_E), its corresponding log larval population (log P_R), and the apparent mortality κ, are shown in Figures 81 and 82.

In most cases, there is no striking correspondence of either log P_E, or κ with log P_R. It appears that the larval population (P_R) is the result of both natality and mortality, with the latter perhaps being the most important influence.

Plots of log P_E, log P_R and κ for two of the alternative host (*B. variegata*) sites are shown in Figure 83. In these the role of natality appears to be more important in population fluctuation than it is in macadamia.

The coefficient of determination (r^2) (Steel and Torrie 1960, p.187) of P_R on P_E gives the proportion of variance in P_R accounted for by P_E (Southwood 1967). Coefficients of determination for each of the graphed populations are shown in Table 96. In *B. variegata*, as well as an overall calculation, certain dates have been excluded and a further r^2 calculated. It is apparent that the importance of natality and mortality in population fluctuations changes during population development.

It appears that in macadamia, mortality is important in determining population size, although there is some variation. These plots only cover the period to the late larval instars - it is believed that mortality is also very important in the prepupal stage (see below).

Southwood (1967) stated that the role of κ may be investigated by studying the regression of κ on log P_E. This regression will reveal any density dependence of the mortality factor. This has not been done in the present case. It is felt that the assumptions underlying the derivation of κ are not sufficiently sound to ensure that misleading results would not be returned. There is a further difficulty in that the observed mortality is undoubtedly the result of a number of different mortalities which individually may have different modes of action. Luck (1971) showed that analysis of such regressions is not suitable if the different mortalities cannot be isolated, identified, and measured.

b Direct examination

Within each site, and season, only low, variable numbers of dead *C. ombrodelta* immatures were detected. It was considered best to pool the data as much as possible, and use the data only to indicate approximate relative rates of apparent mortality.

Table 97 shows the percent mortalities for each immature stage, pooled for each sampling site over the entire season.

The 4th instar appeared to have the greatest mortality and the prepupal and pupal stages the smallest. There was no consistent difference in the mortalities of each stage in tree and fallen nuts. This does not necessarily reflect the severity of mortality in each situation, as deterioration and removal of dead insects is likely to be more rapid in fallen nuts. There appeared to be a lower mortality at Beerwah than at Aspley. These figures, together with the very high population of *C. ombrodelta* at Beerwah (Chapter 14), and the virtual absence of parasites (Chapter 18) could be an indication that the heavy spray schedule in the Beerwah orchard in 1972-73 had reduced the diversity and density of *C. ombrodelta* mortality agents.

To examine the variation in mortality as the season progressed, the sample mortalities from all sites were arranged in three groups: 1st to 3rd instar, 4th to Final instar, and prepupae and pupae, and pooled over all seasons and sites. The different sampling dates were arranged to coincide approximately with those at Aspley in 1972-73. These mortalities are shown in Table 98.

In the 1st-3rd instars there is no definite trend over the season in tree nuts, but in fallen nuts mortality appeared to increase during the season. In older larvae, mortality in tree nuts appeared to increase during the season, but in fallen nuts such a trend was less evident.

The occurrence of dead prepupae and pupae only in mid season is not believed to be significant as the mortality rates for these stages are based on very low numbers, and it was only in this part of the season that appreciable numbers of these stages were found.

The probable causes of death recorded in the samples are shown in Table 99. For more than half the recorded deaths, no cause could be determined; the various causes suggested are:

Cannibalism. These larvae were usually found with others in the same nut. They had black "chewed" marks on their body, sometimes with damaged head capsules.

Gummosis. This only occurred in the younger larvae (see Gummed holes - Table 58). Sap exudate from the newly formed hole trapped the larva.

Predator. Various parts of the larval or pupal body were found, without the characteristic black marks associated with cannibalism. In pupae, the anterior part was usually eaten away.

Drowning. Occurred only under very wet conditions; larvae were unmarked.

Ecdysis. This has also been observed in the laboratory. Either the exuvia was not cast from the posterior end of the larva, or the old head capsule was not shed completely.

Parasite (?) paralysis. Mentioned in Chapter 18. Affected larvae were immobile, often quivering, and unmarked.

Nut shrinkage. Only for pupae, in fallen nuts. After pupal formation, the nut husk shrinks crushing the pupa.

c Deserted holes

The estimated numbers of deserted holes in tree and fallen nuts, on each sampling date in the main macadamia sampling sites for 1972 to 1974 are shown in Table 100, together with the corresponding number of total immatures. For each sampling site the season mean deserted holes

per living larva is shown; in each case this value is greater for fallen nuts than for tree nuts. At Beerwah, the mean for each nut type is much lower than in either of the Aspley varieties. This is a further indication that factors causing larval mortality may be less common in this sprayed orchard than at Aspley.

Figures 84 and 85 show the comparisons of the mean deserted holes per living larva for tree and fallen nuts on each sampling date. It is apparent that the mean is usually higher in fallen nuts. This is expected because fallen nuts carry a relatively large proportion of the population of older larvae and these are likely to leave the nuts in search of pupation sites; it is thought that most do not survive. In addition, all larvae experience harsher conditions in fallen nuts than in tree nuts, this would increase mortality. There appears to be a trend towards an increase in the mean as the season progresses, indicating that conditions become less favourable for larval survival.

(ii) Experimental Populations

a Multiples

A summary of the events occurring in this experiment is set out in Table 101. The large proportion of larvae unaccounted for is disappointing. However, as it is assumed that all larvae moving out of the nuts after they had fallen were detected, and that larvae do not move out of the nuts having once become established (Chapter 17), the number unaccounted for may be considered to have died, and become unrecognizable by the time the nuts were inspected.

This residual "mortality" (for the entire larval life) shown in the last column of Table 101 is much higher than would be expected from a consideration of those mortalities indicated by the regular samples.

The lowest mortality (65.0%) was recorded in those nuts having

only one larva, the highest (95.0%) in those with eight. These results indicate that competition leads to reduced survival.

b Cohorts

The number of immature *C. ombrodelta* found in each of the tree nut samples from the cohort nuts, was corrected for those numbers which had fallen between samples, and those numbers taken in previous samples. The resultant estimate of numbers present is shown in Table 102, together with the stage of development reached at each sampling date. Sample standard error was reduced by the sampling fraction. Even so, as a percentage of the mean, it averaged 150%.

The apparent percent mortality in the early larval stages was much higher in S1 than in H2. This was probably due to the much higher larval densities in S1, resulting from the higher establishment of young larvae in that variety. In the H2's there were fewer nuts with multiple infestations, resulting in a higher survival of those which became established.

The apparently sharp increase in percent mortality between day 23 and 37 is probably not entirely due to death in the nut. At this stage it is probable that a number of mature larvae left the nuts to search for pupation sites elsewhere. The number of such larvae could not be determined.

4. MOBILE PREPUPAE

It is shown in Chapter 17 that a large proportion of mature larvae may leave both tree and fallen nuts in search of pupation sites.

No measure of mortality that such larvae incur was obtained in this study. It is considered that macadamia trees have relatively few

pupation sites. The few mature larvae released on trees showed no ability to discover suitable sites. On the other hand, the ground under macadamia trees usually has many leaves and twigs, and mature larvae released on the ground very quickly found suitable pupation sites (Table 90). However, emergence traps have never caught *C. ombrodelta* emerging from the ground, and examination of the ground during fallen nut counts has not revealed empty pupal cases.

Geier (1963) stated that the majority of mature 5th instar codling moth larvae that he studied died, or could have been assumed to have died before they made a cocoon. Since all codling moth pupae are formed outside the fruit, it is reasonable to believe that they are better adapted to searching for pupation sites than *C. ombrodelta*. Therefore it is assumed that most of the *C. ombrodelta* mobile prepupae also die before pupating. This will need further study.

5. MORTALITY CAUSED BY PARASITES

Bracon sp. This parasite has been found attacking all stages from 2nd instar to prepupae inclusive, but 4th to Final instars are attacked most often (Figure 75). The rate of attack on different stages appears to depend on both host and parasite density, but this is not clearly understood.

When calculating the effect of *Bracon* sp. on population levels, the apparent percent parasitism should be calculated for each of the susceptible stages. As the parasite appears to attack only living larvae, the apparent percent parasitism calculated for each stage may be considered to represent real mortality for that stage.

Apanteles briareus. The relationship of the apparent percent mortality calculated in Chapter 18 and the real population mortality

caused by this parasite is rather complicated.

As only *C. ombrodelta* larvae to the 4th instar are susceptible, the sample apparent percent mortality must be increased in proportion to the number of *C. ombrodelta* emergences arising from larvae older than 4th instar at sampling. In addition, some of the parasite emergence from any particular sample will be from larvae younger than 4th instar at sampling, and the field mortality due to *Apanteles* in these individuals would be expressed at a later date. However, its expression will probably be different from that anticipated as parasitised larvae remaining in the field will presumably be subject to other mortality factors.

To illustrate the above, suppose the following sample was maintained in the laboratory for parasite emergence, with the results shown:

60	1st-3rd instar larvae	yielded	45	*C. ombrodelta*,	15	*A. briareus*
20	4th "	"	"	15	"	5	"
60	older than 4th "	"	"	60	"	0	"
140				120		20	

Apparent percent mortality would be $\frac{20}{140}$ = 14.3%. The real mortality on the sampling date due to *A. briareus* would be $\frac{5}{20}$ = 25%. In this sample no assumption is made regarding the larval stage attacked by *A. briareus*. It may attack all stages to the 4th instar or only the 1st instar. The interpretation of sample results to provide an estimate of real field mortality requires such knowledge.

It is likely though, that this parasite is more important in population regulation than the figures for apparent percent parasitism in Chapter 18 indicate.

C. DISCUSSION

Although there is evidence that mortality is important in *C. ombrodelta* populations in macadamia it is clear from the above descript-

ions of mortality factors, that knowledge of the magnitude, causes, and effect of mortality is inadequate for a confident interpretation of *C. ombrodelta* population dynamics.

Figures 51 to 53 show that successive peaks of unhatched egg absolute populations, estimated in the macadamia samples (Chapter 14) usually have less than a five-fold difference in height; the difference is often much less.

Morris (1957) showed that for an insect with discrete generations, and a fecundity of 200, a constant level of population would result if generation mortality were 99%. The situation is more complicated for *C. ombrodelta* as it has no discrete generations. However, if it were assumed that over a period the mortality of *C. ombrodelta* individuals (egg to egg) was an average 0.98, a steady population level should be achieved, as fecundity of the species is approximately 100 (Chapter 16). To achieve a five-fold increase between periods, the mean probability of mortality would need to fall only to 0.90 (therefore in a cohort arising from 100 eggs, 10 adults would emerge, five would be females, and 500 eggs would result).

Although the effect of an unknown level of immigration and emmigration complicates the assumption, it appears likely that natural populations of *C. ombrodelta* are subjected to a relatively high level of mortality; certainly more than is indicated by the direct examination of sample material described in this chapter. In this case, it may be assumed from Morris' (1957) discussion that relatively small changes in the probability of death will result in comparatively large population fluctuations, e.g. a change to a probability of mortality of 0.99 would result in a population decrease of 50%, a mortality of 0.96 in an increase of 100%.

In the absence of discrete generations, such a change would have to be maintained for a period long in relation to the life cycle. Short

term changes are likely to be compensated for because of the multiple cohorts which contribute to population change.

Morris (1957, 1965) showed that a consideration of the dependence on density of mortality factors, whether they act sequentially or contemperaneously, and their mutual interference are most important in determining the response of a population to the imposition of these mortality factors. A study of the mutual interference of mortality factors may be important in applied control - factors with a low level of interference with those existing, being most likely to result in successful control (Morris 1965).

Populations of *C. ombrodelta* may be affected by density in two different ways. Absolute population density (e.g. the number of insects per 0.5 ha), will affect the response of parasites and predators, and possibly the oviposition behaviour, and migration of the adult. The depletion of food supply by *C. ombrodelta* has never been recorded as a limiting factor in absolute populations.

Insect numbers per nut is the second type of density relationship. Distribution among nuts divides the absolute population into a number of small, discrete units each of which may have disparate processes involved in its survival. A single larva is likely to have a higher probability of survival than larvae in multiple infestations.

The apparently density related reductions in populations observed in Chapter 14 (Figures 54 to 57) are operating on the per nut level. Examination of these figures indicates that a factor reduces the contagion of populations between the egg and 1st instar. In cases where nuts have a single egg, the resultant larvae would be expected to have a relatively constant establishment rate. Where more than one egg is found on a nut, if the larva hatching first becomes established, it is likely that larvae hatching later would locate this establishment hole, attempt to enter, and either be killed or cause the death of the first larva. This would

reduce the contagion.

There is also a reduction in contagion between the 4th and 5th instars. It is thought likely that in multiple infestations larvae can probably avoid contact with each other until each is older than a 3rd instar. After this time cannibalism is likely to reduce contagion.

Other stresses likely to be increased in nuts with multiple infestations are food shortage and food deterioration - at least for the younger larvae, due to the older larvae causing a comparatively early nut fall.

Considerably more work on evaluating these factors must be undertaken early in any future studies. Such work will be labour intensive, and require a large and continuous supply of mated female moths, and a plentiful supply of macadamia nuts on the tree.

In the meantime, the use of computer models, which allow the simulation of different levels of mortality will be instructive. Such models are developed in Section VI.

CHAPTER 21

THE EFFECT OF *C. OMBRODELTA* INFESTATION ON THE MACADAMIA CROP

Ironside (1970 unpublished report) recognized that although some nuts were damaged when the *C. ombrodelta* larva tunnelled into the kernel, much of the crop was also damaged by boring in the husk causing fall of nuts before they attained maturity. He stated that loss occurred not only directly from reduced yields and crop quality, but also indirectly from increased grading costs. Ironside believed that husk damage to nearly mature fruit was unimportant.

In this chapter, the crop damage process is examined in more detail and the probable importance of the different types of damage is discussed. However, such discussion is hampered to some extent by the absence of objective quality measurements in the Australian macadamia processing industry.

A. METHODS

(i) Direct Kernel Damage

Regular nut samples in 1972-73 were examined for nuts with kernels damaged by *C. ombrodelta* attack.

The 1973-74 records from Aspley were not used as the very high populations of *Amblypelta nitida* in this season resulted in an abnormally high proportion of nuts with weakened and damaged shells. The number of *C. ombrodelta* found in kernels was higher than normal.

(ii) Nut Fall Caused by C. ombrodelta Attack

a Multiples

Two small experiments were performed at Aspley S1 in 1974 (these are described in less detail in Chapter 20).

The first was begun on 11.I.74 and finished on 19.II.74. Twenty racemes, each carrying two nuts, were selected. On each nut a number of small holes were made in the husk, and newly hatched larvae were transferred to the surface. The following treatments were used.

5 racemes - on each nut 1 hole, 1 larva

5 racemes - " " " 2 holes, 2 larvae

5 racemes - " " " 4 holes, 4 larvae

5 racemes - " " " 8 holes, 8 larvae

In the second experiment, begun on 7.III.74 and ending on 6.IV.74, 25 racemes each carrying two nuts were used. The treatments were:

5 racemes - on each nut no holes, no larvae (Control)

5 racemes - " " " 4 holes, 0 larvae

5 racemes - " " " 4 holes, 1 larva

5 racemes - " " " 4 holes, 2 larvae

5 racemes - " " " 4 holes, 4 larvae

Each raceme was covered with a fine gauze cage for the full period of the experiment.

After two days, if it appeared doubtful that all larvae had established (the number of frass filled holes was counted), this raceme was discarded, and a new one begun.

After establishment was confirmed, the racemes were inspected daily. The number of days for each nut to fall was converted to hour degrees above 10.43°C, using the temperatures recorded within the orchard. If a nut did not fall, a value of 12,400 hour degrees was used, this being

the thermal constant for *C. ombrodelta* from hatching to adult emergence without regard to daylength (Chapter 13).

On each raceme one nut was designated as "lower", the other "upper", depending on its position on the rachis. The effect of position on fall was tested.

b Regular nut samples

An attempt was made to relate the amount of larval feeding in nut husks to the probability of that nut being found on the ground, or in the tree.

Because there are no data available for the amount of material eaten by each instar - and thus the damage done to each nut by each instar - it is difficult to determine if, for example, a 4th and a 2nd instar in a nut is as damaging as a final instar and a 1st, etc.

As most of the infested nuts sampled, had only one larva (75.38%, p.183), the largest stage present in a nut was considered to be causing the damage. The damaging stages were ranked from smallest to largest, as follows:

1st instar, 2nd, 3rd, 4th, 5A, Final, prepupa, pupa, deserted hole.

Eggs were considered to cause no damage.

Therefore a nut having a prepupa and a 4th instar would be classified as - highest damage, prepupa.

For each sample, the total population of each type of highest damage was estimated for both tree and fallen nuts on that date. The proportion of each highest damage population that was on the ground was then determined. These proportions were compared within and between highest damage classifications.

(iii) The Effect of C. ombrodelta Husk Infestation on Kernel Quality

In the 1973-74 season, nuts taken in S1 on and after 18.I.74, and in H2 on and after 25.I.74, were separated into those having no damage by *C. ombrodelta* and those having *C. ombrodelta* boring in the husk.

The kernels were classified by the grades: Water, 1st, 2nd, and Reject, as described on p. 57-58.

B. RESULTS

(i) Direct Kernel Damage

Samples of nuts taken from the tree revealed few nuts with damaged kernels, and their occurrence was very erratic. For instance, in Aspley S1 1972-73, kernel damaged nuts were recorded in only two samples throughout the season of 12 samples. In H2 in the same year, only two samples of 16 from the tree showed kernel damaged nuts.

Attention was therefore concentrated on the samples of fallen nuts. The results, for both Aspley varieties, and Beerwah trees are shown in Table 103.

When the nut shells are soft, nearly all *C. ombrodelta* infestation results in kernel damage. However, as there is little insect activity at this stage, the number of nuts with damaged kernels, as a percentage of total nuts falling is low.

As the shells harden, there is a steady decrease in the percentage damage which results in kernel damage. The higher percentage of kernel damage in the fallen nuts soon after shells harden is thought to be due mainly to the low probability of undamaged nuts falling in this period.

The persistence of kernel damaged nuts in the fallen nut samples for so long after shell hardening is probably due to the retention of some kernel damaged nuts on the tree. The author has observed several S1 nuts

which were kernel damaged before shell hardening; those retained by the tree developed an apparently normal hard shell, apart from the hole.

It is believed that nearly all kernel damage occurs close to the date on which shells harden; at this point, late December, orchard *C. ombrodelta* populations usually increased substantially. A small amount of kernel damage probably occurs later, in nuts having weak shells, either from abnormal growth, or from damage by *Amblypelta nitida.*

In each variety, the percentage of total potential crop with kernel damage was:

246 (Beerwah)	S1	H2
3.03%	1.02%	0.51%

The difference between varieties is probably a reflection of the intensity of *C. ombrodelta* attack, rather than a measure of their susceptibility to kernel damage.

(ii) Nut Fall Caused by C. ombrodelta Attack

a Multiples

The hour degrees to fall, of each nut, was transformed to log (x). Bartlett's test for homogeneity (Sokal and Rohlf 1969, p.370), performed on the transformed variances of each treatment, within each experiment, did not show that these were heterogeneous. Each experiment was subjected to an analysis of variance. The F values of these analyses, and the untransformed means of each treatment are shown in Table 104. Significant differences between means are indicated.

A difference between means was apparent in the first experiment: the mean period to fall for nuts with one or two larvae was not significantly different, the nuts with more larvae fell sooner. This confirms that husk damage can cause premature nut fall. The experiment does not

allow a clear interpretation of the effect of the type of infestation found in the field, as it was not known how many larvae in each experimental nut remained to the time of fall. In addition, the lack of a control meant that it could not be determined whether fall was due to the initial damage of artificial holes, or to the later damage of larval boring.

The second experiment, having controls, was designed to decide this second point. However, the lack of significance of treatment differences prevented this. Apparently the experiment was started too late in the season. A number of undamaged nuts fell, and many of the damaged nuts died on the tree without forming an abscission layer. Nut death due to borer damage was not considered normal; the Aspley S1's in 1973-74 were showing signs of nutrient deficiency, and this may have contributed to nut death.

b Regular nut samples

The proportions on the ground of each type of highest damage, within each site and season, were extremely variable, often ranging from 0 to 1.00 on consecutive sampling dates. The reason for this appeared to lie in the low numbers of each stage present in each sample. For instance, often there would be only one or two nuts with highest damage of, say 3rd instar, and both would be either on the tree, or the ground.

To overcome this, some pooling of the data was necessary. It was decided to use the classifications:

No damage

1st to 3rd instar

4th and 5A

Final instar and greater.

The resultant proportion of damage (converted to percentages by

multiplying by 100) are shown in Figure 86. The lines in each graph were fitted subjectively, as an estimate of the mean expectation of fall through the season for each type of damage. These estimates will be used as a guide to expected fall in the computer simulation model.

The graph for No Damage is equivalent to those for percent likelihood of fall in Figures 17 and 18, corrected for the effect of insect damage; there is little tendency for undamaged nuts to fall in mid season.

Graphs for each of the damage classifications, indicate that damage does increase the probability of a nut's falling. The higher the damage, the more likely the nut is to fall. Therefore, at least before maximum maturity of the kernel is achieved, feeding by *C. ombrodelta* will cause a loss in crop quantity, or in quality if these immature nuts are collected at harvest.

When the probability of undamaged nuts falling is high early in the season, damaged nuts - few in number - also have a higher than average likelihood of fall. Likelihood of fall of any nut appears to be lowest in late December, early January. This point may be assessed visually in that all nuts have hard sticky shells; kernels are immature (Figures 22 to 27). After this period, the likelihood of fall of each class of damaged nuts increases as the season progresses; this steady increase corresponding approximately to the increase in likelihood of fall of undamaged nuts. It is observed that in highest damage "4th, 5A" and "Final and greater", the increase of the proportion of nuts on the ground levels off near the end of the sampling period. This may have been due to damaged nuts dying without forming an abscission layer, as observed in the Multiples experiment. This behaviour may not be as abnormal as was thought.

(iii) The Effect of C. ombrodelta Husk Infestation on Kernel Quality

Figures 87 and 88 show the results of the maturity tests carried out on S1 and H2 nuts in 1974.

In each variety there appears to be a reduction in kernel quality with *C. ombrodelta* husk infestation. This reduction applies to nuts sampled from both the tree and the ground. It is also seen that the lower quality of fallen nuts compared to tree nuts is not due entirely to *C. ombrodelta* infestations.

The effect of *C. ombrodelta* infestation on the distribution of sampled nuts between the four quality grades used, is shown in Table 105.

In S1 the effect is to reduce the percentage of crop suitable for processing by approximately 9%, and to increase the percentage in the 1st grade by approximately the same amount.

In H2 the effect of husk boring is more severe. The percentage of crop suitable for processing is reduced by approximately 19%, and nuts are reduced in quality to 1st, 2nd, and even Reject grade.

C. DISCUSSION

C. ombrodelta can cause both a quantity and a quality loss of macadamia crop.

Quantity loss - (a) from kernel damage, which is detected in ground collected nuts for most of the season

(b) from premature fall early in the season, before harvesting begins.

Quality loss - from husk boring after harvesting has begun.

An illustration of the type of calculations required to determine the extent of loss caused by *C. ombrodelta* is now given for Aspley S1

1972-73 (all trees). It also illustrates that there is still some information required on crop behaviour in the absence of *C. ombrodelta*. The basic data for the calculations is shown in Table 106.

Total potential crop was discussed on p.62, and defined in Table 37 for S1 1972-73, as 38,194 nuts. For this discussion however, the 11,716 nuts still present in the tree after sampling ceased, are ignored. Therefore potential crop is 26,478 nuts.

It is desirable, before harvesting begins, for the ground under each tree to be cleared of all nuts which have fallen already. These are discarded as they are usually immature. The date on which harvest begins varies with the grower, and local conditions. It has been defined in this case as 21.I.73, when more than 50% of the tree nuts had hard brown shells; a proportion which indicated the onset of rapidly increasing maturity (Figures 23 and 26). This point of development, being readily recognizable, may have application in commercial orchards.

The harvest is divided into two periods. A short early period of increasing nut maturity, and a longer period of maximum nut maturity (defined by tree nut maturity, as this is believed to be least subject to quality variations caused by wet weather, etc.).

The proportions of harvested nuts in each of the four grades in each period, for damaged and undamaged nuts, is shown in Table 106. In 1972-73, water grade was not determined, but the figures shown are a reasonable expectation, based on the grade relationships in S1 1973-74.

It is assumed that only the water grade is suitable for processing, and that the remaining grades have no positive value.

(i) Expected Return without C. ombrodelta

Although it is probable that a proportion of the damaged nuts falling during the early part of the season would have fallen even if the insect had been absent, with the data to hand it is not possible to correctly determine this proportion.

Therefore it is assumed that in the absence of *C. ombrodelta* only 1,371 nuts would have fallen before harvesting began, and that only 115 nuts would have fallen in the period of increasing maturity. It is also assumed that the damaged nuts falling before and during the period of maximum maturity would have all fallen as undamaged nuts during this period.

Thus the harvest would have been:

	Water	1st	2nd	Reject	Total
Increasing maturity	54	1	16	44	115 nuts
Maximum maturity	24,242	0	500	250	24,992 nuts
Total	24,296	1	516	294	25,107
Percentage	96.8	0	2.1	1.1	100.0%

for such a crop of this quality the grower would receive $0.66/kg (J. Simpson[1] 1974 pers. comm.). At 143 nuts/kg, the total amount would be $115.88. From this harvesting and farm processing costs would be deducted.

The cost of clearing the ground of nuts before harvesting begins may be considered an overhead, and is not included.

It is assumed that nut pick up costs $0.11/kg, and that dehusking, at the rate of 2 kg per minute requires one person, being paid $2.50 per

---

1. Mr J. Simpson, Manager, Macadamia Nuts Pty. Ltd., Slacks Creek, Queensland.

hour. It is assumed that no grading is undertaken on the farm.

Therefore, grower return is:

$ 115.88

- $ 19.31 pick up

- $ 3.66 dehusking

$ 92.91

(ii) Expected Return with C. ombrodelta

Before harvest begins 2,628 nuts are discarded. This increase in the number discarded is not considered to have increased the cost of the operation.

The harvest is as follows:

	Water	1st	2nd	Reject	Total
Increasing maturity					
no damage	54	1	16	44	115 nuts
damage	936	278	354	973	2,541 nuts
Maximum maturity					
no damage	4,757	0	98	49	4,904 nuts
damage	14,270	1,298	324	398	16,290 nuts
Total	20,017	1,577	792	1,464	23,850
Percentage	84.0	6.6	3.3	6.1	100.0%

Mr Simpson stated that for such a crop, with more than 10% unsuitable for processing, only the 84% highest grade would be paid for (at $0.66/kg). Costs for pick up, and dehusking were as before, but the total cost would be less, as there were fewer nuts to pick up.

Return is:

$ 92.39

- $ 18.35 pick up

- $ 3.47 dehusking

$ 70.57

Therefore, in this case, *C. ombrodelta* attack is believed to have cost the grower $22.34, or 24.0% of his return without the insect. This is a substantial percentage of return.

It may be seen from the calculations that the loss experienced in any situation will depend on a number of factors, including the time at which insect attack begins and the varietal characteristics of undamaged nut fall, and maturity development.

SECTION VI

MODELLING

CHAPTER 22

THE GENERAL MODEL

The models developed and described in this and the next chapter are concerned mainly with the interaction between *C. ombrodelta* and macadamia. This is only a small part of the *C. ombrodelta* life system, but it is considered that only this part has been studied in sufficient detail to warrant model building. The other parts of the life system studied will be considered in the model input data array. This section will, in effect, summarize the results of the earlier chapters.

Unfortunately, the quantitative nature of the *C. ombrodelta*-macadamia interaction is imperfectly understood because of the difficulties encountered in sampling and experimentation. The development of a model is worthwhile, despite this imperfect quantitative knowledge. Watt (1968, p.371) believed that models, constructed initially with inadequate or unrealistic assumptions, have a valuable self-teaching role, as the pattern of model output suggests how the assumptions should be modified. Similarly, Milner (1972, p.258) suggested that the construction of a model, before all the correct input data were known, was advantageous as it allows major faults in the structure to be detected. In addition, sensitivity analyses make it possible to assign priorities to the order in which subsequent investigations are carried out to improve knowledge of the process under study.

As this study was conceived as being only the first stage of a more extensive investigation of the *C. ombrodelta* life system (see Chapter 3) it is important to construct a model using the available information, to summarize knowledge and test the validity of hypotheses as to cause and effect, so that future studies may be effectively directed.

Before a more sophisticated simulation model for use in the prediction of the effects of certain management or control practices may be constructed the ecological parameters will have to be estimated with precision, or the capability of the computer techniques will not be fully realized (Conway and Murdie 1972, p.197).

This chapter describes the structure of the conceptual model and, using simple hypothetical examples, shows how this framework is a suitable basis on which to build the mathematical description of the *C. ombrodelta* life system.

1. THE BASIC MODEL

The basic *C. ombrodelta*-macadamia model is represented in its conceptual form in Figure 89. This type of "box and arrow" diagram is referred to by Radford (1972, p.278) as an ecological flow diagram. In this case it describes the movement of *C. ombrodelta* in macadamia through time and space, and the resultant loss of nuts.

The "boxes" describe living states of the subject insect; the probability that any of the events described by the arrows linking the states will occur may be determined by appropriate experimentation or sampling.

In this study, the model is deterministic in that no estimate of variability is incorporated in the input data.

(i) The Movement between States

There are three types of movement possible:

(a) survival - an insect in one state moves to the next oldest state; represented in the diagram by vertical arrows from one box to the next

(b) mortality - an insect in any one state moves to the state "dead"

(c) habitat change - an insect in a tree nut may become an insect in a fallen nut, if that nut falls. A prepupa in a tree nut may become a prepupa in the tree. A prepupa in a fallen nut may become a prepupa on the ground. These changes are "horizontal", and occur within the time period under consideration.

The survival and mortality changes are considered to be "vertical" and occur between time periods. This distinction has important consequences in the mathematical treatment of the models.

(ii) Modification of the Model

The model is "open-ended". Any part of it may be expanded and examined in more detail, without affecting its overall integrity. Figure 90 illustrates this for a small section of the model. In a similar way, if a section of the model were found to be relatively unimportant, it could readily be contracted.

In addition, sub-models of other processes may be built around or within it. In Figure 76, a sub-model for *C. ombrodelta* in the alternative hosts is connected to the basic model by migrating adults. Similarly, one or more models for parasite species breeding on *C. ombrodelta* immatures in macadamia could be linked to the appropriate stages by attack, and adult emergence arrows.

Provided data are available the process may be expanded to any level of complexity without major alterations to the basic model.

(iii) Mathematical Applications of the Model

As a population of *C. ombrodelta* moves through time, the probabilities of mortality, survival, and habitat change of the individuals in each state will change due to the extrinsic factors of the environment.

Therefore, to describe a population over an extended period, a series of such probabilities must be prepared. The more variable the probabilities, the more frequently they need to be estimated. For a simplified, hypothetical situation, such a series is illustrated in Figure 91.

To facilitate mathematical manipulation of the model, the life cycle of the subject insect is divided into equal lengths of physiological time (hour degrees). In Figure 91 it has been assumed that young larvae take twice as long to develop as old larvae, so their development time is halved to give early young larvae (A), and late young larvae (B).

The modelled population therefore moves through time in a series of steps. In each step, individuals surviving any state move forward only to the next state. Holling (1963) pointed out that such a procedure preserves the discontinuous and historical characteristics of many biological processes and is suitable for use with a computer. Computer models moving forward in steps, were used by Hughes and Gilbert (1968) and Gutierrez *et al.* (1974).

Pielou (1969, p.34) stated that the use of discrete time units was suitable only if the units were short. Hughes and Gilbert (1968) pointed out that short units, whilst more accurate, increased the amount of computation. After some experimentation, they decided to use periods of 14 day degrees, in a total life cycle (*Brevicoryne brassicae* L.) of approximately 476 day degrees - or 34 periods per life cycle.

The number of periods chosen for the computer simulation model of

C. ombrodelta-macadamia, will be discussed in the next chapter.

2. TIME SPECIFIC MODEL

Each of the flow diagrams in Figure 91 is a time specific model. They show the expectation of events for each time period for which they are constructed. One such diagram by itself describes only one change of state for any individual.

The probabilities of events from a series of such models provide data suitable for use in the computer model. At each step in the computation the probabilities of events for each state at the appropriate period are applied to the number of individuals in each state.

The probabilities of mortality and survival shown in Figure 91 are estimates of real rather than apparent mortality and survival. Therefore the sum of probabilities relating to any state in which a habitat change occurs is more than unity.

The probabilities of events shown on a series of time specific models can be expressed in the form of matrices, which are readily manipulated mathematically (Usher 1972, p.36). However, the occurrence of habitat changes within a time period needs special attention.

A procedure of matrix manipulation which could be used to describe population changes is described. The population illustrated is that shown in Figure 91.

For each time specific diagram, two matrices are constructed. The first (H_n) describes the habitat change within the time unit "t"; the second (T_n) describes the population change between time units t_n and t_{n+1}. For the first time specific model in Figure 91:

H_1 =

	Dead	Mature	TNYL(A)	TNYL(B)	TNOL	FNOL
dead	1.00	0	0	0	0	0
mature	0	1.00	0	0	0	0
TNYL(A)	0	0	1.00	0	0	0
TNYL(B)	0	0	0	1.00	0	0
TNOL	0	0	0	0	0.50	0.50
FNOL	0	0	0	0	0	1.00

where TNYL(A) = Tree Nuts, Young Larvae (A)

TNYL(B) = Tree Nuts, Young Larvae (B)

TNOL = Tree Nuts, Old Larvae

FNOL = Fallen Nuts, Old Larvae.

Thus within the time period, the only change is that half the Tree Nuts, Old Larvae move to Fallen Nuts, Old Larvae.

T_1 =

	Dead	Mature	TNYL(A)	TNYL(B)	TNOL	FNOL
dead	1.00	0	0	0	0	0
mature	0	1.00	0	0	0	0
TNYL(A)	0.40	0	0	0.60	0	0
TNYL(B)	0.20	0	0	0	0	0
TNOL	0.80	0.20	0	0	0	0
FNOL	0.90	0.10	0	0	0	0

i.e. all dead larvae remain dead; Tree Nuts, Young Larvae (A) have a probability of 0.60 of moving to Tree Nuts, Young Larvae (B) etc.

Now, the population structure may be expressed as a row vector P_t.

	Dead	Mature	TNYL(A)	TNYL(B)	TNOL	FNOL
P_1 =	0	0	1000	400	200	100

Two matrix multiplications are then performed:

$$P_{1H} = P_1 . H_1$$

$$P_2 = P_{1H} . T_1$$

In this example:

	Dead	Mature	TNYL(A)	TNYL(B)	TNOL	FNOL
P_{1H} =	0	0	1000	400	100	200
P_2 =	740	30	0	600	320	0

It may be seen from Figure 91 that, apart from the 1500 Tree Nuts, Young Larvae (A) which have been added, this described the state of the population after the passage of one time unit.

The process may be repeated for as many time periods as desired.

Thus, once the probability of the different events has been calculated, the mathematical generation of the population is quite straightforward.

The calculation of the probabilities is a major problem. When overcome, however, it is believed that this matrix approach may prove to be suitable.

It is noted that this form of the matrix is more appropriate to the description of this problem than is the Leslie matrix, which is being adapted for a large number of purposes in biology (e.g. Usher 1972, p.37) as it illustrates the actual changes in the population with fewer hidden components.

In the special case, when habitat changes are not present, the above matrices become the transition diagrams of one step absorbing Markov chains. These with their established algebra would be useful in popul-

ation description.

3. AGE SPECIFIC MODEL

Age specific models may be constructed from a series of time specific models. One constructed from the first four time periods of Figure 91 is illustrated in Figure 92. Provided the habitat changes are dealt with in a similar way as above, these models describe the fate of a real cohort, and may be used as a basis for a conventional analysis of population processes. However, to account for changes and variations in development time it is probable that a computer programme such as that used by Southwood *et al.* (1972) would be required. In addition, the calculation of I (the generation index) would not be easy because *C. ombrodelta* breeds continuously, and a form of weighted summation is probably required.

CHAPTER 23

APPLICATIONS OF THE MODEL

This chapter deals with the construction of a model compatible with the present imperfect knowledge of the *C. ombrodelta* life system.

Rather than attempt to build a model designed to predict the outcome of various management or control practices, emphasis is placed on producing a model which describes, explains, and tests present hypotheses concerning population processes. In the present case, this has resulted in a rather complex and costly model, which will certainly need to be modified before a "management" simulation model is achieved. The conceptual model described in the last chapter forms the basis of the model to be described.

The first mathematical test of the structural validity of the conceptual model will be described, and its shortcomings explained. The development and testing of a computer model designed to overcome these difficulties and shortcomings will then be discussed.

1. A DESK CALCULATOR MODEL

The first mathematical test of the conceptual model was made soon after the 1972-73 sampling season. It dealt only with insect populations in tree nuts - therefore there were no habitat changes. Calculations were performed on a desk calculator.

(i) The Description of the Model

The population modelled was that of Tree 194 at Beerwah between 27.XII.72 and 21.II.73 inclusive. Much of the input data was compiled

from a consideration of the sampling results in that tree during that period. As Goodall (1972, p.185) and Clark *et al.* (1967, p.169) pointed out this is unsatisfactory, as a comparison of model output with the real situation is then not independent. At that stage in the model development the use of these data was considered justified.

The assumptions on which the model was based were:

(1) Temperature was constant throughout the period at 24°C.

(2) Development time of the immature stages of the insect was as recorded in Table 56.

(3) 60% of the larvae had 6 instars, 40% had 5 instars.

(4) Oviposition was as recorded in sampling.

(5) The probability of fall of nuts with highest damage:

1st to 3rd instar	was	nil
4th instar	"	0.09
5A instar	"	0.17
Final instar	"	0.34
Prepupae and pupae	"	0.43.

(6) The occurrence of larvae in multiple nut infestations was that recorded in the sample on the appropriate date.

(7) The only mortality was 0.40 probability of death between egg hatching and larval establishment.

The time specific diagram describing the model is shown in Figure 93. Because of the simplifying assumptions, the only parameter to change between each step was that relating to multiple nut infestations (point 6 above). This is designated C (for "contagion") in Figure 93.

The entire period of immature development was divided into units of 326 hour degrees; equivalent to 24 hours at 24°C. Thus for eggs there were 6 periods, for 1st instars 4, and so on.

(ii) Running the Model

A flow chart summarizing the calculations performed is shown in Figure 94. They are described below:

Initial larval age structure. Although no larvae were detected in the field sample of 27.XII.73, the presence of mature larvae on the next sampling date indicated that there must have been approximately 80 2nd, 3rd and 4th instar larvae present on 27.XII. Therefore the initial age structure was set at 80 larvae approximately evenly distributed within the nine age periods (326 hour degrees) representing 2nd, 3rd and 4th instars.

Daily oviposition. On each date of input, the number of eggs present in the tree was estimated from the sample (e.g. Figure 53 eggs). This number was then divided into six groups (at 24°C eggs hatch in six days) representing the different age classes of eggs. If oviposition appeared to be increasing, most eggs were placed in young age classes; if declining, most were in the older age classes.

Decrease by establishment factor. The numbers of larvae in the first six larval age classes were reduced by 0.40.

Nut fall. The number of nuts which fell was obtained by multiplying the total number of 4th instars present by 0.09, the total number of 5A instars by 0.17, and so on. The resulting numbers were recorded as nut fall in the following week to that in which the calculations were performed. Insect numbers in each instar were reduced by the same value.

Contagion factors. The expectation of different combinations of larvae being in each nut was determined for each calculation date from the corresponding field sample. Larval numbers were then decreased (i.e. in addition to the decrease caused by direct nut fall) by the appropriate amount. For example, were it determined that nuts with one pupa as the highest damage had a probability of 0.20 of having a 1st instar, and 0.40 of having a 2nd instar, then if five nuts, each with a pupa fell, 1st instar numbers would be reduced by one, 2nd instars by two. In this case a decision would be required as to which of the four time periods for 1st instars should lose this larva (and similarly for 2nd instars). Random numbers were employed to decide this.

Move forward. After the above calculations the numbers in each age class were moved forward seven age classes. Some then became adults; these were not considered further.

The cycle was then repeated.

(iii) The Results

The results are shown in Figure 95. There is a reasonably good correspondence of insect numbers on each date, except on 14.II. and 21.II. when the expected numbers of mature larvae were much greater than sampling indicated.

Nut fall, although following the actual pattern, was underestimated. This is probably due to the failure to account for the increasing tendency of all nuts to fall as the season progresses. Had this been done it could have also corrected the excess numbers of mature larvae predicted by the model, on 14.II. and 21.II.

(iv) Difficulties Encountered

The major difficulty encountered in this model is the calculation of multiple infestations in nuts ("contagion" - C), and the effect of these on the insect population, and number of nuts falling.

The present form of the model could cope with this if appropriate equations describing the numbers of each combination of larvae at all densities could be formulated. (Although at a future date it may be determined that only a few of such combinations are important; this would reduce the magnitude of the task.) However, it appears that the occurrence of multiple infestations and their type (mixture of larval ages) depends to a great extent on the history of the infestation. This complicates the determination of these equations.

Estimating daily natality is also difficult. This is more a sampling problem than one of computation. More frequent samples are probably the only solution to this difficulty.

2. A COMPUTER MODEL

(i) The Structure

In describing populations of *C. ombrodelta* in macadamia it is important that the concept of the total population being composed of small, discrete units of population (nuts) be retained. The desk calculator model failed to do this; it treated the population as a homogeneous, undivided group of insects. This representation led directly to the difficulty of manipulating the contagion factor - "C" of Figure 93.

Computer facilities offer the opportunity to overcome this difficulty. In the model developed below, a sample group of orchard nuts is represented in computer storage as discrete units, and populations of *C. ombrodelta* are

developed on these according to hypotheses of cause and effect developed in the study. "Nut" loss can be generated. Parts of the model are treated stochastically.

(ii) Processes to be Modelled

The processes involved in the computer generation of *C. ombrodelta* populations in macadamia are shown in Figure 96. They are discussed below.

a Time periods

The model was used to generate all or part of a normal macadamia fruiting season - November to March. The season was divided into shorter periods, each of 2,000 hour degrees. Depending on the temperature conditions being considered, the number of such short periods per season would vary, but is of the order of 25.

The life cycle of the insect was also divided into periods of 2,000 hour degrees. Individuals having five larval instars completed immature development in 7 periods, those with six larval instars required 8. The complete development of insects in each instar series was divided as follows.

5 INSTARS

Periods	1	2	3	4	5	6&7	8-10
	egg	1st&2nd	3rd&4th	5th	pre-pupa	pupa	adult

6 INSTARS

Periods	1	2	3	4	5	6	7&8	9-11
	egg	1st&2nd	3rd&4th	5th&6th	6th	6th & prepupa	pupa	adult

A comparison of these divisions with the thermal constants in Table 56, shows that such division is only an approximation. The model was originally developed for periods of 1,000 hour degrees. This allowed a more accurate description of the life cycle. Such a division proved more costly to run and difficult to programme.

Within each period, the calculations shown in Figure 96 were performed and the population was aged one period. The cycle was then repeated as often as required.

b The nuts

The nut population used in the model was considered to be a representative sample of nuts present in an orchard. Ideally its size should be set by sampling considerations. For instance, suppose the model were to be of an insect population similar to that in Aspley S1, 1973-74, and that the sample size was set so that the length of the 95% confidence interval of the mean 3rd instars per nut was no more than 10% of that mean. In the sample results of S1 1973-74 the smallest mean for 3rd instars (excluding zero) was $\bar{x} = 0.0033$ instars/nut, with a variance of $s^2 = 0.0033$, the largest was $\bar{x} = 0.0400$ with $s^2 = 0.0390$. Using the formula given by Steel and Torrie (1960, p. 86) the number of nuts/sample in each case, to achieve the desired confidence interval, was 3,745,000 and 422,000.

Unfortunately the cost of computer memory storage, and the number of repetitive searches of the memory array meant that such a number was too expensive to be considered. Much of the development work on the model was carried out with only 200 nuts in the initial sample and some with only 60. This was later increased to 1,000 to 4,000 nuts.

At the beginning of the first time period all nuts were considered

to be in the tree and unaffected by *C. ombrodelta*. Chapters 7, 8 and 21 provide data from which the nuts' likelihood of fall, development, and maturity could be predicted for use as input data for each period.

c The insect

Oviposition (Boxes 1-7, Figure 96). In the model no provision was made to account for the proportion of total eggs laid on tree parts other than the nuts. The eggs are laid on either damaged tree nuts or undamaged tree nuts in accord with the formula

$$\text{Egg ratio} = \frac{\text{mean eggs/damaged nut}}{\text{mean eggs/undamaged nut}} = \frac{26.29}{(\%\ \text{crop damage})^{0.709}}$$ (Chapter 16)

Box 1. The percent damage of tree nuts is calculated for use in the above formula. A damaged nut is defined as having, or having had, an insect stage as great as or greater than a 1st in it.

Box 2. The number of eggs laid in the orchard depends not only on adult emergence within the orchard - which can be generated by the model but also on adult immigration. Approximate estimates of such immigration may be obtained from the sample results for early season samples (e.g. Figures 51 and 52). In this step eggs from each source are added for a total estimate.

Box 3. As the proposed relationship of egg ratio and % crop damage is hyperbolic and approaches infinity as crop damage approaches zero, it is thought to be unrealistic at low crop damage levels. If damage is equal to or less than 1%, all eggs are considered to be laid on all available nuts (Box 3 goes to Box 6).

Box 4. If crop damage is greater than 1% the total eggs are divided between undamaged nuts and damaged nuts according to a formula derived from that describing the egg ratio.

$$\text{Eggs on damaged nuts} = \frac{\text{total eggs} \times \text{egg ratio} \times \text{total damaged nuts}}{\text{egg ratio} \times \text{total damaged nuts} + \text{total undamaged nuts}}$$

Eggs on undamaged nuts = total eggs - eggs on damaged nuts.

Box 5. Within each class of nuts the contagion of eggs is described by formulae developed in Chapter 16:

For damaged nuts $s^2 = 1.357\ \bar{x}^{1.154}$

For undamaged nuts $s^2 = 1.346\ \bar{x}^{1.043}$

The mean is calculated from the figures derived in Box 4 and the variance from these formulae. Then the frequency of occurrence of nuts which carry 0, 1, 2, 3, etc. eggs may be calculated from formulae for the negative binomial distribution (Kendall and Stuart 1963, p.129). Similar operations are carried out in Box 6 if necessary, using the formula for undamaged nuts.

Box 7. The groups of eggs are allocated randomly to the nuts available. For example, if 10 nuts each are to receive one egg, 10 random numbers in the appropriate range are selected and each receives the correct number of eggs.

Movement of prepupae out of nuts (Box 8). The number of insects in the prepupal stage is multiplied by an emigration factor to give the numbers of external prepupae, either in the tree or on the ground.

Mortality of insects in nuts (Boxes 9 and 10). As explained in Chapter 20, mortality is imperfectly understood. However, basic values

were proposed for each stage such that mortality of the insect from egg to adult emergence would approximate 98% - which would, if maintained, result in a constant population size. Each mortality factor is presumed to be density independent, which is probably not true. (Although a peculiarity of the programme provides that if a nut is selected more than once for egg placement, that nut has a higher than average probability of being selected for the allocation of egg mortality. Thus a type of density dependence - probably undercompensating - exists for egg mortality.) Figure 97 shows the basic steady state mortalities which are proposed. Mortalities for tree and fallen nuts are shown separately, those for fallen nuts being higher than those for tree nuts, except in the case of pupae and prepupae free on the ground. In these it is thought that conditions on the ground are more favourable to pupation than in the tree.

Obviously the final emergence of adults depends very much on the proportion of larvae which fall, and at what stage in their life this occurs. It also depends on the proportion of prepupae which leave nuts, so deduction of the correct mortality is very difficult.

The stage "larvae" in Figure 97 immediately after eggs, is a "dummy" stage. Increments of 2,000 hour degrees are too large to incorporate this stage which is less than 24 hours (*ca.* 400 hour degrees) in duration, so that the basic mortality used in the model for egg to 1st and 2nd instar is 0.47 for tree nuts i.e. (1.00-(1.00-0.03).(1.00-0.45)) and for fallen nuts 1.00.

Box 9. Records are kept of the total number of insects in each development stage, for tree, and for fallen nuts. Each total is multiplied by its appropriate mortality factor which gives the number of deaths expected. Nuts with the appropriate stage are then selected randomly, and one insect is removed from each nut until the desired mortality is reached (Box 10).

d Population totals

Box 11, 12. Counts are made of each class of nut:

Ground - Damaged

Undamaged

Tree - Damaged

Undamaged

Box 13. Counts are made for the numbers of each development stage in both tree and fallen nuts.

Box 14. The number of adults which emerge from nuts during the period under consideration is calculated from the numbers of old pupae present in nuts.

e Nut fall

Box 15. The expected fall for damaged and undamaged tree nuts is obtained by multiplying the number of such nuts by their corresponding probability of fall.

Box 16. The required fall is effected by taking nuts at random from each class of nuts until the required number has been selected, each selected nut and its entire contents being transferred from tree to ground.

f Stages external to nuts

Prepupae and pupae (Boxes 17 and 18). Mortality factors are applied to these (Box 17), and the number of adults which have emerged in the period under consideration is calculated (Box 18) and moved to the calculations

dealing with adults.

Adults (Boxes 19-21). The number of adults emerging from nuts is added to the number which emerged from external pupae (Box 19). Adults in each age class are reduced by emigration and mortality factors (Box 20). No data are available for these factors, but estimates are chosen such that emigration is at a maximum in the mid age period of adults and mortality increases with increasing adult age. Basic values suggested are:

Age class	1	2	3
Emigration	0.20	0.40	0.05
Mortality	0.15	0.45	1.00

These may be varied to test the effect of different values.

Box 21. The number of eggs laid by the remaining adults is calculated from the mean oviposition rates for laboratory adults (Table 79). For each age period these are:

Age period	1	2	3
Eggs laid	62	41	4

These egg numbers are transferred to the beginning of the next loop.

g Monetary value of nuts

Box 22. At certain periods during the season, viz: when harvest begins, when maximum maturity occurs, at the end of the season, the nuts which had fallen were assessed for their commercial value. This depended on the time of season, and proportion damaged. The calculation to determine crop value is the same as that outlined in Chapter 21, p.233-237.

h Move stages forward

Box 23. Every stage is aged by one time period, both for external insects and those in nuts. These updated records are carried forward to the next period if required.

i Time increment

Box 24. If the end of the season has been reached, calculation stops. Otherwise the procedure is repeated.

(iii) Conversion to the Computer

The calculations outlined above formed the basis for a computer programme titled MACSAV. This consisted of a main programme and 15 subroutines and one function subroutine, as well as certain internal subroutines. The arrangement of the different components is outlined in Figure 98. Subroutine MOOV is written in Macro, the remainder of MACSAV is written in Fortran IV.

The author is indebted to Mr W. Goodman, of the Department of Agriculture in the University of Queensland for assistance with the programming. The author prepared the flow chart detailing the operations to be carried out and provided the initial Fortran coding for the subroutines MAYN, ADULT, PPOUT, MONEY, and ROUNCK. Mr Goodman conceived and coded the remaining subroutines, attached all subroutines to the main programme, refined all coding, and provided valuable assistance in debugging the entire programme.

The basic calculations of MACSAV are now described. Descriptions of the more detailed aspects are given in Appendix D, where a copy of MACSAV is presented, together with examples of its input and output data.

a The nuts

Each nut is represented in the computer memory storage by one 36 bit word. Such a storage device allows the contents of each nut to be treated either in part - as required for the allocation of insect mortality, or as a whole - which is required should the nut fall from the tree.

A schematic representation of a "nut" is illustrated in Figure 99. Bits are numbered 0 to 35, each may have a value of "0" or "1" (off or on). Each word is divided into a number of regions which are now described.

Bits 0 and 1. These two bits are "flag" markers showing the nut's condition. The four possible combinations are 0 0, 0 1, 1 0, 1 1 - which indicate respectively that the nut is Ground, no damage; Ground, damage; Tree, no damage; Tree, damage. Therefore causing a nut to fall merely involves a change in bit 0. Damage may be similarly altered; a 1 is placed in bit 1 when an insect passes through development stage 2. It is not removed, even if the insect should subsequently die (in which case the nut has a deserted hole).

Bits 2 to 11 are free. The insect developmental stages are represented in bits 12 to 35 of the word. Each stage occupies 3 bits so that a maximum of seven individuals may be present in any stage. (A bit pattern of 1 1 1 is read right to left in the following manner $2^2 + 2^1 + 2^0 = 4 + 2 + 1 = 7$.)

During programme development, when periods of 1,000 hour degrees were being considered, a maximum of 15 insect development stages were required. To accommodate these stages, each nut consisted of two 36 bit words. The 9th to 15th insect development stages were accommodated in the 1st to 21st bits of the second word, with the remaining bits free.

To minimize the cost of core storage for nuts, and reduce the

volume of calculation, advantage was taken of the fact that only a small number of total nuts are affected by *C. ombrodelta* at one time.

The total nut sample was represented by a single variable - CNUT, and a fixed size array called NUT was set up in memory core. NUT need have space for no more than 20% of the total nut sample. Accounting relating to NUT is performed in MAYN.

At the beginning of a run, NUT is empty. In each loop only the number of nuts required to carry newly laid eggs is added to NUT (and subtracted from CNUT). In some cases no new nuts will be required as, due to egg death, sufficient "clean" nuts will be in NUT already. Subsequent searches and calculations are performed on only the number of nuts present in NUT - thus in most cases the actual nut numbers under consideration is less than 10% of the total. When NUT becomes three quarters filled a clearing operation deletes all fallen nuts having no insect stages and moves all remaining nuts to one end of the array.

As an example of the effectiveness of the operation, one run was made with an initial sample (CNUT) of 4,000 and maximum NUT size of 200 nuts; mean oviposition per loop was 40.40 eggs, the maximum number of nuts to be searched in any loop was 165, and the mean number per loop only 97.76. To have placed the full 4,000 nuts in NUT and performed each calculation with 4,000 nuts would have been prohibitively expensive.

b The programme

MAIN is a short programme which specifies the nut numbers being modelled. As it is so short it can be altered at little cost. Subroutine MAYN - originally the main programme is shown as a continuation of MAIN (Figure 98).

Numerical format. Any value relating to number of nuts or insects

is expressed as an integer. If during calculation decimal places appear, these are rounded to the nearest integer value or truncated, as desired. For this reason it is an advantage to model a large sample of nuts (certainly not less than 200), or rounding errors become appreciable.

Random numbers. By selecting the starting point in the random number generator according to the time of day, each run generates a different sequence of random numbers.

Data input. DATA is the input file containing input data. This relates to the number of eggs laid in each period by migrant adults, likelihood of fall for nuts of the different damage classes, the mortality data for insects, etc.

Scratch files. Subroutine OPEN prepares the way for scratch (temporary storage) files to be written of the number of insects in each stage of development. For eight development stages eight files are required.

Scratch files are not stored in memory core, and may be of variable length, from zero if no stage is present, to the maximum size of the population. Their use represents a saving in memory cost, as the alternative is to open in the memory core a fixed size array of dimensions (development stages x nut numbers) - e.g. for eight stages and 200 nuts (8 x 200); much of this space would not be required, as many nuts would have no insects.

Loop counter. For a season length of 25 periods the programme executes 25 major loops. The execution stops before this if the tree nut crop has been depleted. The number of loops required is typed in at the teletype at the beginning of each run.

Eggs laid. The total eggs for allocation equals eggs laid by

immigrant moths (DATA file) plus eggs laid by adults emerging in the orchard (generated by the model).

Percent damage. If percent damage is not greater than 1% all eggs are allocated to all nuts without regard to damage. Otherwise a division of eggs is made, and eggs on damaged and undamaged nuts calculated. In either case the number of nuts carrying 0, 1, 2, 3, 4, or 5 eggs is determined. These calculations are described in (ii)c above.

Check egg numbers. To ensure that eggs have been allocated in a realistic manner, the main programme calls subroutine ROUNCK.

ROUNCK first checks that there are no more than two nuts carrying five eggs each as more would not be realistic. If there are more an error message is printed on the teletype and the execution stops.

If this test reveals no difficulties, the subroutine tests actual egg numbers with total eggs allocated. If the difference is more than five eggs it is believed to be greater than could have arisen through rounding errors and an error message to that effect is printed at the teletype and the execution stops. Otherwise the difference is corrected by adjusting the number of nuts with one egg, e.g. if the difference were -1, and four nuts carried one egg, this would be altered to five nuts with one egg. This procedure results in a temporary imbalance in egg distribution and nut accounting. It is considered minor compared with the difficulties which would otherwise arise.

Records of crop status and insect numbers. So that subsequent calculations may be performed, a record of the number of nuts, damaged and undamaged nuts in the tree, and the number of insects present in each developmental stage in tree and fallen nuts must be compiled. Subroutine SRCH performs this task; subroutines INDEX and RANFIL are called from SRCH.

An array called ITEMPT is used to store the index (e.g. nut 1, nut 49 etc.) of each tree nut in NUT. ITEMPT consists of half as many 36 bit words as are in NUT, i.e. if there are 200 nuts, ITEMPT is 100 words. Each word is divided in two, and one index is stored in each half word. Undamaged nut indices are stored from left to right, damaged nut indices from right to left.

SRCH examines the value of the first two bits in each nut (flag bits). If the nut is on the ground (flag value 1, or 2) subroutine RANFIL is called and the numbers of each insect developmental stage are determined and recorded in the appropriate scratch files. For a tree nut (flag value 3 or 4) INDEX is called. INDEX determines where in ITEMPT the index should be placed. SRCH places the nut accordingly and calls RANFIL which performs the operation described above.

Place eggs on tree nuts. Subroutine ALLOC is called, first for undamaged nuts, later for damaged nuts.

ALLOC calls Function IRANDX to select a nut index from ITEMPT at random from those nuts available for the allocation. ALLOC then adds the appropriate egg numbers onto the nut, and adjusts the numbers in the egg scratch file. Single eggs are allocated first, then groups of two, three, and so on. Ideally a nut should be selected only once. However, in MACSAV multiple selection is possible. To correct this would mean extensive modification to ROUNCK, which was not undertaken as development costs were high in relation to the author's budget.

Calculate prepupal movement out of nuts. The numbers of prepupae or mature larvae which move out of nuts are determined by multiplying the numbers in the scratch file for stage 6 (6th instars and prepupae) by the appropriate emigration factor, firstly for the ground, then for the tree.

Subroutine PPOUT is called. This adds the numbers which moved out into the first position in a 1x3 array called by OUTPP. Mortality is applied to each value in the array, the highest mortality occurs in the first array position (most recent emigrants) as establishment mortality is considered to be the most important in these external insects. The number of adults emerging in the time period under consideration is recorded as the number of pupae in the last position of OUTPP. All values are then moved forward (aged) one time period.

Mortality of the insects in the nuts. Subroutine MORTAL is called.

The mortality for each stage is read. This depends on whether the insect is in a tree or fallen nut. Each mortality may be changed as often as 24 times in a programme run, or held constant for as many loops (periods) as desired.

Mortality in fallen nuts is considered first, then that in tree nuts. For each insect stage, from eggs to pupae, the number of insects present is multiplied by the mortality factor - this gives the number of insects which should die. Indices of nuts containing the stage under consideration are selected randomly and one insect removed from each nut. The process is repeated until the correct number of insects has been "killed". A nut may be selected any number of times.

For mature larvae and prepupae (developmental stage 6), the mortality factor applied is a combination of mortality for insects in nuts, and the proportion which moved out of nuts (see PPOUT above).

Calculate totals etc. These operations are performed by subroutine SRCH2, which also calls subroutines MOOV and OUT.

SRCH2 examines each nut in turn, regardless of its position (tree, ground).

Adult emergence: the number of insects in the last developmental

stage (8) are recorded as adult emergence at the end of the period under consideration.

Nut records: the flag bits of each nut are examined and the totals for fallen nuts - undamaged; fallen nuts - damaged; tree nuts - undamaged; tree nuts - damaged, are incremented as appropriate.

Insect stages: the number of insects in each stage of development is recorded and a running total is made separately for fallen nuts, and for tree nuts.

Ageing insect stages: subroutine MOOV moves all the insect stages forward three bits (one stage). Those in the last three bits are lost. Of those insects in the 4th stage, a percentage jump one stage (the 5 instar series), the remainder move only the one stage (6 instar series). Adjustment for the stage jump is made in SRCH2.

Output: subroutine OUT is called. From the array of developmental stages (compiled before MOOV was called), the numbers of eggs, 1st & 2nd instars, 3rd & 4th instars, 5A instars, Final larval instars, and pupae, in fallen and tree nuts is calculated, and output in each loop. These values are placed with the previous output from MAYN.

The counts of damaged and undamaged tree nuts, made before MOOV was called, are referred to as pre-MOOV counts. After MOOV returns these will be out of date, as some eggs will have hatched, resulting in an increase in damaged nuts. Therefore, at the end of SRCH2 a check is made of the new damage and totals for damaged and undamaged tree nuts are adjusted accordingly.

Calculate fall. The numbers of damaged and undamaged nuts present are each multiplied by the probability of fall (read from DATA for the appropriate period). The resultant number of nuts which should fall, is then allocated randomly in each class of tree nuts by subroutine FALRAN. Nut numbers used are the pre-MOOV counts from SRCH2. Therefore nuts damaged

by 1st & 2nd instars only, fall with the frequency of undamaged nuts. All other damaged nuts fall with a higher frequency.

FALRAN selects a nut index randomly from ITEMPT and checks that this nut has not already been selected. If it has been selected before, another index is picked, otherwise the first flag bit in the appropriate nut is changed - and the nut "falls". If dealing with damaged nuts, the total for damaged tree nuts is decreased appropriately, if dealing with undamaged nuts a check determines whether the selected nut is in fact undamaged or damaged by a 1st & 2nd instar. The appropriate adjustment is then made to either damaged or undamaged nut totals.

Calculate eggs laid in orchard. Subroutine ADULT is called. This subroutine is similar to PPOUT. It adds the number of adults emerging from external pupae to those from nuts, and places the total sum in the first position of a 1x3 array - ORCHAD. Factors for emigration and mortality are applied to each of the values in the array reducing their numbers, and the total eggs laid is calculated by multiplying ORCHAD by a 3x1 array of the egg expectation for adults of different ages. Each adult value is then moved forward one place (age) in the array.

Running total of fallen nuts. Continuous records are kept of the accumulative total fall of damaged and undamaged nuts.

These are subtotaled at different periods in the season. Firstly when harvest begins, secondly when nuts attain maximum maturity, and thirdly at the end of the season.

Calculate nett return of crop. At the end of the season subroutine MONEY calculates the gross return of nut sales, deducts labour costs and writes the nett return.

(iv) Deficiencies in the Programme

The programme is in a relatively early stage of development - only six weeks have elapsed since the initial coding to the time of writing, and several major structural changes have taken place in that time. Each resulted in a number of arithmetic and logical difficulties which added to the cost and time involved.

Further effort was not devoted to overcoming the difficulties outlined below, both because of the time and money restrictions, and because future workers may wish to develop the model along different lines.

a Nut fall

With the exception of causing nuts damaged by 1st & 2nd instars to fall with the frequency of undamaged nuts, gradation of likelihood of fall with increasing damage is not incorporated in the model. Figure 86 suggests that there is such a gradation, and it is thought to be quite an important feature in macadamia-*C. ombrodelta* interactions.

To incorporate such a feature would have increased memory storage costs, as it appeared that an extra ITEMPT array would be required. It would also have increased the cost of searches and processing of data relating to nuts.

b Allocation of eggs

It has been mentioned that nuts selected for allocation of eggs may be chosen more than once in any loop. This occasionally results in excess allocation. During five runs in which a total of approximately 7,000 eggs were allocated, one nut received seven eggs and one nut eight.

In the second case no eggs would be recorded on that nut as eight is represented by a bit pattern of (1 0 0 0) and only the right hand three bits would be written. This deficiency of eggs may cause an infinite loop to develop in MORTAL, as the computer searches for eggs which are not present. A count in MORTAL causes the search to be abandoned after 20 attempts, when an appropriate error message is typed. The run then continues.

At this stage in model development this symptomatic correction is considered preferable to the extensive changes in ROUNCK and ALLOC which would otherwise be required.

c Mortality

Mortality factors are read from the DATA file while the programme is running. Therefore, although they be changed 24 times in any run, such changes must be arbitrarily decided before the run begins. No self correcting device for density dependence is incorporated in the model calculations. Such a calculation should be relatively easily and cheaply incorporated when knowledge of *C. ombrodelta* mortality factors is more complete.

More costly, would be the incorporation of disparate mortalities for young larval establishment in damaged and undamaged nuts, and for older larvae in multiple infested nuts and nuts with single infestations. Either extra scratch files for nut index storage of the different types of nuts would be required, or there would have to be an extra check on the developmental stage bits before mortality was applied, with a subsequent adjustment to the mortality factor before it was applied.

d Programming language

Mr Goodman believes that a considerable increase in the efficiency of the calculations involved could be achieved if the entire programme was rewritten by a competent MACRO programmer.

(v) Running the Model

So that model output may be compared with actual sampling data, the results of samples taken in Aspley S1, 1972-73 and 1973-74 have been regraphed in groups of immature stages similar to those used in the model (Figure 100). For a comparison of actual nut populations and fall the reader is referred to Figures 15 and 18.

a Features of the model

Six runs were required to achieve a combination of immigrant egg laying, and mortality factors which produced an output similar to that achieved by sampling at Aspley S1. Figure 101 shows the output of the fifth and sixth runs in the series. The data used in these runs are shown in Table 107. The variation in immature mortality from the 5th to the 6th run was an average 6.3% increase in fallen nuts, and an average 3.4% decrease in tree nuts.

The pattern of oviposition generated by these model runs is similar to that found in orchard samples - with wide fluctuations in egg numbers from period to period. In the model, a sharp increase in egg numbers occurs in the 11th and 12th loops, when the first adults of the season emerged from "orchard" nuts. It would appear that the sharp increase in egg numbers in orchard samples observed in late December (Figure 100) is also due to the first emergence of adults within the orchard, supplementing

the continued immigration of adults. Such emergences, in both model and orchard, also coincide approximately with the lowest probability of nut fall. This indicates that the high fall of nuts early in the season reduces within orchard survival of immatures in nuts.

Both these model runs were made with an initial sample (CNUT) of 1,000 nuts, and a maximum NUT array size of 200; only 112 nuts were placed in NUT for run 101A and only 137 for 101B. Cost of the runs was $1.50 for A and $2.30 for B. A larger run made with 4,000 CNUTs and twice the number of immigrant eggs cost $4.50.

The fluctuating pattern of immigrant eggs used in the input was deduced from a consideration of the fluctuations of male catch in Orfamone II lures around the Aspley orchard in 1973-74 (Figure 77). Egg population intensity in the first seven loops, at about 0.02 eggs per loop, is comparable to the sample results. In the field sampling results the level of the December, January increase in eggs was about x4. Inspection of Figure 101 shows that the corresponding increase in the model was only x2. During early development runs (200 CNUTs) egg population intensity following orchard emergence of adults was so high that the run stopped (in ROUNCK). To overcome this, the egg expectation from adults of different ages was approximately halved from that shown on p. 257 and this value has been retained to give a safety margin, even though nut numbers have since been increased. This also reduced costs, whilst still allowing for the observation of qualitative variation in model populations.

Because of the lack of data, emigration has been assumed to be nil in these runs.

For all larval and pupal stages in the model output there is a greater proportion of population on the ground than was found in field samples. For stages older than 2nd instars, the absolute populations in the tree are lower than expected from a comparison with field samples. These discrepencies suggest that some improvement is required in the mort-

ality values chosen. However, they are probably largely due to the lack of a gradation in the model of likelihood of nut fall with increasing damage.

Table 108 gives a comparison of some of the basic statistics generated by the model with those obtained by field sampling. The model statistics are compiled from an output of the NUT array in loop 14 of each run. The field sampling results are for dates in 1972-73 and 1973-74 falling in approximately the same seasonal period as loop 14 of the model. Only tree nuts are compared as in the model, nuts on the ground accumulate over all 14 loops - comparative data from the field are not available.

The results are broadly similar, although model means are usually less than field means, and the variances higher for comparable means. This indicates either that the fault in the allocation of eggs (ALLOC) is having an appreciable effect, or that density dependent mortality (not incorporated in the model) is important in reducing the numbers of multiples in the field. Probably both conditions are true. Only in model runs E and F are the ratios of variance to mean comparable to those obtained in field samples, and in these cases, deserted holes per living larva are higher than expected. In each of these runs (E and F) the mortality for tree nut eggs was approximately 90% compared to the more normal 46%.

Nett return in the model was only $0.68220 for run A, and $0.61778 for run B. Each result should be multiplied by 73 to bring it to initial nut numbers comparable to Aspley S1 1972-73. The returns are then $49.80 (A) and $45.10 (B) which is considerably lower than in the calculation for field data ($70.57, pp. 233-237). As the values for maturity, prices and costs were the same, this difference in return indicates that the combination of egg laying, mortality, fall etc., used in these runs needs adjustment. Even though low, the nett return calculation indicates, by its variation, the different effect on the crop of different input values.

b Elementary simulation and sensitivity

After the very early development runs only egg laying and mortality were varied. To have tested variations in other factors would have given rise to a very large number of combinations of test data.

An elementary simulation of spraying was carried out to determine how the model behaved with variations in mortality factors. The results of two sprayed runs are shown in Figure 102. In 102A, spray which reduced the survival of eggs and 1st and 2nd instars in tree nuts to only 10% and 50% respectively (*cf.* the usual 54% and 25%) was applied only in the 2nd and 3rd loops.

The result on the subsequent population was dramatic. Orchard generation of adults did not recover until the 24th loop. Such a response to spraying is considered most unreal, in the light of comparison with the Beerwah experience. The fact that the model responded in this way shows that the density independent mortalities used are unrealistic, and input mortality also fails to take account of a probable reduction in natural enemy populations after spraying.

102B shows the results of one spray run which attempted to simulate a post-spray population resurgence. Data, apart from the mortalities, were identical to that used to give the results shown in Figure 101B.

Spray was applied in the 3rd and 4th and 14th and 15th loops. The spray reduced the survival of eggs to 10% and mortalities for later stages decreased and then gradually returned to normal. The data are shown in Appendix D (Figure D12). This run is thought to have produced a more realistic result, but the dependence on an arbitrary input of mortalities before the run begins is clearly unsatisfactory.

A similar simulation was made with the release of an "egg parasite" which reduced the survival of eggs to 10%. Whilst the release was in pro-

gress mortalities of later stages were lower than normal, to mimic the effect of reduced intra-specific competition. Populations were reduced during the release, returning to normal levels soon after the release finished. Until a subroutine dealing with parasite generation is incorporated in the model, such releases are operationally identical to the effect of spraying.

At present the model is sensitive to any change in egg input or mortality. A 10% increase in egg input should result in a 10% increase in adult emergence, and changes in mortality would similarly affect output. Slight variations will occur due to rounding errors and the randomness of nut fall. More detailed experiments on mortality factors of *C. ombrodelta* should provide data suitable for the incorporation in the model of density dependent mortalities, when more interesting experiments on sensitivity analysis may be performed.

SECTION VII

CONCLUSIONS

CHAPTER 24

CONCLUSIONS OF THE STUDY

The present study of *C. ombrodelta* covered a wide range of aspects of its life system in Southeast Queensland, and because of this, had to be carried out on a strict time-scheduling which has left data for many processes incomplete. However, the study has established a basic knowledge of the life system from which future work may be directed efficiently.

1. GENERAL CONCLUSIONS

(i) Difficulties Encountered

1. The division of a site population into small discrete units (the fruit) means that it is desirable to use one fruit as a sampling unit (p. 124). This small unit size, usually containing only one or two insects (Table 59), combined with the arduous dissection of units for examination, militates against precision in field sampling - even when the insect is causing appreciable economic damage.

2. The occurrence of different developmental stages of the insect in multiple habitats (e.g. eggs on leaves, branches and fruit (Table 69), prepupae in soil, branches and fruit (pp. 183-186)) makes it difficult to achieve sampling precision with acceptable cost.

3. Field sample results are difficult to analyse because of the continuous breeding of the insect, and the large fluctuations in its rates of increase and decrease (Figures 49-53).

4. The variations in the physiological development time of the immature stages with changing daylength (p. 114), combined with variation likely to be imposed by changes in food quality etc. complicate the prediction of field population development.

5. Accurate identification of larval instars is hindered by the variable instar numbers, with consequent overlapping head capsule widths (Chapter 12). (Precise identification may not be necessary, as a reasonable interpretation of population change was achieved in the present study by grouping certain instars (Figure 101).)

6. The failure of a wide range of conventional traps to record appreciable female *C. ombrodelta* catch (Table 74) indicates that the study of migration may be hindered.

7. The characteristics of the macadamia crop cause some complications in sampling - nuts have extremely variable distribution between and within trees, and their stability varies throughout the season (Chapter 7).

(ii) Computer Model

Having the construction of the computer model as a goal has achieved the desired effect of directing the work carried out.

The process of constructing the model was instructive in evaluating the status of the knowledge, as were the limited number of runs made. Although much work has yet to be done on improving the input data and on model construction, these runs have proved to be helpful in imparting an awareness of the processes involved.

In general, the hypotheses of cause and effect, proposed in the study and incorporated in the model, appear to result in a fairly good sim-

ulation of observed field populations. This indicates that the study has contributed to an understanding of the *C. ombrodelta* life system.

2. MAJOR CONCLUSIONS

The major conclusions reached are now given under the headings of the aims of the study (p. 2).

(i) Definition of Damage Caused by C. ombrodelta

It is concluded that *C. ombrodelta* may cause a substantial loss of crop in macadamia.

The major sources of loss are an increased fall of nuts early in the season before kernels are sufficiently mature to be harvested (quantity loss), and after harvesting begins but before maximum maturity is achieved (quality loss).

Direct insect damage to the kernels of nuts is likely to be of little consequence in the *integrifolia* types of macadamia now being grown (p. 230), although its effect on increasing handling and grading costs must not be overlooked.

There is evidence that, contrary to previous beliefs, husk damage by *C. ombrodelta* after maximum kernel maturity is achieved may cause a significant loss of quality (Table 105, Figures 87 and 88). This has not been confirmed by commercial process tests, but if proved the present toleration of *C. ombrodelta* infestations late in the season will have to be revised, as such infestation would not only reduce gross return, but also increase handling and grading costs.

The studies on crop development reported in Chapter 8 show that there are a number of useful visual characteristics of the nut which

assist in the definition of the type of crop loss occurring at any time, and in setting times for harvesting operations e.g. the point at which 50% of nut shells were hard brown is used in this study to define the date on which harvest should begin (Table 106). It appears from the data of this study that use of this easily defined seasonal point minimizes the collection of immature kernels, and the loss of mature kernels.

(ii) Determinants of Abundance and Persistance

a Alternative hosts

It is concluded that in the Aspley area the large, and diverse extra-orchard alternative host populations (Figure 28) are of primary importance in the production of abundant orchard populations each year.

The Orfamone II lure traps placed around the orchard in 1973-74, showed that there is a high production of *C. ombrodelta* adults from these hosts from early spring to early autumn, and that only in late summer does production of adults in the orchard approach comparable levels (Figures 78 and 79).

Orchard nut samples (Figures 49-53) indicate that egg laying in the orchards early in the season is due to immigration of moths from extra-orchard hosts. Large increases in orchard oviposition occurred only in December, January when the first emergences of adults from nuts could be expected. That this is so is supported by the computer model runs (e.g. Figure 101).

b Macadamia

It is thought that macadamia may not be a very suitable host plant for *C. ombrodelta*, although this may depend on the variety under

consideration. The reasons for this supposition are:

(a) Young larvae experience difficulty in entering undamaged nuts, especially in H2 (Table 95).

(b) The adult's preference for laying on damaged nuts (Figure 65) eases larval entry but it is likely to result in a much lower probability of such larvae maturing; the nut will probably fall from the tree too early for the larvae to complete development, and cannibalism is more likely.

(c) Mortality appears to play a more important part in determining population levels in macadamia than in the alternative hosts (Figures 81, 82 and 83).

(d) In varieties with a restricted fruiting season, it is believed that overwintering does not occur in macadamia orchards (p. 187).

It may be postulated that macadamia may not have been important in the evolution of *C. ombrodelta* as the insect's behaviour appears more suited to hosts with larger fruit and more accessible seeds, which do not have such a high probability of fall after infestation.

The above points are made from a consideration of sampling results in the unsprayed Aspley and Inala orchards. The very high populations arising in the Beerwah trees studied in 1972-73 may have been due to unknown factors which make 246 variety a suitable host for *C. ombrodelta*, the fact that spraying in the orchard reduced natural mortality factors, or an unusual combination of extrinsic factors. If further studies, under a variety of conditions confirm the population patterns at Beerwah, the supposition that macadamia is not a good host would have to be revised.

c Weather

Prevailing weather conditions are thought to be an important influence in the persistence and abundance of *C. ombrodelta*. The 1972-73 season was relatively hot and dry, and populations in the Aspley orchard were high, with a high level of adult emergence within the orchard (p. 205). In contrast, 1973-74 was a cooler, and very wet season. Although populations of *C. ombrodelta* were high outside the Aspley orchard (Figure 78), within the orchard populations were low, and adult emergence very low (p. 205). A similar difference in populations between seasons was observed at Beerwah, although the situation there was complicated by a variable spray regime.

As early egg populations in the Aspley orchard were similar in both seasons, the difference is thought to reflect a sharply decreased establishment of young larvae in nuts due to their having been washed from the nut surface (p. 215). Absolute larval population levels confirm this view (Figure 51 and 52).

There is little evidence to show how weather affects migration of adult *C. ombrodelta*. However, the early level of eggs in Aspley in 1973-74 was at least as high as in 1972-73, so that migration is probably not affected greatly by wet windy weather.

d Natural enemies

Parasites were the only natural enemies recorded in abundance, although predators were probably also important. Disease seemed to play no major role in population regulation.

Because populations reach such high levels in the alternative hosts (Figures 58, 59) and apparent percent parasitism remains low

(Figures 73, 74) the natural parasites do not appear to be effective in limiting population growth in these hosts.

Control by natural biological agents appears to be no greater in macadamia. However, in late summer when populations of *C. ombrodelta* are high, parasites have increased, and the host population is experiencing difficulties due to mature nut fall and increased intra-specific competition, the small extra mortality imposed by parasites may provide sufficient extra pressure to reduce host populations. Little relief from crop damage is then obtained.

(iii) Direction of Future Work

a Probable control

The present study confirms the view of Ironside (1974) that a purely chemical control is likely to be ineffective in reducing *C. ombrodelta* populations. The trees are difficult to spray, and the desired control period occurs during the wet season. Most importantly, the continuous breeding of *C. ombrodelta* means that chemical control must rely on a continuous spray cover for the low density immigrant egg populations during the early part of the season.

The most effective course in reducing loss due to *C. ombrodelta* is likely to be one of avoidance. Future plantings could be in isolated areas - the extra costs of transport to and from such farms could well be offset by the saving in crop damage.

Avoidance will not always be possible, especially in existing macadamia orchards. In these, it is important to prevent the within orchard emergence of adults and so avoid the sharp increase in *C. ombrodelta* populations in December, January. It would be difficult for natural enemies within the orchard to control the low density pest populations due to immigration. By the time natural enemy populations responded to the

December, January pest population increase, there would be considerable crop damage.

The most acceptable control is likely to be the release and encouragement of one or more natural enemies which can suppress the spring alternative host populations, and thus reduce the probability of appreciable *C. ombrodelta* migration to the orchards. As native natural enemies do not at present exercise such control, introduced species will probably be required, although with suitable management the native parasites may be effective.

b Experimental programme

The following programme of research and investigation is recommended to ensure that macadamia crop losses due to *C. ombrodelta* are minimized. The potential for loss due to this insect (up to 20% of the crop return, Chapter 21) is great enough to warrant the expenditure involved.

The present study has indicated that each site, and each variety of macadamia is likely to exhibit variation in loss due to *C. ombrodelta*. It is therefore most important for studies to be localized at specific commercial sites, and concern the most common varieties of macadamia.

Economic crop damage threshold.

At several sites, a number of trees should be given full protection (probably chemical) against *C. ombrodelta*; others should be unsprayed. The number of trees in each group should be sufficient to provide enough nuts for fortnightly records of crop infestation levels, and fortnightly nut samples of a size suitable for commercial processing. There should be sufficient replicates to provide statistical precision. Records

should be kept of nut fall in each group, and correlated with infestation levels and time of season.

The nut samples should be processed commercially and the yield of first grade nuts, the handling and grading costs, and value of each sample should be recorded. Special attention should be given to the variation in yield between husk damaged and undamaged nuts late in the season.

These results will allow the definition of the economic threshold of infestation at different times during the season. Such a definition is essential to the evaluation of any control measure.

C. ombrodelta studies

Infestation potentials. The areas around orchards should be surveyed to determine the species and number of alternative hosts present. Grids of Orfamone II lure traps as described in this study (pp. 199-200) will be useful in locating sites of *C. ombrodelta* breeding and confirming the survey results.

Such information will assist in defining the likely importance of *C. ombrodelta* to each orchard. In addition, the species and number of such hosts may determine the control. If alternative hosts are few, and in well defined areas, extra orchard chemical or mechanical (digging up the species or collecting the fruit) control may be feasible. If the hosts are widespread and in private gardens such controls would probably not be acceptable.

Mortality. A proper definition of the natural mortality factors and their mode of action is most important. This should be done in macadamia so that the effect of a proposed control measure in the orchards may be predicted. For instance, an egg parasite may reduce the density of larval populations to such an extent that normal intra-specific compet-

ition becomes negligible, with the result that a high percentage of adults mature from those eggs escaping the parasite.

Similar studies should also be undertaken in the seasonally important alternative hosts, e.g. *Bauhinia* spp., and *Cupaniopsis anacardioides*, as mortality in these will probably be important in deciding on the final suitability of a control measure.

Such studies will be hampered by the difficulties mentioned at the beginning of this chapter. Results will best be achieved by the intensive study of a series of experimental populations carried out on site. Fruit should be caged for a short period, subsequent egg population densities artificially reduced to normal levels, and the resulting populations monitored intensively, with emphasis given to the time and manner of insect death in the nut, and of insects leaving nuts.

Migration studies. A more precise definition of the migration of *C. ombrodelta* would assist in predicting the infestation potential of an orchard area.

Flight mill studies of females will determine the maximum potential distance of immigration. Experiments on the behaviour of adult females will determine whether migration is predominately accidental, or purposeful. Especially in accidental migration, a knowledge of wind directions prevailing in spring would assist in predicting sites from which migration may be expected.

Natural enemy studies

Initially the parasites *Apanteles briareus* and *Bracon* sp. should be investigated more thoroughly. Particular attention should be given to means of increasing their populations in the spring period - either by

food supplements in their natural environment, or by a mass release.

Extensive searches for exotic parasites should not be undertaken until these studies on native parasites have defined their potential more clearly. Literature surveys concerned with natural control will assist in narrowing the search should it prove necessary.