BIOLOGY, ECOLOGY AND MANAGEMENT OF WHITE WAX SCALE, *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE), ON *CITRUS* AND *SYZYGIUM*

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Doctor of Philosophy

by

Waktola Wakgari

Department of Entomology and Nematology

Faculty of Agricultural and Forestry Sciences

University of Stellenbosch

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Promoter: Professor J. H. Giliomee

Declaration

I, the undersigned hereby declare that the work presented in this dissertation is my own original work and has not previously been submitted in its entirety or in part in candidature at any university for any other degree.

ABSTRACT

The population density of the white wax scale, *Ceroplastes destructor* Newstead, has increased since 1994 in certain areas of Western and parts of Eastern Cape Provinces of South Africa where citrus is grown, particularly on *Citrus reticulata* (Blanco). A study was conducted to investigate its morphology, biology and ecology as contributions to the development of a sound integrated management programme.

Characteristics of the immature stages and adult females were described and illustrated from field-collected and slide-mounted specimens. A key to the different stages and morphometeric characteristics useful for separating them are provided. No significant differences in female fecundity were found between orchards ($P > 0.05$). However, fecundity varied significantly between female size classes from the same orchard ($P < 0.001$). Female body-size also differed significantly between orchards ($P < 0.05$) and was significantly positively correlated with fecundity ($P < 0.01$). *C. destructor* has one discrete generation per year in South Africa. Oviposition commenced in November and continued through to the end of December with a few females ovipositing until mid January. Population density of the second instar peaked in February while the third instar extended from March to the end of July, followed by a peak population of adults in August. Seven primary and three secondary parasitoids, as well as four predator species attacking *C. destructor* were identified. *Aprostocetus (= Tetrastichus) ceroplastae* (Girault) was the dominant species, accounting for 78.87% of the total primary parasitoids reared. Peak numbers of parasitoids and predators were synchronized with peak emergence of susceptible scale stages, indicating that the host-

parasitoid/predator system contained a density-dependent regulatory mechanism. Key mortality factors varied slightly between two of the orchards. Key stage mortality determined from a cohort life table was generally in the third instar (LIII) and pre-ovipositional female (POF) stage. Significant density-dependent mortality factors were demonstrated for the first instar (LI) and POF stage.

Dispersal of *C. destructor* is by first instar nymphs and the numbers caught on a series of yellow sticky traps varied significantly between crawler densities at the source, trap distances and trap directions from the source ($P < 0.001$). The numbers caught were positively correlated to the initial crawler density at the source ($P < 0.01$), suggesting that dispersal was density dependent. Trap distance and the numbers caught were inversely correlated ($P < 0.01$). Evaluation of effects of different densities of *C. destructor* on growth, survivorship and reproduction of scales as well as on leaf bearing ability of trees and area of leaf surface covered with sooty mould fungus was carried out on naturally infested *Syzygium (= Eugenia) malaccensis* (L.) plants. Scale body size and fecundity were inversely related to scale density ($P < 0.01$), suggesting density-dependent intraspecific competition. Scale survivorship generally declined with increasing density whereas scale parasitism and predation were positively correlated with density ($P < 0.05$). At high scale densities production of new leaves was significantly reduced ($P < 0.01$), reducing the resource base for subsequent generations of scale. Scale density and leaf area covered with sooty mould fungus were significantly positively correlated ($P < 0.05$).

The toxicity of four synthetic insecticides against the three immature stages of *C. destructor* and of eight insecticides against the parasitoid *A. ceroplastae* was evaluated. Development of the first and second instars of *C. destructor* was completely arrested by

the chemicals. Female fecundity, fertility and body sizes of survivors of treatments applied at the LIII stage were not significantly affected by any of the chemicals ($P > 0.05$). All the chemicals exhibited high toxicity to *A. ceroplastae* and hence are not recommended for integrated management of *C. destructor* in citrus orchards where *A. ceroplastae* plays an important role.

OPSOMMING

Die populasiedigtheid van die witwasdopluis, *Ceroplastes destructor* Newstead, het sedert 1994 toegeneem in sekere gebiede van die Weskaap en Ooskaap provinsies van Suid-Afrika waar sitrus verbou word, veral op *Citrus reticulata* (Blanco). 'n Studie van hierdie insek se morfologie, biologie en ekologie is onderneem as bydrae tot die ontwikkeling van 'n geïntegreerde bestuursprogram.

Die karaktertrekke van die onvolwasse stadia en die volwasse wyfies is beskryf en geïllustreer vanaf eksemplare wat in die veld versamel is en op glasplaatjies gemonteer is. 'n Sleutel vir die verskillende stadia en morfometriese kenmerke wat nuttig is om hulle te onderskei, word voorsien. Geen beduidende verskille in die vrugbaarheid van wyfies van verskillende boorde is gevind nie ($P < 0.05$). Vrugbaarheid het egter betekenisvol verskil by die verskillende grootteklasse van wyfies uit dieselfde boord ($P < 0.001$). Die liggaamsgrootte van wyfies uit verskillende boorde het betekenisvol verskil ($P < 0.05$) en was betekenisvol positief gekorreleer met vrugbaarheid ($P < 0.01$). *C. destructor* het een generasie per jaar in Suid-Afrika. Eierlegging het in November begin en aangehou tot aan die einde van Desember, met enkele wyfies wat nog tot in middel Januarie eiers gelê het. Die populasiedigtheid van die tweede instar het 'n hoogtepunt in Februarie bereik, terwyl die derde instar van Maart tot aan die einde van Julie geduur het, gevolg deur 'n piekbevolking van volwassenes in Augustus. Sewe primêre en drie sekondêre parasitoïde asook vier predator spesies wat *C destructor* aanval, is geïdentifiseer. *Aprostocetus (=Tetrastichus) ceroplastae* (Girault) was die dominante spesies wat 78.87% van die totale aantal primêre parasitoïde wat uitgeteel is, uitgemaak

het. Die pieke in die getalle van parasitoïde en predatore was gesinchroniseer met pieke in die verskyning van die gevoelige stadia, wat dui op die aanwesigheid van 'n digtheidsafhanklike regulatoriese meganisme. Die sleutel mortaliteitsfaktore het effens gevarieer tussen twee van die boorde. Die sleutelstadium van mortaliteit, soos bepaal m.b.v. 'n kohort lewenstabel, was gewoonlik die derde instar (LIII) en die pre-oviposisionele wyfie (POW). Betekenisvolle digtheidsafhanklike mortaliteitsfaktore is aangetoon vir die eerste instar (LI) en die POW.

Die verspreiding van *C.destructor* vind plaas deur die eerste instar nimfe en die getalle wat op 'n reeks van taai geel valle gevang is, het betekenisvol gewissel volgens kruiperdigthede by die bron, asook die afstand en rigting van die valle vanaf die bron ($P < 0.001$). Die getalle wat gevang is, was positief gekorreleer met die aanvanklike kruiperdigtheid by die bron ($P < 0.01$), wat daarop dui dat verspreiding digtheidsafhanklik was. Die afstand van die valle en die aantal wat gevang is, was omgekeerd gekorreleer ($P < 0.01$). 'n Evaluering van die invloed van verskillende digthede van *C. destructor* op die groei, oorlewing en reproduksie van dopluise, asook die vermoë van bome om blare te dra en die area van die blaaroppervlak wat met roetskimmel besmet is, is uitgevoer op plante van *Syzygium (= Eugenia) malaccensis* (L.) met 'n natuurlike besmetting. Die liggaamsgrootte en vrugbaarheid van die dopluise was omgekeerd gekorreleer met hulle digtheid ($P < 0.01$), wat dui op digtheidsafhanklike intraspesifieke kompetisie. Die oorlewing van die dopluise het oor die algemeen afgeneem met toenemende digtheid, terwyl parasitisme en predasie positief gekorreleer was met digtheid ($P < 0.05$). By hoë dopluisdigthede het die produksie van nuwe blare betekenisvol afgeneem ($P < 0.01$), wat die hulpbronbasis vir daaropvolgende generasies

van dopluise verswak. Die dopluisdigtheid en blaaroppervlak wat met roetskimmel bedek was, was positief gekorreleer ($P < 0.05$).

Die toksisiteit van vier sintetiese insektemiddels teenoor die drie onvolwasse stadia van *C. destructor* en van agt insektemiddels teenoor die parasitoïd *A. ceroplastae* is geëvalueer. Die ontwikkeling van die eerste en tweede instars van *C. destructor* is heeltemal stopgesit deur die middels. Die fekunditeit, fertiliteit en liggaamsgrootte van wyfies wat toedienings op die LIII stadium oorleef het, is nie betekenisvol ge-affekteer deur enige van die middels nie ($P < 0.05$). Al die middels was baie toksies teenoor *A. ceroplastae* en word dus nie aanbeveel vir die geïntegreerde bestuur van *C. destructor* waar *A. ceroplastae* 'n belangrike rol speel nie.

To Dad and Mom who educated me

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CHAPTER 1

GENERAL INTRODUCTION

Citrus is believed to have originated in subtropical and tropical regions of Asia and is currently grown in tropical, subtropical and Mediterranean regions (40°N to 40°S) (Cartwright, 1977; Spiegel-Roy & Goldschmidt, 1996). Its introduction to South Africa in 1654 is often regarded as a historical landmark in South African agriculture. The initial stock that arrived at Cape of Good Hope included only sweet orange and rough lemon (Walter *et al.*, 1967), whereas easy-peel cultivars ('Clementines' and 'Satsumas') were introduced most recently (Van Rensburg, 1988). The first selections of Satsuma mandarin in South Africa were obtained from Fort Beaufort in 1934, but major plantings were made only in 1978 (Van Rensburg, 1988). Clementine mandarin originated about 80 years ago from seedlings of Mediterranean easy-peel crosses but major selections were made only during the early 1980s (Van Rensburg, 1988). Records indicate that more than 18, 655,000 citrus trees are grown on 47, 422 hectares of land in South Africa (Bedford, 1998) (Fig. 1). About 18.5% of these trees are grown in the Western Cape, although recent additions of easy-peels are not included. Annual export amounts to nearly 40 million cartons of 15 kg each (Bedford, 1998).

Citrus provides a suitable habitat for various sedentary and mobile insect pests. Bedford (1998) reported more than 150 insect species as pests of citrus in South Africa. Among the complex of insect pests associated with citrus is the white or soft wax scale, *Ceroplastes destructor* Newstead (Hemiptera: Coccidae). *Ceroplastes* is the second described genus of the family Coccidae after the Linnean *Coccus*, and was raised to generic rank by Vigor in 1829

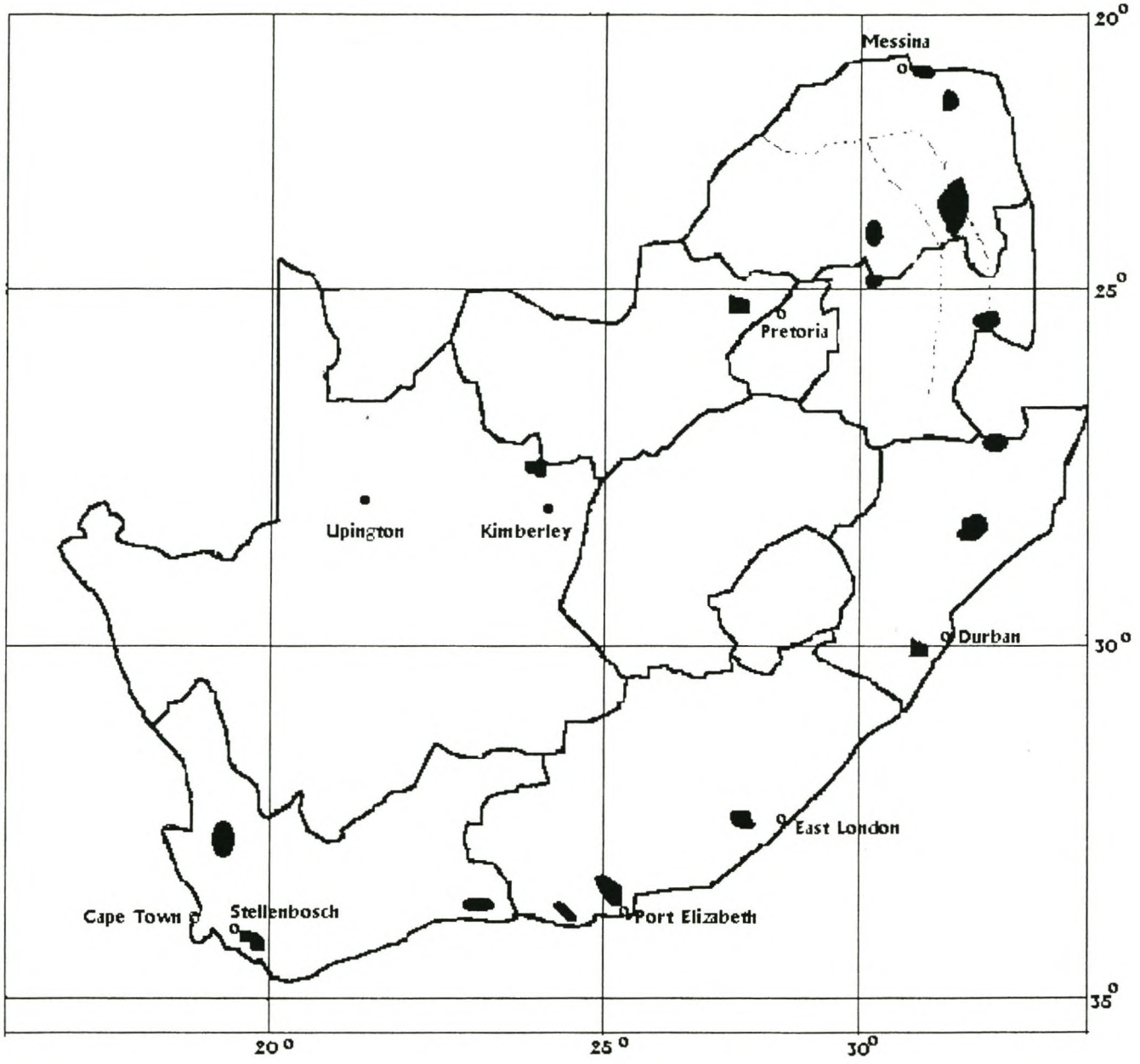

Figure 1. Major citrus producing areas in South Africa (re-sketched from Bedford, 1998).

(Hodgson, 1994). Giliomee (1967) studied the adult males of the family Coccidae and found that the genus *Ceroplastes* was very close to *Coccus*. He suggested that the subfamily name Ceroplastinae should probably be sunk as a synonym of Coccinae. Nonetheless, the subfamily Ceroplastinae is valid to date, but according to Hodgson (1994) it requires a total revision to clarify the status of some genera.

De Lotto (1965) argued that the genus *Gascardia* Targioni Tozzetti is morphologically related to *Ceroplastes* Gray, but could be separated by differences in the shape and way in which the spiracular setae are arranged around the spiracular clefts. He emphasized that the adult females of *Gascardia* are characterized by possession of a 'round or oval compact' group of spiracular setae that extend over the dorsum, whereas the adult females of *Ceroplastes* have an 'elongate' group of spiracular setae that are more peripherally situated. He then erected *Gascardia* as a separate monophyletic genus based on these differences, a decision supported by Hodgson (1994). However, Gimpel *et al.* (1974) had expressed difficulty in applying De Lotto's concept of *Gascardia* because they found that some species such as *Ceroplastes ceriferus* (Fabricius) and *C. cirripediformis* Comstock have intermediate states between 'elongate' and 'round or oval compact' groups of spiracular setae and aptly regarded it as a junior synonym of *Ceroplastes.* Williams & Watson (1990), Ben-Dov (1993), Qin & Gullan (1994), among others, supported this decision. In a cladistic analysis of wax scales, Qin & Gullan (1995) have concluded that all wax scales should be included in the one genus *Ceroplastes*. They suggested that further generic splitting will make *Ceroplastes* paraphyletic or polyphyletic. The generic name *Ceroplastes* is maintained here for *C. destructor*, which De Lotto (1965) placed in *Gascardia*.

C. Gowdey was the first to collect specimens of *C. destructor* in 1902 on *Antigonon* sp. from Uganda and sent the material to Newstead for identification (De Lotto, 1955; Snowball, 1969; Williams & Watson, 1990). Newstead described the material as *C. ?ceriferus* in 1910 and

later redesignated it as *Ceroplastes destructor* (Newstead, 1910; 1917). Hall (1931) described specimens collected in Zimbabwe as *C. destructor var. brevicauda* but De Lotto later raised the variety to specific rank (De Lotto, 1955). De Lotto also erected *C. luteolus* as valid species to represent the white wax scale commonly occurring in East Africa where *C. destructor* also occurs. He subsequently synonymized *luteolus* with *brevicauda* and transferred both *brevicauda* and *destructor* to *Gascardia* (De Lotto, 1965).

Based on the localities where its type species was originally designated, *C. destructor* is believed to have originated in Africa (Zeck, 1934; Edwards & Shedley, 1955; De Lotto, 1965; Snowball, 1969; Smith, 1970). A cladistic analysis of the phylogeny of the scale insects by Qin *et al.* (1994) predicted that *C. destructor* is a native of the Afrotropical region. *C. destructor* is now a cosmopolitan species. It has been recorded from the following zoogeographic regions of the world: Austro Oriental (Papua New Guinea); Australian (New South Wales, Queensland); Ethiopian (Angola, Cameroon, Congo, Ivory Coast, Kenya, Mozambique, South Africa, Uganda, Zambia, Zimbabwe); Madagasian (Madagascar); New Zealand and Pacific region (New Zealand, Norfolk Island, Solomon Islands), and Oriental (India) (Williams & Watson, 1990; Ben-Dov, 1993).

Ceroplastes destructor is widely distributed in the Sub-Saharan Africa where it is recorded from various unrelated plant species. In this region it has been collected on *Coffea arabica*, *C. robusta*, *Gymnosporia* sp., *Citrus maxima, Hibiscus sp., Agave* sp., *Thevetia peruviana and Croton* sp. (De Lotto, 1955; 1965; Snowball, 1969; Cilliers, 1998). In South Africa, *C. destructor* has been recorded on *Citrus* from Grahamstown in the Eastern Cape Province, Naboomspruit in the Northern Province and Hazyview in Mpumalanga (Cilliers, 1998) (see Fig. 2). Other host records in Southern Africa include: *Psidium guajava,* custard apple and avocado in Transvaal, Naboomspruit and Nelspruit, Syringa (*Melia azedarach*) in Botswana, *Poncirus trifoliata* in Buffelspoort, *Trichilia emetica, Nidorella resedifolia, Maytenus*

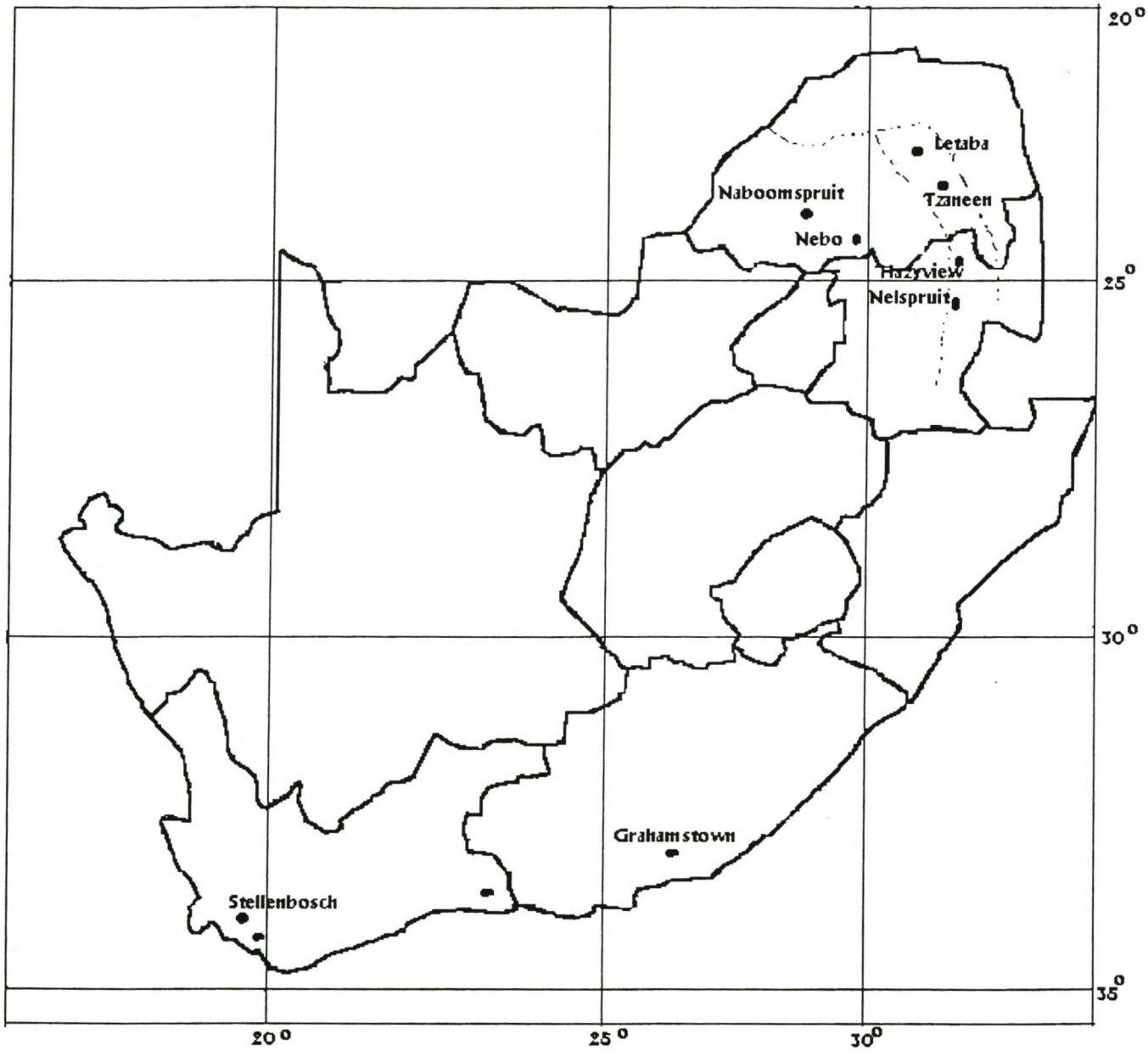

Figure 2. Distribution map for *Ceroplastes destructor* in South Africa (from description by different authors).

senegalensis, Schinus molle, Gardenia australis and *Ekebergia capensis* (Brain, 1920; De Lotto, 1965; Snowball, 1969; Cilliers, 1998). *C. destructor* is commonly found in the Western Cape Province on *Citrus reticulata* (Blanco), *Syzygium* (=*Eugenia) malaccensis* (L.) (Fig. 3) and *Gardenia thunbergia* L. f. (Wakgari & Giliomee, 1998). In Australia it has been recorded on citrus, pears, persimmons, apricots, apples, christmas tree, ti-tree, blue-bell, pink myrtle, groundsel, oleander, guava, lillypilly and gardenia (Jenkins *et al.*, 1953; Smith, 1970). Brimblecombe (1956) reported at least 79 plant species as hosts for *C. destructor* and Snowball (1969) extended the list to 106 plant species. Ben-Dov (1993) listed 37 plant species from 22 families as hosts of *C. destructor*.

The biology, economic importance, ecology and population dynamics of *C. destructor* has not been studied in the tropics despite its wide-scale distribution in this region. *C. destructor* is a uniparental species with three nymphal instars and an adult female. Reproduction is by parthenogenesis. Females are copiously fecund, laying from several hundred to several thousand eggs. After eclosion, crawlers move onto the leaves of the host plant from the 'brood chamber' and settle along the veins, mainly on the adaxial leaf surface of young branches (Milne, 1981; 1993) or on leaf petioles and young twigs especially when the population density is high (Manefield, 1955; Smith, 1970; Wakgari & Giliomee, 1998). Immature stages (rosettes) on leaves produce waxy secretions to form a central pad and lateral rays leaving part of the body exposed. When the scales reach the third instar stage they move back onto the twigs where they permanently reside and their dorsal surface subsequently becomes completely covered with wax (Milne, 1993; Wakgari & Giliomee, 1998).

Ceroplastes destructor has never hitherto been considered as a pest of economic importance in South Africa. Cilliers (1967), for instance, states that *C. brevicauda* (Hall) was the only soft scale of economic importance in South African citrus orchards whereas *C. destructor* was regarded as a potential pest that had been under effective control by complexes of natural

enemies. However, it was reported as an important pest of citrus in Australia (Manefield, 1955; Gellatley, 1968; Smith, 1970; Snowball, 1970; Smith & Ironside, 1974; Hely *et al.*, 1982; Sands *et al.*, 1986; Qin & Gullan, 1995) and in New Zealand (Olson *et al.*, 1993; Lo, 1995). *C. destructor per se* might not cause serious economic damage although in some cases sucking of plant sap causes minor damage. Moreover, it is a prolific producer of honeydew, which often covers the leaves, stems and fruits of the host and acts as a growth medium for black sooty moulds, which give an unsightly appearance to the host. In some cases the sooty moulds cover the fruits of host plants (e.g. citrus) and cause severe blemishes and heavy in-season fruit discard (e.g. Georgala, 1979). In some instances substantial packhouse cull due to sooty moulds is possible (Van Dijk, 1998). The sooty moulds also reduce the rate of leaf light transmission (Tedders & Smith, 1976; Wood *et al.*, 1988), the rate of photosynthesis in plants (Wood *et al.*, 1988; Kaakeh *et al.*, 1992) and fruit yield (Brun, 1986). The mould defaces the fruit, rendering it unmarketable (Amitai, 1969), and is difficult to remove even if fruit is washed or brushed before packing (Jenkins *et al.*, 1953). In the case of easy-peel cultivars, the fact that the fruits are susceptible to damage after harvest makes removal of sooty moulds with high pressure sprays in the packhouse ineffective (Hattingh *et al.*, 1998). Under heavy infestation, a general decline in vigour and, in some cases, dieback of the hosts has been observed (Gimpel *et al.*, 1974). Although various scale insects are known to transmit pathogenic organisms to their hosts via their feeding habits, such a possibility has not been investigated for *C. destructor*. However, honeydew exuded by Homoptera may encourage colonization of the host plant by pathogenic fungi (Haines & Haines, 1978a, b). Ants tending honeydew secreting soft scales usually suppress the effectiveness of parasitoids and predators of some important insect pests of citrus like the red scale (*Aonidiella aurantii* (Maskell)) and lead to drastic population increases of the pest (Bedford, 1968).

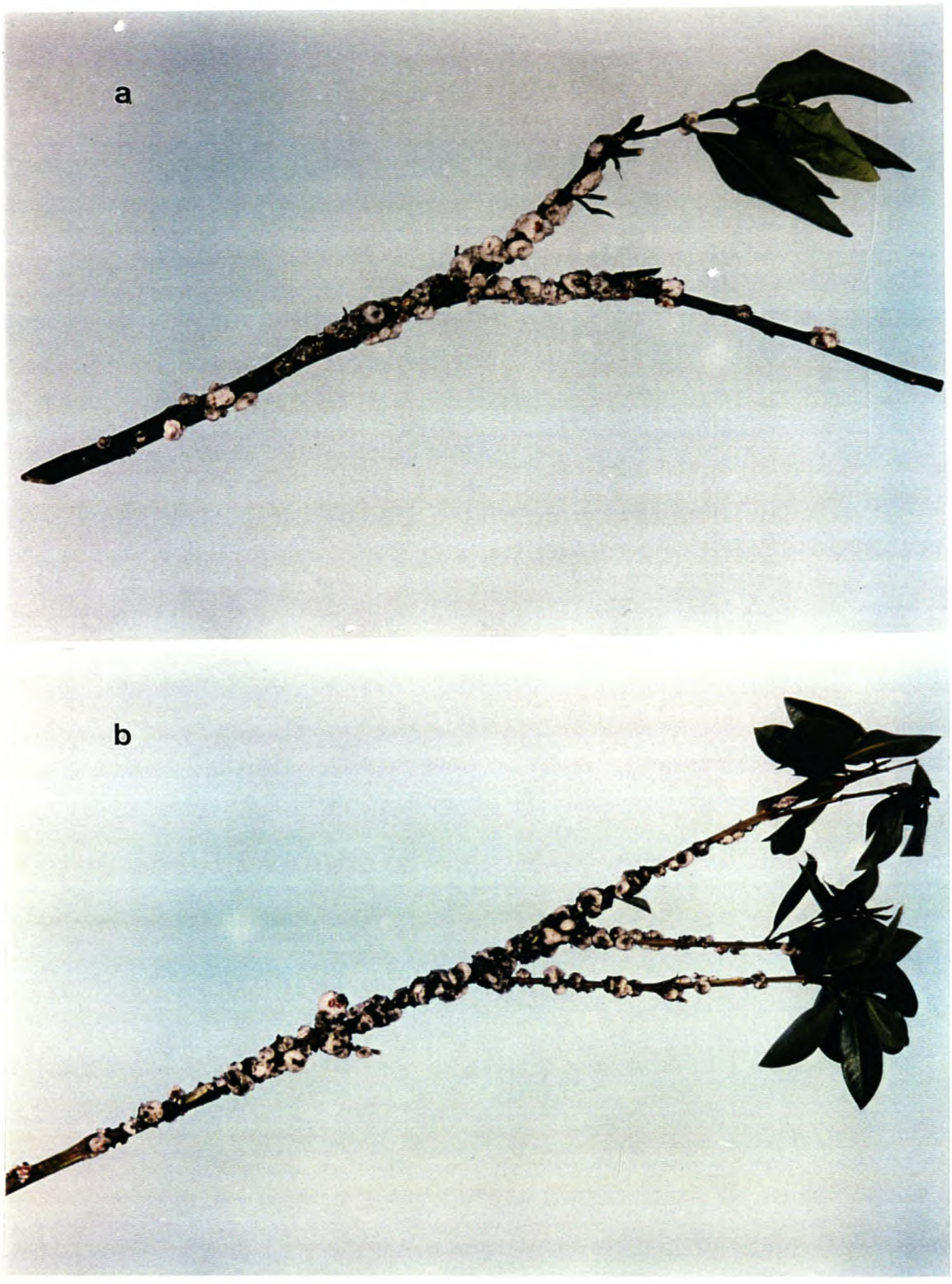

Figure 3. *Ceroplastes destructor* on twigs of *Citrus reticulata (a)* and *Syzygium malaccensis* (b).

Ceroplastes destructor has recently increased in abundance and distribution in some citrus groves, and particularly in areas where easy-peel citrus (*C. reticulata*) is grown in the Western Cape Province of South Africa (Wakgari & Giliomee, 1998). The concurrence of this resurgence with the expansion of easy-peel citrus could be attributed, amongst other things, to *C. reticulata* providing a suitable habitat for the reproduction and survival of this species. The main stimulus for this study was this recent expansion of *C. destructor* infestations, despite the presence of a large endemic natural enemy complex and a wide arsenal of chemical control options available. In view of the stringent aesthetic and sanitary requirements by fruit importing countries, it is essential to control insects such as *C. destructor* for mould-free export fruits. The control of such insect pests requires a good understanding of their seasonal population dynamics and the biological processes involved in the changes. These are investigated in this study.

The development of *C. destructor* to pest status could be attributed to the injudicious use of persistent pesticides against major insect pests of citrus and deciduous trees grown adjacent to easy-peel citrus. Insect Growth Regulators (IGRs) such as triflumuron (Alsystin®) and pyriproxyfen (Nemesis®) are frequently used against false codling moth (*Cryptophlebia leucotreta* (Meyrick)) and red scale (*A. aurantii*), respectively. Likewise, parathion has been and, in some orchards, is still sprayed against red scale, often several times in one season. Although some researchers (e.g. Peleg, 1988; Eisa *et al.*, 1991; Darvas *et al.*, 1994) have advocated that IGRs are innocuous to hymenopteran parasitoids of different scale insects, this is not the case with some predators. For example, Nemesis and Alsystin have been demonstrated to have caused extensive disruption of the biocontrol of cottony cushion scale provided by the coccinellid *Rodolia cardinalis* (Mulsant) and of red scale provided by *Chilocorus nigritus* (Fabricius), in South Africa (Hattingh & Tate, 1995). Snowball (1969) observed at Hazyview in South Africa that in Marsh grapefruit orchards sprayed with parathion and dimethoate, *C. destructor* had attained pest status with heavy tree infestation, while an adjacent orchard that had

received no insecticidal treatment for two years was very lightly infested. *C. destructor* is no more an occasional or sporadic pest in the Western and parts of Eastern Cape Provinces as it was a few years ago, but is now more widespread and a common pest of economic importance on citrus, and particularly on easy-peel cultivars. It is, therefore, conceivable that the frequent use of some broad-spectrum insecticides may have upset the biological balance and resulted in the current steady increase in the pest status of *C. destructor*. Assessment of the potential effects of regular chemical control practices on the natural enemies of *C. destructor* in the agro-ecosystem appears essential and will be addressed in this study.

The potential of the existing natural enemy complexes in checking the population of *C. destructor* in South Africa and in the tropics in general, has not been properly documented, although Cilliers (1967) and Snowball (1969) listed various parasitoids and predators reared from this species. In view of the changing citricultural and ecological conditions, the appraisal of the role of natural enemies on the epidemiology of *C. destructor* is desirable. A comprehensive knowledge of the various components of the ecosystem, the pest and its natural enemies is one of the main prerequisites for the successful establishment of integrated pest management (IPM) programmes. It is therefore imperative to investigate the individual and integrated effects of available control options in order to develop sustainable, environmentally benign and effective integrated management strategies for this spreading insect pest.

This study was initiated with the broad objective to investigate the biology and ecology of *C. destructor* and contribute to the development of an integrated management programme based on the results. Each of the Chapters that follow deal with specific objectives set to attain the above stated broad objective.

I. To describe and illustrate the different developmental stages of *C. destructor* so that they can be identified in the field and microscopically as an aid to effective control.

II. To establish the biology (fecundity and fertility in relation to body size, and phenology) of *C. destructor* under South African climatic conditions.

III. To determine the species composition and regulatory effects of the natural enemy complex of *C. destructor*.

IV. To assess the population dynamics and the biological processes involved in population changes of *C. destructor*.

V. To assess the effect of crawler densities on the rate and distance of crawler dispersal.

VI. To determine the effect of scale density on scale growth, body size and fecundity and on the growth of infested plants.

VII. To determine the effects of some common commercial IGRs and insecticides against different phenological stages of *C. destructor* and its major parasitoid.

VIII To contribute to the development of a sound IPM programme for *C. destructor*.

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CHAPTER 2

DESCRIPTION OF IMMATURE STAGES AND ADULT FEMALE OF THE WHITE WAX SCALE, *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE)[†].

ABSTRACT

The white wax scale, *Ceroplastes destructor* Newstead, has recently increased in numbers and distribution in some easy-peel (*Citrus reticulata* (Blanco)) orchards in the Western Cape Province of South Africa. A study was conducted to investigate its micro- and macro-morphology. Characteristics of the immature stages and adult females are described and illustrated from field-collected and slide-mounted specimens. A key to the different stages is provided. Morphometeric characteristics useful for separating the stages are discussed.

1. INTRODUCTION

The white wax scale, *Ceroplastes destructor* Newstead, is a unisexual and polyphagous species with three nymphal instars and an adult female stage (Cilliers, 1967; Snowball, 1969; Qin & Gullan, 1994). The adult continues to grow after the final moult until oviposition commences. This stage can therefore be subdivided into young, mature and ovipositing stages, although distinct morphological demarcation is difficult. Descriptions and illustrations

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of adult *C. destructor* were provided by De Lotto (1965) and Qin & Gullan (1994). However, detailed morphological descriptions and illustrations of the different nymphal instars are lacking, although brief descriptions were presented by Cilliers (1967). Without detailed knowledge of the external characters and illustrations, incorrect identification of the different stages of development are possible (Amitai, 1969; Beattie *et al.*, 1990; Camporese & Pellizzari, 1994). Detailed and correct identification of the stages is essential for proper timing of control programmes.

Ceroplastes destructor is believed to have originated in Africa (Zeck, 1934; Edwards & Shedley, 1955; De Lotto, 1965; Qin & Gullan, 1994), but it has been a pest of only minor economic importance in South Africa. A complex of natural enemies kept it under excellent control for decades (Cilliers, 1967). *Ceroplastes destructor* has recently increased in numbers, and is spreading rapidly in different easy-peel (*Citrus reticulata* (Blanco)) orchards in the Western Cape Province of South Africa.

In some instances, variations in opinions on the number of instars is reported (see Snowball, 1970; Sands *et al.*, 1986). This is probably because of the fact that field differentiation of instars based on their external morphology is often difficult, particularly where the wax growth and casting of exuviae is not regularly observed. The aim of this study was therefore to provide a key for the identification of different instars of *C. destructor* based on macro- and micromorphological characteristics. Detailed morphological descriptions and illustrations of each instar are presented.

2. MATERIALS AND METHODS

2.1. Field observations

Infested easy-peel citrus trees (*C. reticulata*) from two sites at Stellenbosch (34°54'S 18°54'E) (Welgevallen Experimental Farm and Rustenburg Estate), Drakenstein (Rhodes

Fruit Farms) (33°54'S 18°57'E) and Grabouw (WhiteHall Farming Trust) (34°14'S 19°06'E) (see Chapter 3, Table 1 and Fig. 1 for details of orchard descriptions) were marked and observed at bimonthly intervals for a period spanning a year to establish the number of moults and subsequent wax growth. Infested twigs were sampled at random and taken to the laboratory for slide mounting and micromorphological examination of the instars. Voucher specimens of *C. destructor* were deposited in the insect collection of the Department of Entomology and Nematology, University of Stellenbosch, South Africa.

2.2. Slide mounting

Scale-infested materials were collected from the field on *C. reticulata* (Rutaceae), *Syzygium* (=*Eugenia) malaccensis* (L.) (Myrtaceae) and *Gardenia thunbergia* (Rubiaceae) and mounted on slides for microscopic examination of the ultrastructures. Twigs or leaves infested with scales were placed in glass dishes containing equal volumes of 90% alcohol and xylene to remove the wax (Sands, 1984). Permanent slides were prepared in three ways as described below:

i. Denuded insects were carefully detached from the twigs/leaves with needles and transferred into Nesbitt's Fluid (mixture of 40 g chloral hydrate, 2.5 cc hydrochloric acid, and 25 cc distilled water) in test tubes and heated for 10 minutes in a hot water bath while occasionally removing the tubes from the boiling bath and shaking. Once the specimens were cleared they were transferred to distilled water for about 10 minutes after which a few drops (usually 2-3) of acid fuchsin were added. The specimens were left in the mixture for at least 1 hour (sometimes up to 12 hours) and then mounted in Hoyer's medium. The slides were cured at 50 °C for 48-72 hours.

ii. Denuded specimens were punctured across the dorsum with needles and placed in a test tube containing 90% ethanol. The tubes were placed in a beaker containing water and then heated on a hot plate at a temperature below 70 °C for 10 minutes. The alcohol was replaced with 10% potassium hydroxide and specimens heated at just below boiling point for 10 minutes. The translucent specimens were transferred to distilled water in a glass plate and pressed gently with fine forceps to expel the body contents. Specimens were heated again in 10% potassium hydroxide when the body content was not yet sufficiently macerated and placed in a dish of distilled water from 1 hour to several hours. Specimens were then transferred through grades of increasing ethanol concentration (40% to 90%) and retained in 90% ethanol for 1 hour. They were transferred into a mixture of 3 parts carbol xylene and 1-part phenol crystals and kept in the mixture for 1 hour to remove wax droplets or particles inside and outside insects' body. Scales were placed in 90% alcohol for another hour before transferring them through grades of decreasing alcohol strength down to pure water. A few drops (usually 2-3) of acid fuchsin stain, made by mixing 100 g phenol + 100 ml lactic acid + 100 ml glycerine + 200 ml distilled water + 0.625 g acid fuchsin, were added and the specimens retained in the stain for about 1 hour. They were then transferred into glacial acetic acid for 10 minutes before retaining them in clove oil for 1 hour to clear. Heavily stained specimens were left in the oil for longer for better clearing. Scales were then mounted in canada balsam and the slides cured at about 50 °C for two to four weeks.

iii. A method described by Ben-Dov & Hodgson (1997) was also used. In short, this method involved fixation in acetic acid, maceration, dehydration, staining, washing in glacial acetic acid, clearing with xylene, final fixation in clove oil, mounting in

canada balsam, and curing. While the second and third methods provided good permanent slides, a reasonably good preparation was obtained in a short time using the first method.

2.3. Micromorphological examinations

Egg size was determined by placing randomly selected, 12-24 hr old eggs, under a stereomicroscope fitted with an eyepiece micrometer and measuring the length and width along the midline. The size of first (LI), second (LII) and third (LIII) instar nymphs was measured from mounted slides. Mounted specimens were studied under a phase-contrast compound microscope equipped with an eyepiece micrometer, and important morphological structures were measured. Drawings were made from images reflected onto drawing paper from a *camera lucida* attached to the microscope. All drawings were not made to the same scale. This also applied to the same structures of the different instars. Body size (length and width) of the adult female was measured from dewaxed unmounted specimens under a stereomicroscope, the length was measured dorso-medially from between the eyespots to the tip of the anal plates. The width was measured across the dorso-medial region from between the two spiracular clefts. The sizes of the immature stages were measured from slide mounts using a compound microscope in a similar manner to the adult female. Measurements of the body and important morphological structures are presented as ranges with mean values in parenthesis. The total leg length was measured on each leg by adding the measurements of individual segments. Descriptions and measurements were based on 24 specimens of each developmental stage. The morphological terminology used here is adopted from Qin & Gullan (1994).

3. KEY TO DIFFERENT STAGES OF *CEROPLASTES DESTRUCTOR* NEWSTEAD

1. Anal plates with a pair of long slender apical setae and a pair of fringe setae..... 2

   Anal plates without long slender setae and with more than one pair of fringe setae 3

2. Three quinquelocular disc pores in area between spiracular clefts and atrium; one pair of interantennal setae (Fig. 3) ..... 1st instar

   Four to seven (five) quinquelocular disc pores in area between spiracular clefts and atrium; two pairs of fringe setae on anal plates; two pairs of interantennal setae (Fig. 5) ..... 2nd instar

3. Twelve to eighteen (fifteen) quinquelocular disc pores in area between spiracular clefts and atrium; 6-10 (7) spiracular setae in each spiracular groove arranged in irregular rows; three pairs of fringe setae on the anal plates (Fig. 7) ..... 3rd instar

   Fifty eight to seventy eight (sixty three) quinquelocular disc pores in area between spiracular clefts and atrium; 48-57 (53) spiracular setae in each of anterior spiracular groove and 49-61(58) in each of posterior groove ; four pairs of fringe setae on anal plates (Fig. 9) ..... Adult female

4. MORPHOLOGICAL DESCRIPTION

4.1. Female oviposition and characters of the egg

The body of a gravid female becomes full and swollen with eggs before oviposition commences. The venter becomes vaulted to form a 'brood chamber' in which the eggs are pushed forward. Eggs are laid singly, and upon emerging covered by a mass of fine white powder secreted by the multilocular pores of the adult female. The powder persists even when eggs are soaked in water, and is believed to prevent eggs from coalescing. Nonetheless,

sometimes eggs were seen attached to one another like a chain, particularly those laid close to the cessation of oviposition.

Eggs are ellipsoidal in shape and yellowish in colour when they emerge but turn brick-red in few days and remain so until hatching. They are 0.26-0.32 (0.30) mm long and 0.14-0.18 (0.16) mm wide (N = 82); the egg stage lasted 15-19 (17) days at 27 °C and 65 ± 5% RH. This was shorter than the 24-35 days at 27 °C and 38% RH reported by Cilliers (1967) for *C. brevicauda* Hall. Prior to hatching a long, thin, transparent, longitudinal line is formed over the chorion; the chorion turns white and conspicuous during hatching. It gradually cracks open from one end due to pressure exerted by the emerging crawler. When the crawler wriggles out, the empty eggshell remains round or elliptical. All appendages of the crawler can be seen clearly inside the chorion immediately before hatching. When all eggs have hatched the brood cavity of the dead female is filled completely with mass of eggshells.

4.2. Field characters of first instar nymph (Fig. 1, 2a, 2b)

Body. Oval; dorsal wax pad appears as a thin white marking 3-4 days after crawler settling on the leaf surface along the mid-rib or on leaf petioles (Fig. 1). The following wax tests can be seen one week after settling (Fig. 2a):

i. one undivided dorsal wax pad;

ii. three wax rays anterior to the dorsal pad;

iii. six wax rays lateral to the dorsal pad on each side;

iv. one wax ray on each side in front of the anal plates; and

v. one wax ray on each side lateral to the anal plates.

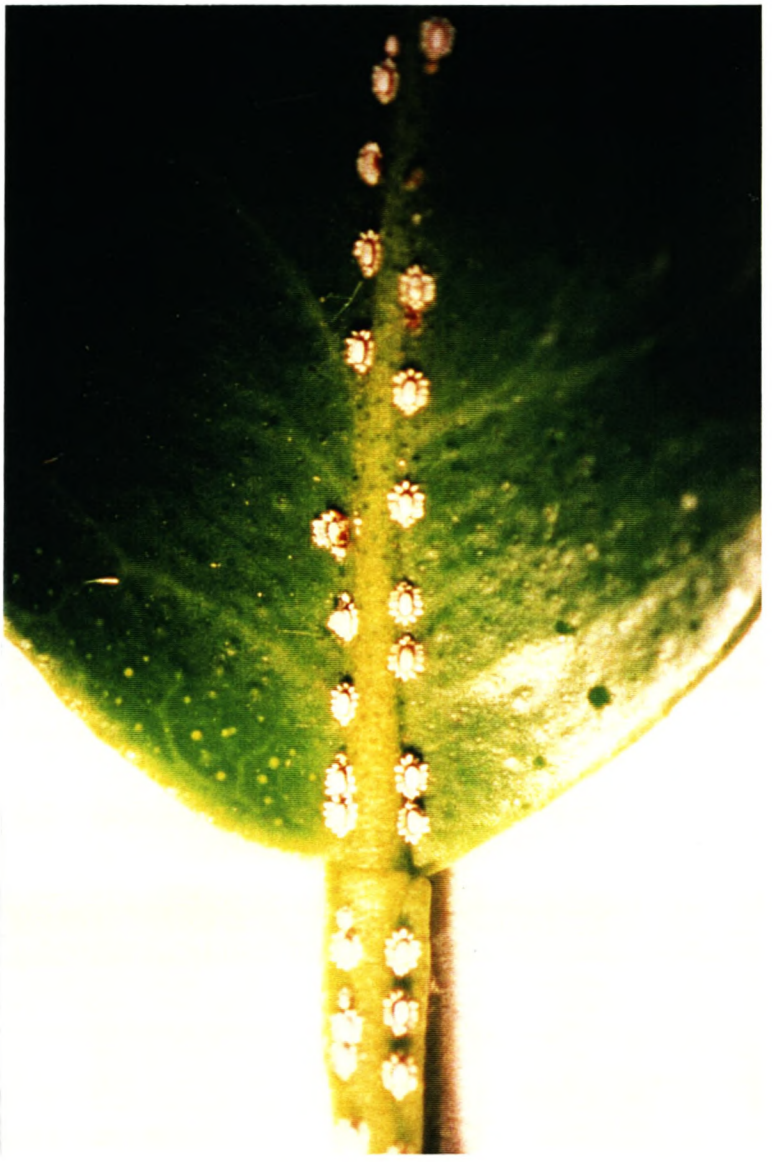

Figure 1. *Ceroplastes destructor* on *Citrus reticulata;* first instar nymphs on leaf petiole and midrib.

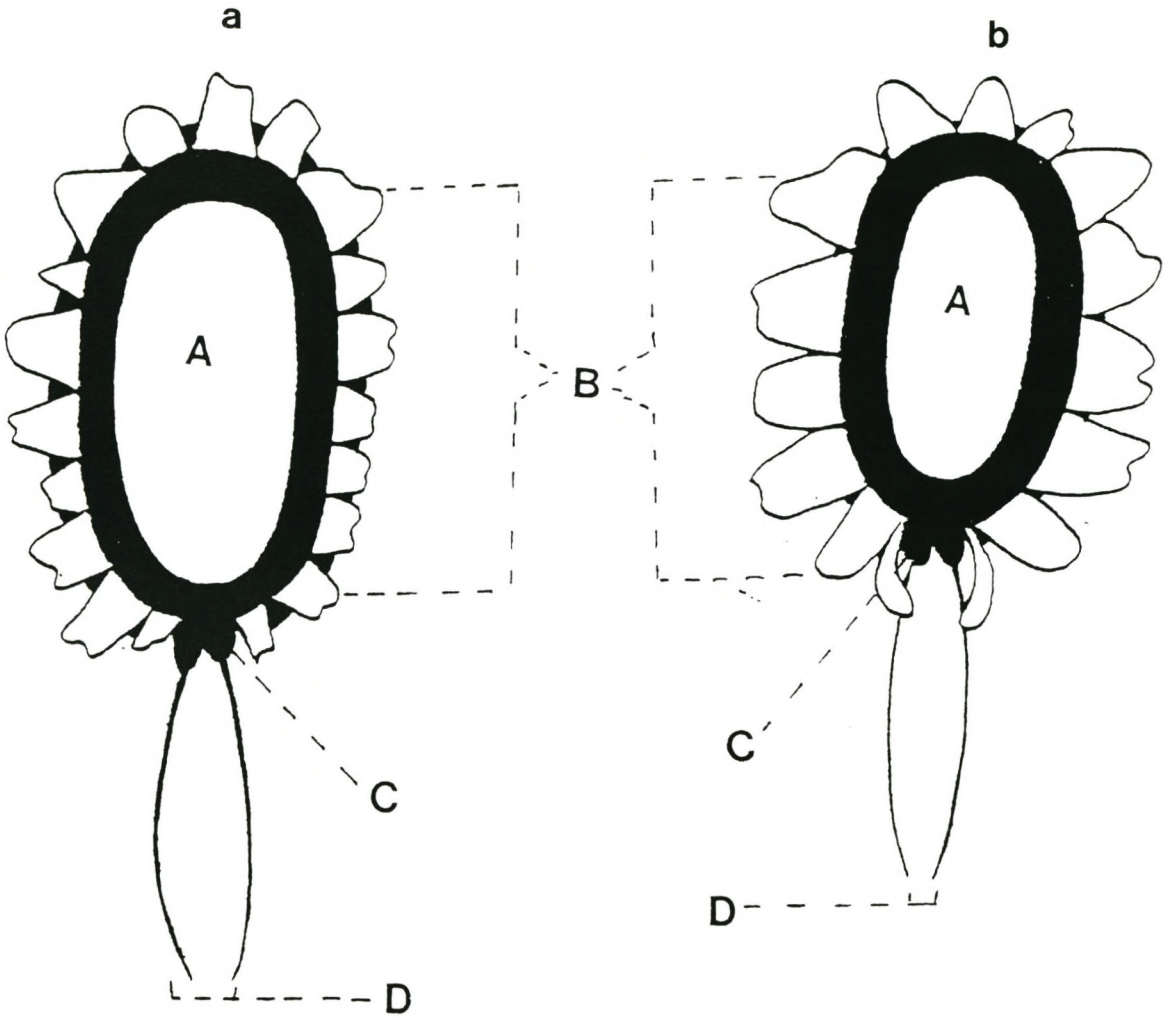

Figure 2. *Ceroplastes destructor* wax-test of first instar nymph; a. one week after settling; b. one month after settling; **A**. dorsal wax pad; **B**. wax rays; **C**. anal plate; **D**. apical setae.

At this early growth stage the rays are not clearly separated from each other or from the dorsal wax pad. The rays become progressively distinct and separated from each other into individual rays. One month after settlement, the following distinct wax processes can be identified (Fig. 2b):

i. one undivided dorsal wax pad;

ii. three wax rays anterior to the dorsal pad;

iii. four wax rays lateral to the dorsal wax pad on each side;

iv. one wax ray on each side in front of the anal plates;

v. one wax ray on each side lateral and posterior to the anal plates.

A pair of long, slender anal plate setae (apical setae) is discernible until the first moult.

4.3. Characters of slide-mounted first instar nymph (Fig. 3)

Body. Dorsolaterally flat, oval-shaped, 0.32-0.50 (0.40) mm long and 0.16-0.26 (0.21) mm wide. Heavily pigmented eye-spot present on dorsolateral part of the head region on each side.

Margin. Marginal setae flagellate, each 5.56-8.25 (6.58) μm long, distributed as follows: 5-8 between eye spots, 2 between eye spots and anterior spiracular furrow on each side, 2-3 between anterior and posterior spiracular furrow on each side, 7 between each posterior spiracular furrow and anal cleft. Three conical spiracular setae present in each spiracular groove, the middle seta more than twice the size of the others, each 2.75-6.00 (4.10) μm long with basal boss 1.70-2.45 (2.20) μm wide.

Dorsum. Derm membranous with no dorsal clear areas. Dorsal setae and dorsal pores absent. Anal plates surrounded by anal lobe, 28.50-55.75 (36.50) μm long, combined width 39.75-57.25 (44.95) μm, 4 pairs of dorsal setae present of which one pair (apical setae) is

very long, each 120.25-244.00 (183.10) μm; a pair of ventral setae and a pair of fringe setae present.

Venter. Submarginal and ventral setae absent. Antennae six-segmented, each 86.80-122.30 (110.50) μm long with third segment the longest. A pair of interantennal setae present, each 5.50-24.25 (12.67) μm long; a pair of prevulvar setae present, each 14.35-21.75 (19.25) μm long. A few cruciform pores present in submarginal areas; three quinquelocular disc pores in each spiracular groove between spiracular setae and spiracular atrium. Multilocular disc pores and tubular ducts absent. Legs well developed, without tibiotarsal sclerosis; tarsal digitules of equal size and knobbed, claw without denticles; claw digitules unequal, one slender the other stout; both apically knobbed. Leg lengths in μm:

Segments	**First leg**	**Second leg**	**Third leg**
Coxa	20-29 (24)	22-33 (29)	23-33 (28)
Trochanter + Femur	37-61 (54)	42-64 (55)	46-60 (54)
Tibia + Tarsus	46-96 (73)	50-82 (74)	50-85 (72)
Claw	5-14 (11)	7-17 (11)	8-14 (11)
Tarsal digitules	21-27 (26)	20-36 (28)	17-34 (26)
Claw digitules	12-15 (14)	10-18 (14)	10-18 (13)
Total	**143-241 (200)**	**153-249 (210)**	**155-242 (203)**

4.4. Field characters of second instar nymph (Fig. 4)

Body. Oval with dry wax which can be easily removed. The fully grown second instar has the following distinct and well separated wax processes:

i. one undivided dorsal wax pad;

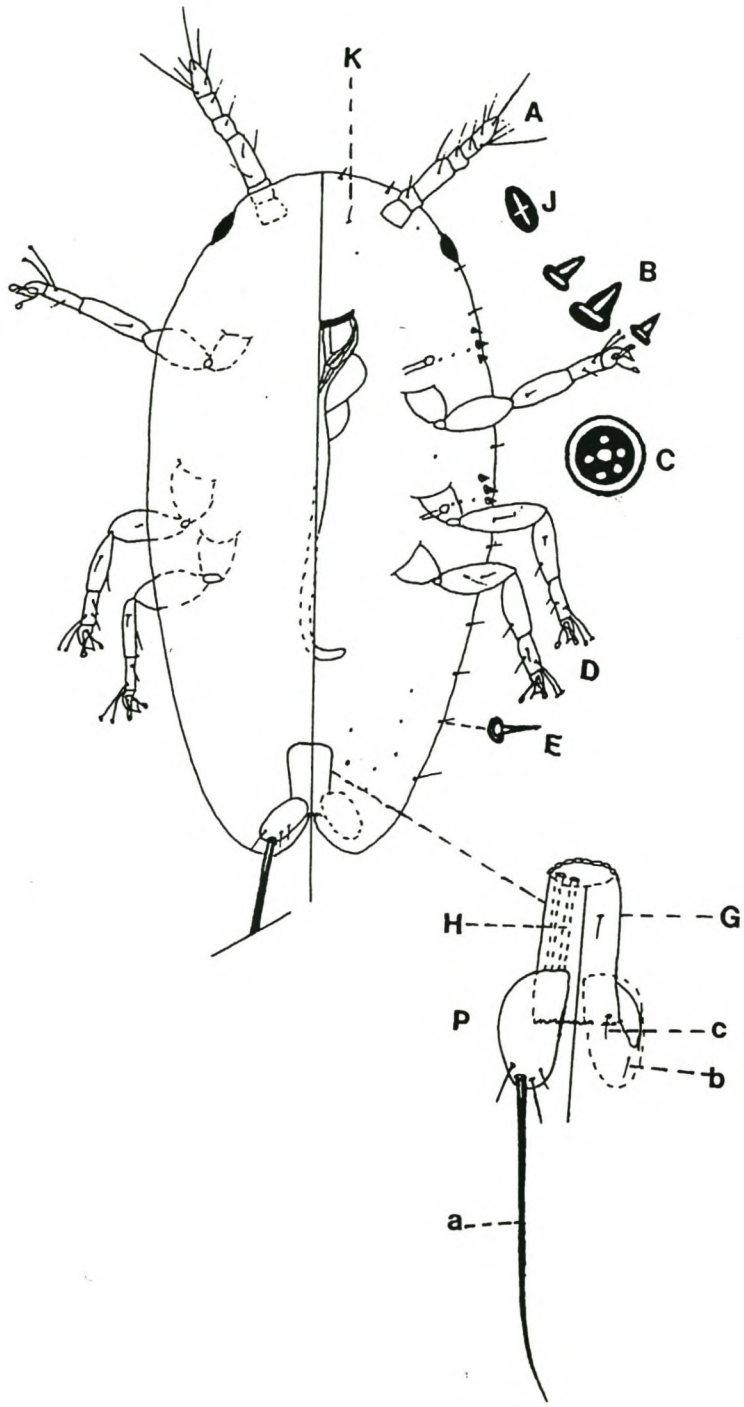

Figure 3. *Ceroplastes destructor* first instar nymph; A. antenna; B. spiracular setae; C. quinquelocular pore; D. leg; E. marginal seta; G. anal ring; H. anal ring setae; J. cruciform pore; K. interantennal setae; P. anal plates: a. apical seta; b. ventral seta; c. fringe seta.

Figure 4. *Ceroplastes destructor* on *Citrus reticulata;* second instar females on a leaf midrib.

ii. three wax rays anterior to the dorsal pad;

iii. four wax rays lateral to the dorsal pad on each side;

iv. one wax ray on each side in front of anal plates;

v. one wax ray on each side lateral and posterior to the anal plates.

4.5. Characters of slide-mounted second instar nymph (Fig. 5)

Body. Oval, 0.65-0.70 (0.68) mm long and 0.38-0.43 (0.40) mm wide; derm membranous; pigmented eye-spot present dorsolaterally on each side.

Margin. Three cone shaped spiracular setae in each spiracular furrow, each 8.75-14.13 (12.21) μm long with basal boss 5.06-5.75 (5.43) μm wide. Marginal setae flagellate, each 6.25-8.25 (7.30) μm long with basal boss 2.90-3.30 (3.10) μm wide, distributed as follows: 4-6 between eye spots, 2 between eye spots and anterior spiracular furrow on each side, 2 between anterior and posterior spiracular furrows on each side, 6-7 between posterior spiracular furrow and anal cleft.

Dorsum. Derm membranous with very few simple minute dorsal pores scattered in submarginal areas; dorsal setae absent; dorsal clear areas not defined. Anal plates surrounded by anal lobe, 43.50-58.50 (52.20) μm long, combined width 57.50-62.5 (60.00) μm, with 4 pairs of dorsal setae, 1 pair of ventral setae and 2 pairs of fringe setae.

Venter. Submarginal setae bristle-shaped, each 3.75-4.40 (4.00) μm long with basal boss 2.44-3.00 (2.69) μm wide. Antennae six-segmented, each 112.75-129.75 (119.75) μm long; two pairs of interantennal setae, the longer pair 17.50-27.50 (22.00) μm long, shorter pair similar to submarginal setae. A pair of prevulvar setae present, each 20.00-26.25 (23.12) μm long. Cruciform pores present in submarginal area. Four to seven (five) quinquelocular disc pores found between the spiracular setae and spiracular atrium. Multilocular disc pores

and tubular ducts absent. Legs without tibiotarsal sclerosis; tarsal digitules equal in size and knobbed; claw denticles absent; claw digitules unequal, one broad and the other slender, both apically knobbed. Leg lengths in μm:

Segments	**First leg**	**Second Leg**	**Third leg**
Coxa	21-29 (26)	22-46 (31)	25-30 (28)
Trochanter + Femur	56-66 (61)	46-73 (65)	60-74 (69)
Tibia + Tarsus	72-90 (82)	70-93 (86)	84-97 (91)
Claw	8-15 (11)	8-17 (10)	8-12 (10)
Tarsal digitule	20-26 (24)	22-30 (28)	24-29 (27)
Claw digitules	9-16 (13)	13-17 (15)	12-15 (14)
Total	**189-240 (215)**	**184-274 (235)**	**216-255 (239)**

4.6. Field characters of third instar nymph (Fig. 6)

The young third instar is similar in appearance to the second instar but after about two weeks wet wax starts accumulating underneath the dry wax of the second and first instars and builds up like a cone, hence, the name 'peak stage'. Lateral and a dorsal wax of the earlier instars can be seen as three and one small dots or faint markings at early stages of the third instar, but later these are incorporated into the wet wax that flows around the dorsum. The wet wax eventually collapses and the late third instar attains its characteristic oval shape. In the fully-developed third instar only the dorsal dry wax of the earlier stages is visible.

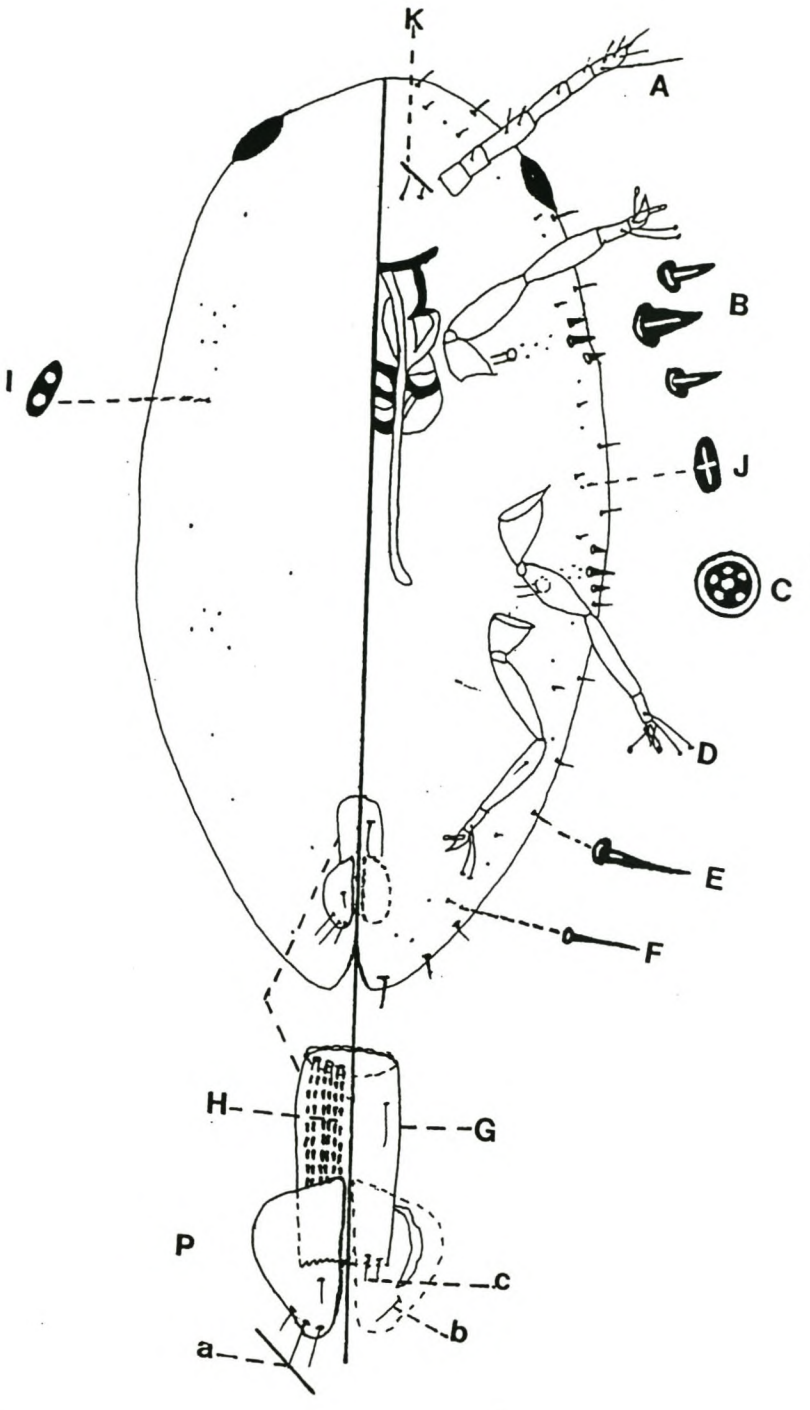

Figure 5. *Ceroplastes destructor* second instar female; A. antenna; B. spiracular setae; C. quinquelocular pore; D. leg; E. marginal seta; F. submarginal seta; G. anal ring; H. anal ring setae; I. dorsal pore; J. cruciform pore; K. interantennal setae; P. anal plates: a. dorsal setae; b. ventral seta; c. fringe setae.

Figure 6. *Ceroplastes destructor* on *Citrus reticulata;* third instar females on a twig.

4.7. Characters of slide-mounted third instar nymph (Fig. 7)

Body. Oval, 0.85-1.20 (1.06) mm long, 0.70-0.90 (0.82) mm wide; eye-spots black and located dorso-laterally on each side.

Margin. Marginal setae flagellate, occasionally clavate to capitate, each 7.80-10.68 (9.34) µm long with basal boss 3.56-4.40 (3.95) µm wide, distributed as follows: 5-6 between eye spots; 2-4 between anterior spiracular furrows and eye spots on each side; 3-5 between the anterior and posterior spiracular furrows on each side; 7-11 between posterior spiracular furrows and anal cleft on each side. Six to nine (eight) conical spiracular setae situated in each of the anterior spiracular furrows and 7-10 (9) in each of the posterior furrows, each 10.63-15.75 (14) µm long with basal boss 8.20-10.50 (9.31) µm wide. The large middle seta in each groove is usually bifurcated.

Dorsum. Derm membranous with one anterior and six lateral clear areas; anal process absent. Dorsal pores oval trilocular, triangular trilocular and bilocular, scattered sparsely over dorsum. A few monolocular pores present dorso-medially. Dorsal setae few in number and sparsely distributed over dorsum, but absent in dorsal clear areas. Anal plates 66.75-80.00 (73.59) µm long, combined width 74.75-89.00 (80.34) µm, each with 4 pairs of dorsal setae, 1 pair of ventral setae and 3 pairs of fringe setae.

Venter. Ventral setae bristle-like, sparsely distributed in submedian area of abdominal region. Submarginal setae similar in shape to ventral setae, each 6.00-11.16 (7.82) µm long with basal boss 2.91-3.91 (3.65) µm wide. Antennae six-segmented, 155.13-201.25 (168.64) µm long; two pairs of interantennal setae, the longer pair 41.25-48.75 (45.00) µm long and shorter pair 7.50-16.25 (10.00) µm long. A pair of prevulvar setae, each 43.25-58.30 (51.47) µm long is located immediately anterior to vulva. Cruciform pores sparsely distributed in submarginal area around the entire body. Multilocular pores and tubular ducts absent. Twelve

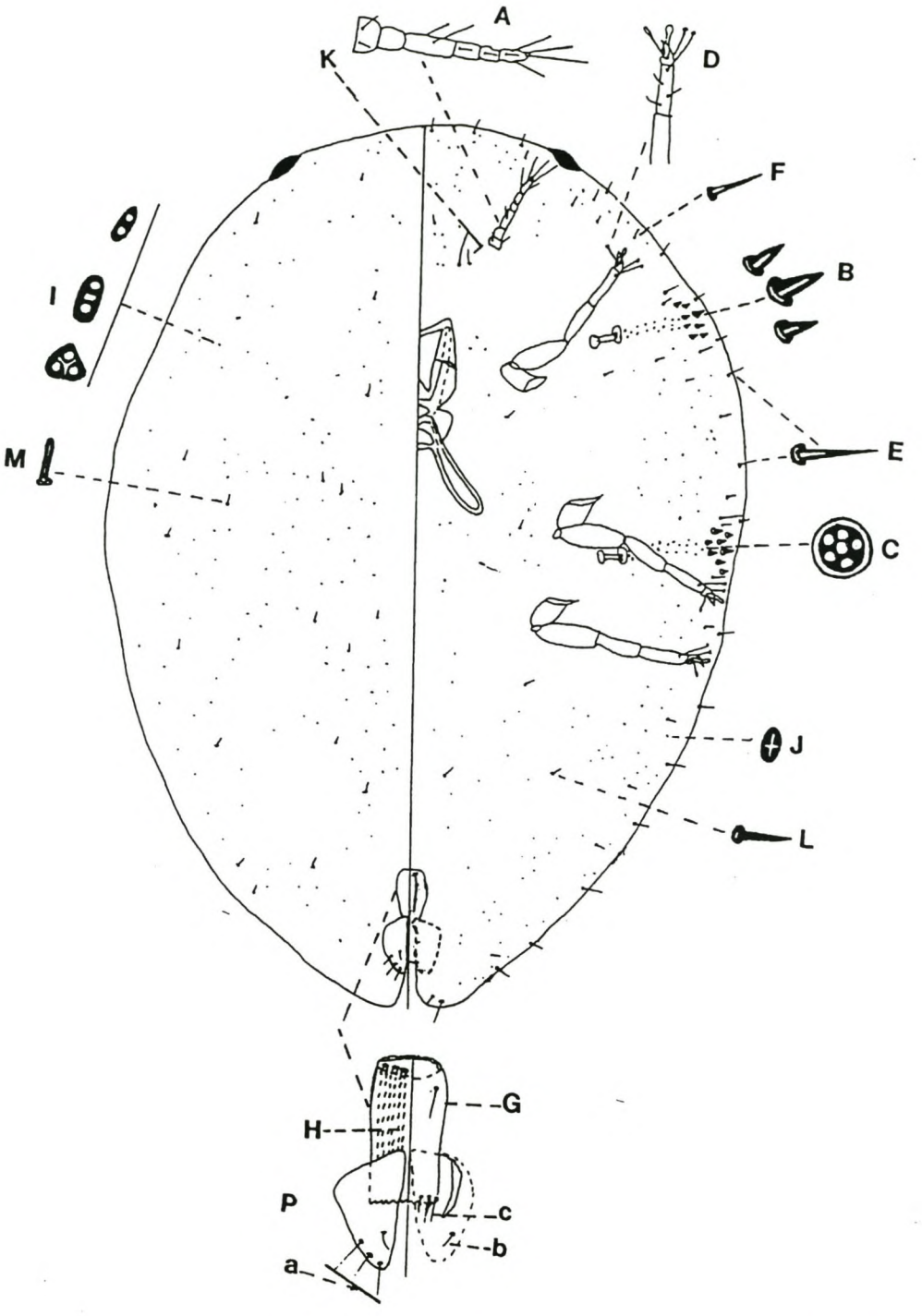

Figure 7. *Ceroplastes destructor* third instar female; A. antenna; B. spiracular setae; C. quinquelocular pore; D. leg; E. marginal seta; F. submarginal seta; G. anal ring; H. anal ring setae; I. dorsal pores; J. cruciform pore; K. interantennal setae; L. ventral seta; M. dorsal seta; P. anal plates: a. dorsal setae; b. ventral seta; c. fringe setae.

to eighteen (15) quinquelocular disc pores present between the spiracular setae and spiracular atrium. Legs without tibiotarsal sclerosis; tarsus and claw with well developed and knobbed digitules; tarsal digitules equal in size; claw without denticles; claw digitules unequal, one slender, the other stout. Leg lengths in μm:

Segments	**First leg**	**Second leg**	**Third leg**
Coxa	32-47 (35)	40-51 (43)	32-48 (40)
Trochanter + Femur	80-93 (88)	87-99 (93)	88-104 (95)
Tibia + Tarsus	106-122 (116)	119-125 (121)	120-125 (122)
Claw	11-16 (14)	14-18 (15)	13-18 (15)
Tarsal digitule	23-34 (29)	25-34 (30)	26-34 (31)
Claw digitule	14-20 (18)	14-20 (18)	15-22 (18)
Total	**266-312 (300)**	**299-347 (320)**	**3294-351 (321)**

4.8. Field characters of adult female (Fig. 8a, 8b)

Body. The early immature adult females have their body only partly covered with wet wax while part of the body remains naked and appears brownish, hence, the name 'brown stage'. In about two weeks, body becomes completely (*in toto*) embedded in white, creamy white or dirty white wet wax which forms irregular ridges and furrows; wax-covered body oval in dorsal view, averaging about 5.2 mm long (*in extenso*) and 3.4 mm wide. Dry wax of the first and second instars discernible only in young adults as a small central cap. Lateral rays of the third instar seen only in young adult as small dots around the margin. The spiracular wax bands present as a thin white thread arising from each spiracular furrow and extending over dorsum. Although the anal ring appears to be completely immersed in wet

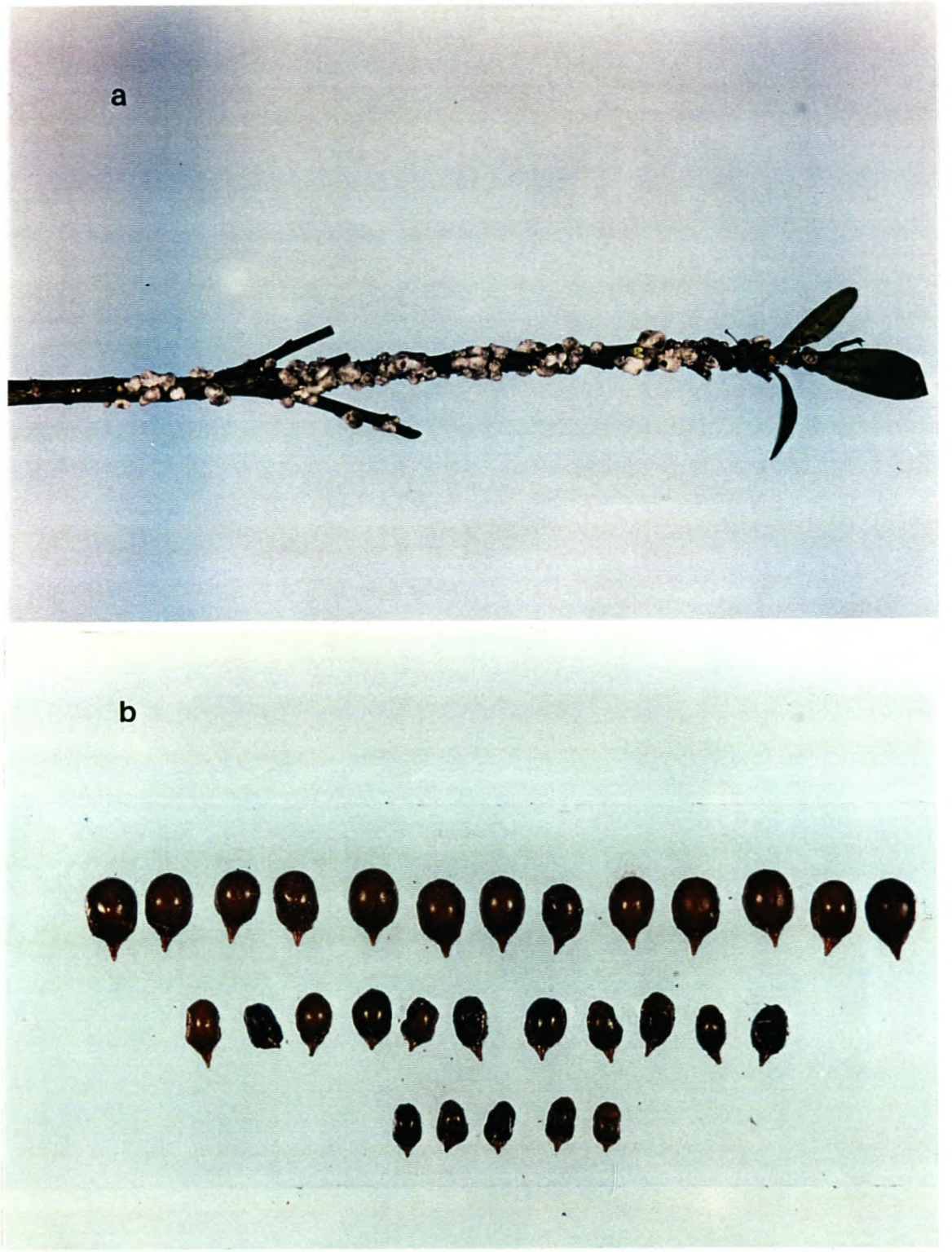

Figure 8. *Ceroplastes destructor* a. adult females on twigs; b. denuded adult females showing caudal process and different size groups.

wax when viewed dorsally, closer examination reveals it to be rather exposed and raised slightly from host surface. This facilitates easy expulsion of honeydew. In majority of females, anterior or cephalic end is oriented downwards or away from leaf or twig terminus (Table 1). This could be an adaptive behaviour to avoid honeydew fouling. Denuded adult reddish-brown with a long, sclerotized caudal process (Fig. 8b). Six lateral, one dorso-medial and one anterio-dorsal tubercle present on dorsum.

Table 1. Orientation of adult female *Ceroplastes destructor* on twigs of *Citrus reticulata* and *Syzygium malaccensis*. *Cephalic end facing towards the twig terminus; **Cephalic end facing away from the twig terminus.

		Orientation	
Host	**N**	**% upwards***	**%downwards****
S. malaccensis	280	4.64	95.36
C. reticulata	320	11.25	88.75

4.9. Characters of slide-mounted adult female (Fig.9)

Body. Generally oval with some marginal indentations; body 2.5-6.4 (4.5) mm long and 1.5-4.3 (2.8) mm wide measured dorsally; eye-spots visible as black spots dorso-laterally on each side of head region.

Margin. Marginal setae bristle-like, each 7.8-18.2 (12.8) μm long with a basal boss 4.6-5.4 (5) μm wide. A total of 32-53 marginal setae distributed as follows: 4-9 between eye spots; 2-5 between eye spots and anterior spiracular furrow on each side; 4-7 between anterior and posterior spiracular furrows on each side; and 6-14 between posterior spiracular

furrow and anal cleft. The last 2 on anal lobe are distinctly longer than the others. Forty-eight to 57 (53) conical or bullet-like spiracular setae located in each anterior spiracular groove and 49-61 (58) in each posterior groove, arranged in 4-6 irregular rows; each 11-18 (15) μm long with a basal boss 10-17 (14) μm wide.

Dorsum. Membranous in young adult, with one anterior and six lateral clear areas. Dorsal pores randomly scattered: oval trilocular, triangular trilocular, and a few quadrilocular and bilocular types distributed dorso-medially and submarginally; maximum dimension of each pore about 5-6 μm, with short inner filaments discernible only under higher magnifications. Dorsal setae cylindrical, some with capitate apices, scattered over the dorsum except in dorsal clear areas; each 7-9 μm long with basal boss 4-5 μm wide. Anal plates 85-150 (113) μm long, combined width 112-121 (117) μm, with 4 pairs of dorsal setae, a pair of ventral setae and 4 pairs of fringe setae.

Venter. Ventral setae bristlehair-like, sparsely distributed across the venter, each 8-14 μm long with basal boss 4-6 (5) μm wide. Submarginal setae more than 100 in number, each 8-13 (11) μm long with basal boss 4-5 μm wide. Quinquelocular disc pores in the spiracular furrows 58-78 (63) per groove, arranged in 6-8 irregular rows between the spiracular setae and spiracular atrium. A pair of short and pair of long prevulvar setae present anterior to vulva, short pair 42-49 (45) μm long and long pair 55-75 (65) μm long. Cruciform pores distributed in submarginal area around entire body. Multilocular disc pores present in rows around vulva and, as can be seen in well-prepared slides, on the heavily sclerotized anal process, each with 10-12 loculi. Tubular ducts sparsely distributed anterior to vulva and submarginally on abdominal region. Antennae six-segmented, each 185-244 (216) μm long;

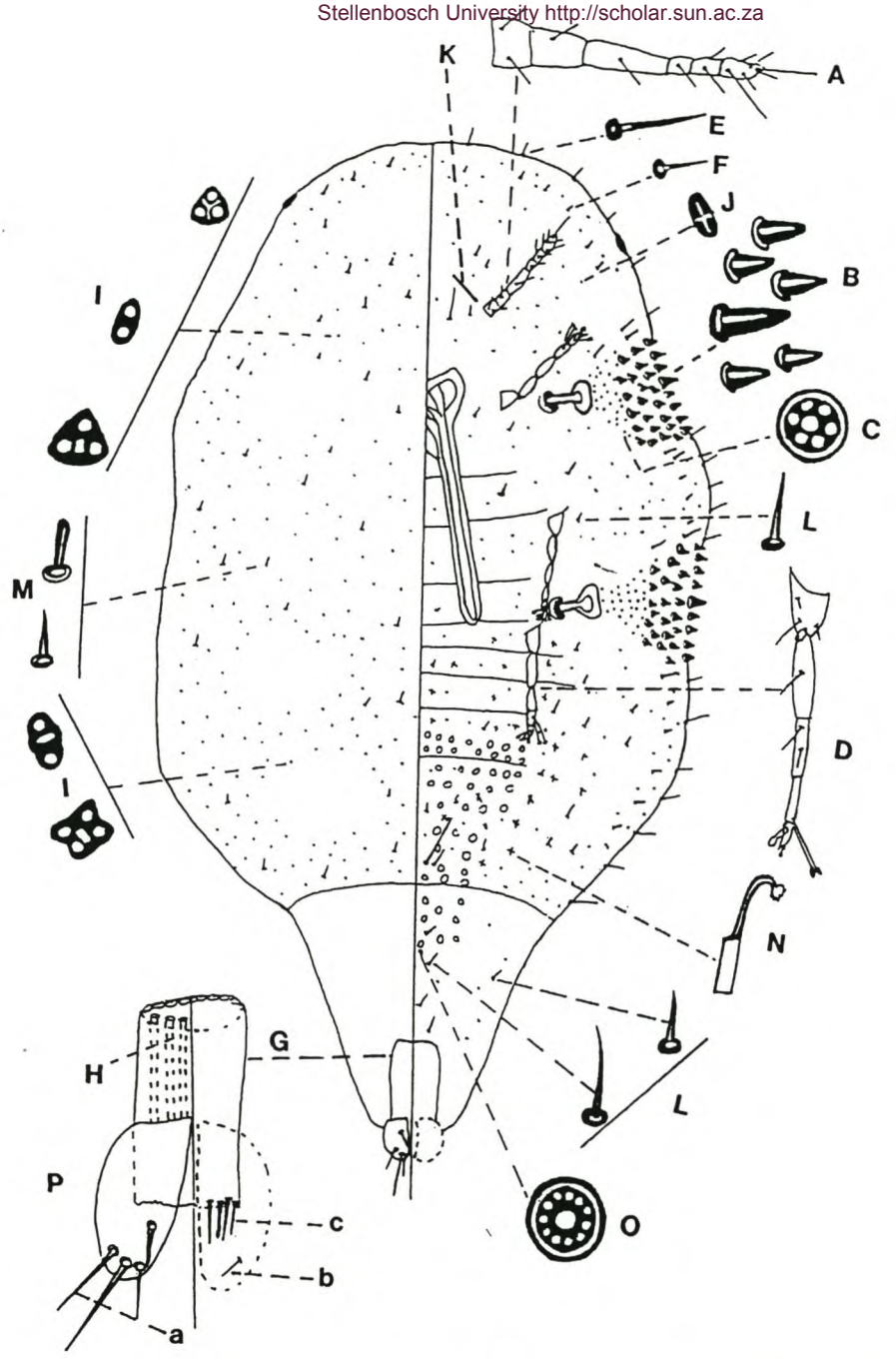

Figure 9. *Ceroplastes destructor* adult female; A. antenna; B. spiracular setae; C. quinquelocular pore; D. leg; E. marginal seta; F. submarginal seta; G. anal ring; H. anal ring setae; I. dorsal pores; J. cruciform pore; K. interantennal setae; L. ventral setae; M. dorsal setae; N. tubular duct; O. multilocular pore; P. anal plates: a. dorsal setae; b. ventral seta; c. fringe setae.

two pairs of interantennal setae present, longer pair 56-77 (66) μm long, shorter pair 11-19 (16) μm long. Legs without tibiotarsal sclerosis, tarsus with equal-sized pair of digitules and claw with one of digitules slender, other stout; both tarsal and claw digitules well developed and apically knobbed; claw without denticles. Leg lengths in μm:

Segments	**First leg**	**Second leg**	**Third leg**
Coxa	35-56 (47)	41-55 (48)	32-47 (43)
Trochanter + Femur	65-84 (74)	87-99 (94)	85-123 (110)
Tibia + Tarsus	96-114 (103)	107-126 (112)	85-123 (110)
Claw	12-17 (15)	12-17 (15)	11-18 (15)
Tarsal digitules	27-34 (32)	22-35 (32)	24-35 (32)
Claw digitules	19-28 (23)	16-22 (20)	15-22 (19)
Total	**243-333 (294)**	**285-354 (321)**	**247-347 (312)**

5. DISCUSSION

The ability to identify the different stages of *C. destructor* in the field is important in directing control operations at the most susceptible developmental stage/s. Wax secretions are perhaps the major field characteristics that differentiate the different stages, although both Amitai (1969) using *C. floridensis* Comstock and Camporese & Pellizzari (1994) using *C. japonicus* Green, have disputed the importance of the wax cover, indicating that using this character is unreliable for instar separation. In the first instar the wax rays are not clearly separated from each other and from the dorsal wax pad, but in the second instar they are clearly distinguishable as separate rays. The gap between rays also seems to increase with age. Two long apical setae are discernible in the first instar. This structure is greatly reduced and can only be seen in slide-mounted second instar nymphs. Separation of the third instar

from the second is almost impossible until about two weeks after the second moult when wet wax starts to be deposited underneath the dry wax of the second instar. The wet wax eventually covers the lateral rays of the earlier stages and only the dorsal dry wax of the earlier stages can be seen as a small dot in fully-grown third instar nymph. Although Cilliers (1967) reported that second instar *C. destructor* is covered by wet and watery wax, both field and laboratory observations in the current study indicated that this stage produces only dry wax as was also described by Gimpel *et al.* (1974).

The major micromorphological characteristics that distinguish the different stages on slide mounts are: size of apical setae, number of quinquelocular disc pores between the spiracular atrium and spiracular setae, number of spiracular setae in each of the spiracular grooves and the presence or absence and/or number of dorsal pores. The first and second instar nymphs can be differentiated by the length of the apical setae, which are much longer in the former stage. The number of quinquelocular disc pores in first instar is always three while in the second instar it ranges from 4-7. There are few dorsal pores in the second instar but none in the first instar. Whereas the first instar has only one pair of interantennal setae, the second instar has two pairs. The second instar can be separated from the third by differences in the number of spiracular setae and quinquelocular disc pores. The third instar has more spiracular setae and quinquelocular disc pores in both the anterior and posterior grooves than the second instar. Furthermore, there are more numbers of dorsal pores in the third instar than the second. Dorsal trilocular pores are absent from the second instar nymphs. The dorsal clear areas are distinct in the third instar but not in the second instar. Adult female has large number of dorsal pores, spiracular setae and quinquelocular disc pores in both the anterior and posterior grooves than the third instar nymph. Dorsal quadrilocular pores and tubular ducts are absent in the third instar.

The description of adult female *C. destructor* presented here generally agrees with that of De Lotto (1965) and Qin & Gullan (1994). The slight variation in the size of some morphological structures of the adult female found in this study from that reported by these authors could be attributed to differences in metereological, edaphic and host nutrient conditions in the ecosystem where the specimens were collected.

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CHAPTER 3

BIOLOGY OF WHITE WAX SCALE, *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE), ON *CITRUS* AND *SYZYGIUM*[†] .

ABSTRACT

The population density of *Ceroplastes destructor* Newstead has steadily increased since 1994, particularly on *Citrus reticulata* (Blanco), in areas of Western and Eastern Cape Provinces of South Africa. The fecundity, body size and phenology of *C. destructor* were studied with the aim of providing a more informed basis for control programmes. No significant differences in fecundity were found between orchards ($P > 0.05$). However, fecundity varied significantly between female size classes from the same orchard ($P < 0.001$). Female body-size differed significantly between orchards ($P < 0.05$) and was significantly positively correlated with fecundity both in 1997 and 1998. Different size groups had varying oviposition periods, larger individuals having a longer oviposition period. No differences in egg fertility were found between orchards ($P > 0.05$). *Ceroplastes destructor* had one discrete generation per year in the Western Cape Province of South Africa. Oviposition commenced in mid November and continued till the end of December with a few females ovipositing until mid January. The decline in population density of the second instar nymphs in February was

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[†]*African Entomology* (2000), **8**(2): 233-242.

followed by a steady increase in that of the third instar. The third instar stage extended until the end of July followed by a peak population of adults in August.

1. INTRODUCTION

The white wax scale, *Ceroplastes destructor* Newstead (Hemiptera: Coccidae), is widely distributed in Sub-Saharan Africa from where it is believed to have originated (De Lotto, 1965; Snowball, 1969). It is a polyphagous species that infests various trees, shrubs and ornamentals. Ben-Dov (1993) recorded it from 22 plant families, while Snowball (1969) and Qin & Gullan (1994) considered that it was found on almost all citrus cultivars. In South Africa, it has been recorded from *Citrus* spp., *Psidium guajava* (L.) and *Ponocirus trifoliata* (L.) (De Lotto, 1965; Cilliers, 1998). In addition, Wakgari & Giliomee (1998) have recorded it from *Citrus reticulata* (Blanco) (Rutaceae), *Syzygium (= Eugenia) malaccensis* (L.) (Myrtaceae) and *Gardenia thunbergia* L. f. (Rubiaceae) in the Western Cape Province of South Africa. Although it has never been regarded as a pest of major economic importance in South Africa, its population density has steadily increased since 1993/1994 and it now has attained pest status in some citrus growing areas in the Western and Eastern Cape Provinces, particularly in areas where easy-peel citrus (*C. reticulata*) and *S. malaccensis* are grown.

Ceroplastes destructor generally has a long prereproductive, a very short reproductive and no post-reproductive period. Its fecundity has been determined on citrus in Australia by Zeck (1934) and Smith (1970), and in New Zealand by Lo (1995) but no information is available for South Africa.

The ratio of various age groups in a population can be used to determine the current reproductive status and trends in population density expected in the succeeding generations (see Krebs, 1978). However, it could be difficult to separate the generations and age

distribution in some species because of lack of synchronization in their life cycle. As the overlap in time of successive stages increases, it becomes difficult to obtain estimates of the total population in any specific stage. *Ceroplastes destructor* is one of the species that exhibit an overlap of stages and generations in some places depending on climatic conditions. For instance, studies in Australia showed that *C. destructor* is bivoltine with a considerable degree of stage overlapping in the hot humid coastal areas of New South Wales (Smith, 1970; Smith & Ironside, 1974), but univoltine further inland (Gellatley 1968; Beattie *et al.* 1990). In New Zealand it is also univoltine (Olson *et al.,* 1993; Lo, 1995). No study has been conducted on its phenology in South Africa and the present study was therefore aimed at determining the fecundity, fecundity in relation to body size, and phenology of *C. destructor* under the environmental conditions of the Western Cape Province. Studies on these aspects may provide useful information on the proper timing of action/s for effective control of susceptible stages and in the optimization of the contribution of natural enemies to scale mortality.

2. MATERIALS AND METHODS

2.1. General description of study orchards

Field experiments presented in this dissertation were conducted in four easy-peel (*C. reticulata*) orchards and on *S. malaccensis* in the Western Cape Province (Fig. 1) from June 1997 to January 2000. Information on the citricultural and orchard protection histories of the study orchards presented in this section was obtained from owners/managers of the respective orchards using structured questionnaires.

Welgevallen Experimental Farm (WEF) is an experimental orchard of the University of Stellenbosch located about 5 km to the south of Stellenbosch (34°54'S 18°54'E). Various Clementine and Satsuma selections raised on different rootstocks are grown on an area of about 4 hectares.

Rustenburg Estate (RUS) is a commercial orchard located about 4 km to the north of Stellenbosch (34°54'S 18°54'E). Mainly Satsuma and a few Clementine selections are grown on an area of about 15 hectares. Both orchards (WEF and RUS) are situated at an altitude of about 230 meters and have similar climatic conditions.

Rhodes Fruit Farms (RFF) is located at 33°54'S 18°57'E, about 20 km to the northeast of Stellenbosch at an altitude of 362 meters. Various Satsuma and Clementine selections are grown over an area of about 12 hectares.

WhiteHall Farming Trust (WFT) is located at 34°14'S 19°06'E about 65 km to the southeast of Stellenbosch at an altitude of about 340 meters. Different Clementine and Satsuma selections are grown over an area of 28.25 hectares (see Table 1 for details). The last three are commercial orchards. *S. malaccensis* is a tree of Australian origin widely grown in and around Stellenbosch, mainly as an ornamental and occasionally as refugia for natural enemies of *C. destructor* around citrus orchards.

Monthly average temperatures and humidities at all sites during the course of these experiments are presented in Figs 2-4. There is substantial variation among orchards with respect to these physical factors. In particular, monthly maximum and minimum relative humidities are generally higher at Stellenbosch and WFT than at RFF (Figs 2-4). Temperature and humidity are the two most important abiotic factors that have a direct bearing on the

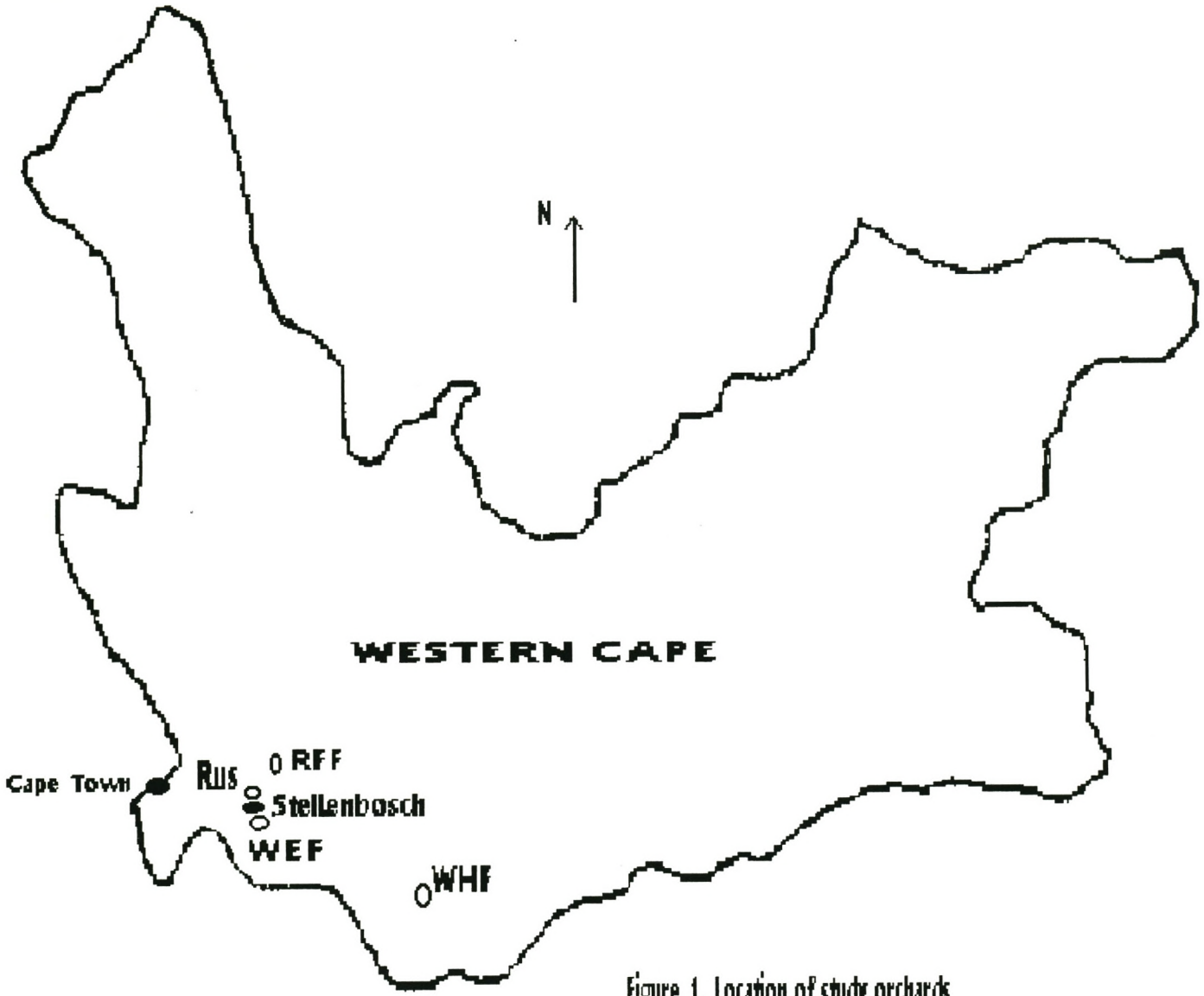

Figure 1. Location of study orchards

Table 1. Retrospective view of citricultural and pest protection histories of the study orchards (see text) based on information gathered using questionnaires.

Characters	Orchard			
	WEF	**RFF**	**RUS**	**WFT**
Rootstocks	Nine different types; mainly Troyer citrange & Carrizo citrange	Troyer citrange, few Volkemariana	Carrizo 1220, Troyer Citrange	For Satsuma: Carrizo Citrange, Swingle Citrange, Rough Lemon; For Clementine: Carrizo citrange, Swingle citrange, Volkemariana & Rough Lemon
Trees planted in	1992	Satsuma: 1988 Clementine: 1987	1986	1986-1996
Cultivars	different varieties of Satsuma & Clementine	Satsuma, Clementine	Satsuma, Clementine	different varieties of Satsuma &Clementine
Mean no. trees/ha	1111	888	889	666,727, 888, 1000, 1111, 1666
Synthetic fertilizers	LAN* at 500g/tree x 3 KCl** at 500g/tree x 3 micronutrients x 2/year	LAN at 400g/tree x 3 KCl at 400g/tree x 2	LAN at 800g/tree/season KCl at 400g/tree/season	LAN at 400g/tree x 3 KCl at 200-400g/tree x 2; Maxifos at 150-200g/tree in August
Irrigation	as per moisture reading	weekly in summer depending on soil moisture content	every 10 days	every 5-14 days depending on neutron probe reading, weather and tree needs
Agronomic problem/s	??	Genetic = fruit size small	Shallow soil, wind damage, and sunburn	??

* LAN= Limestone Ammonium Nitrate; **KCl = Potassium Chloride

Table 1. ***Continued;*** FCM = False codling moth.

Insect pest ranking	waxy scale, brown soft scale	red scale, FCM, citrus red mite, wax scale	FCM, Psylla, red scale, brown soft scale, citrus red mite, brown rot	Psylla, red scale, wax scale, brown soft scale, mealybug, red mite, snails
Importance of white wax scale	very important since 1994	very important since 1995	not much important	sporadic outbreaks since 1992
Loss due to white wax scale	quality loss; cannot quantify	difficult to quantify	?	cannot quantify
Damage by white wax scale	indirect, messy	sooty mould	sooty mould	sooty mould on leaves, branches and fruits
Reason/s for white wax scale increase	unknown	may be use of OPs vs red scale	may be use of IGRs vs FCM	unknown
Chemicals *Vs* white wax scale	chlordane, lannate Nov./Dec.	none so far	lannate and NRD oil Dec./Jan.	lannate in January, burning heavily infested plants
Chemicals to control other major insect pests	citrmet trunk application x 4/year	2 x alsystin vs FCM, Dec. & Feb.; 2 x parathion, superthion, ultracide, chlorpyriphos vs red scale, Aug. & Oct.	phosdrin vs Psylla alsystin vs FCM in Feb.	parathion, ultracide, mevinphos; phosdrin, torgue, dipel, mesurol plus bran mix vs snail, snail pellets
Annual average cull (%)	≅10% due to small fruit size & insect attack	≅ 25% due to wind stroke, size, red scale, other insects	sunburn ≅ 5-8 % wind stroke ≅ 10% insects ≅ 10% injury ≅ 5%	varies from year to year, average 10-30% mainly, due to wind scars, red scale, wax scale, mealybug and snails

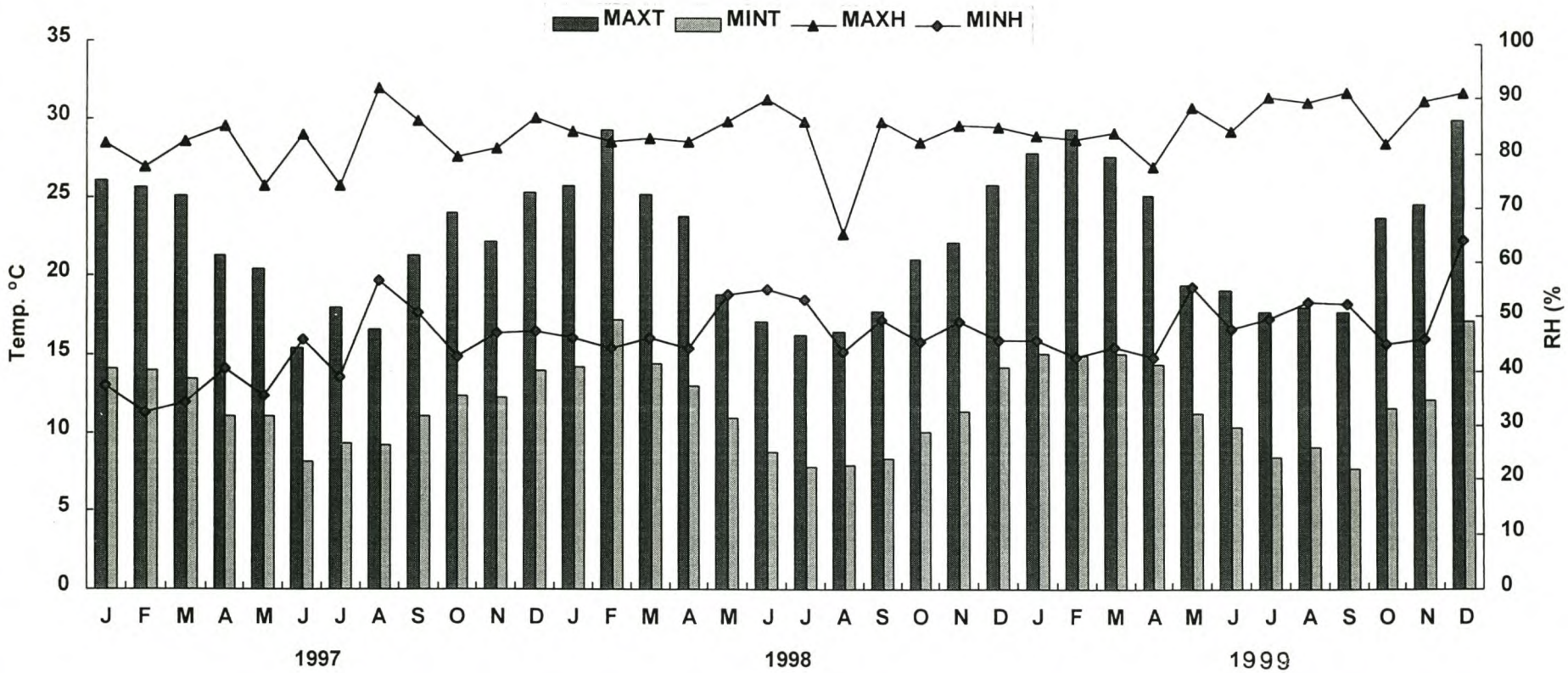

Figure 2. The maximum and minimum monthly temperatures (°C) and relative humidity (%) at Stellenbosch (WEF & RUS) (January 1997 – December 1999).

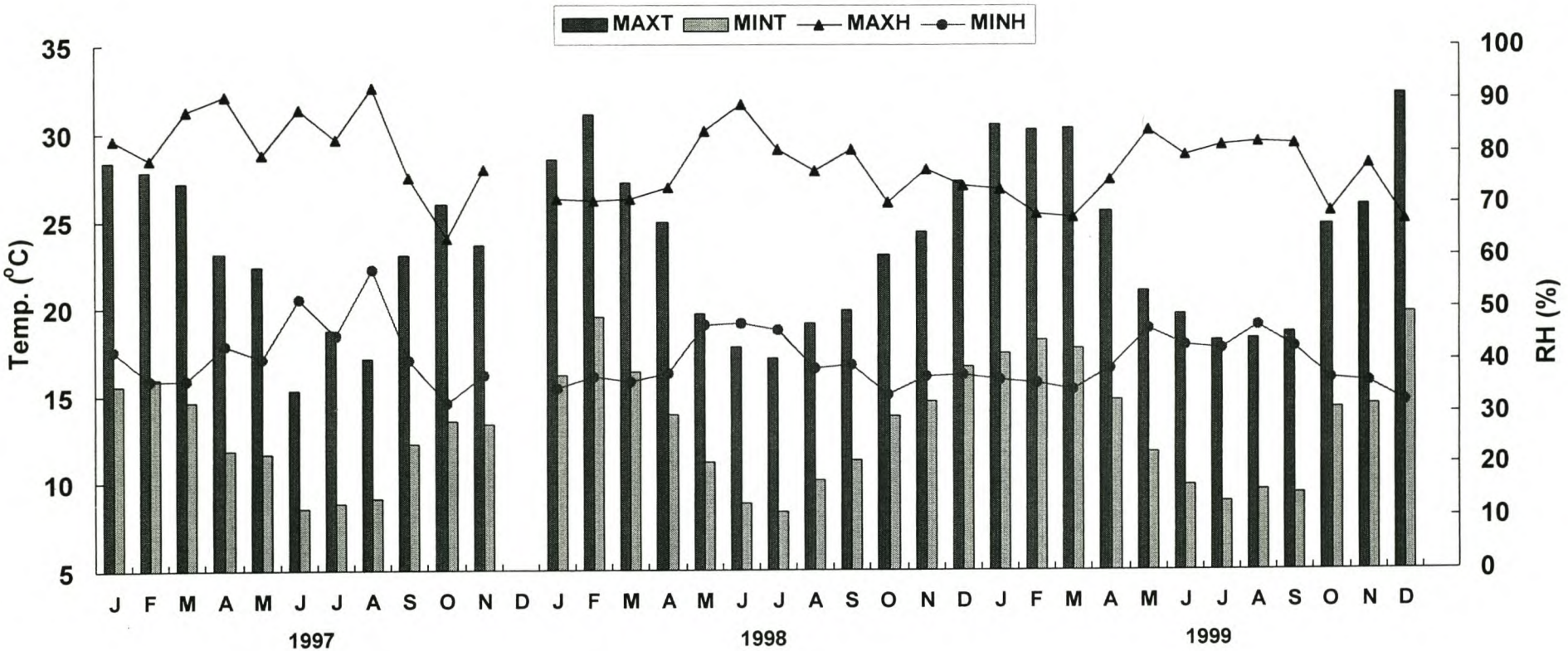

Figure 3. The maximum and minimum monthly temperatures (°C) and relative humidity (%) at Rhodes Fruit Farms (January 1997 – December 1999).

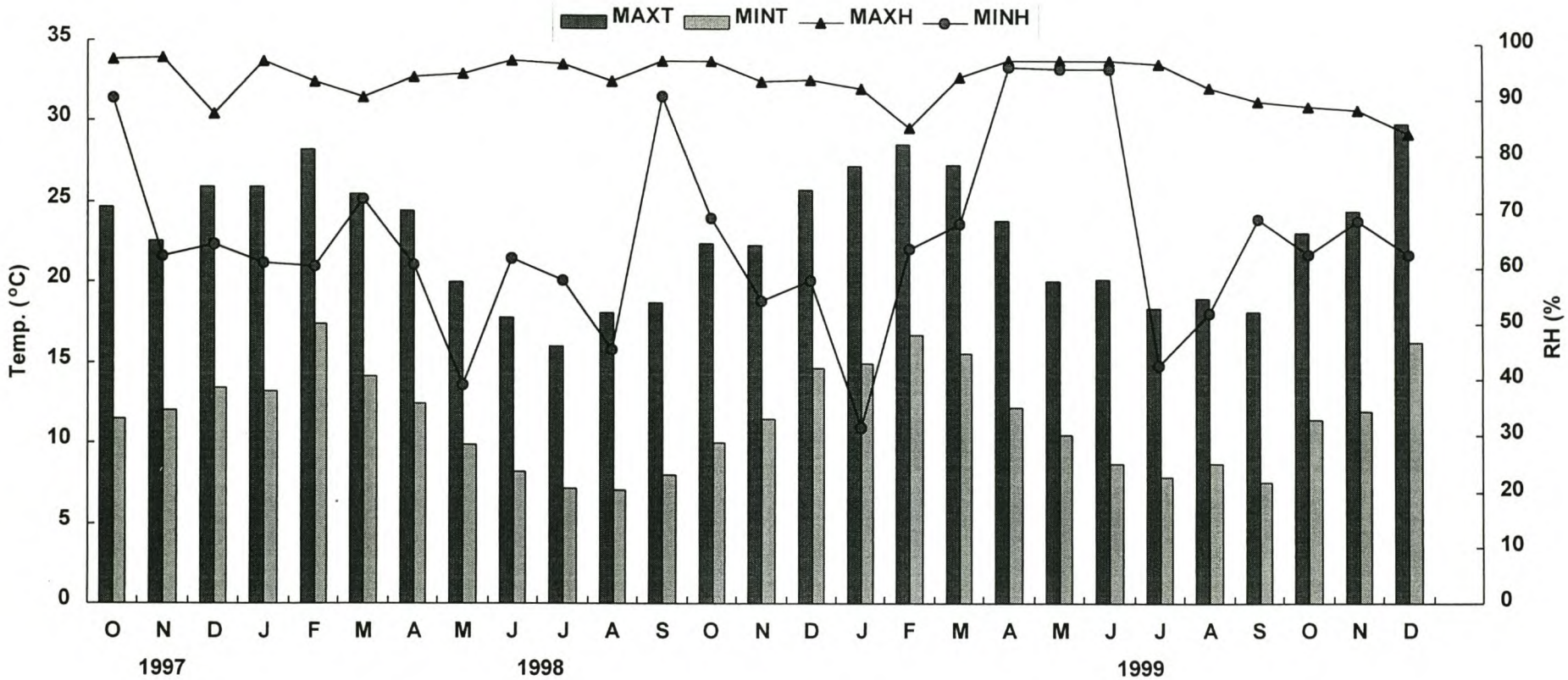

Figure 4. The maximum and minimum monthly temperatures (°C) and relative humidity (%) at WhiteHall Farming Trust (January 1997 – December 1999).

physiology and biology of *C. destructor* and other citrus pests. The effects of these factors will be discussed in relevant Chapters of this dissertation.

2.2. Fecundity and size

I. *Daily oviposition by individual females.* Gravid females were collected from twigs with both isolated and over-crowded populations of adult females in approximately equal proportions. Each female was overturned with dissecting needles and observed under a stereomicroscope for the presence of eggs beneath its 'brood chamber'. Only females that had not yet started egg laying were used; these are recognizable because the venter of the abdomen contracts in gravid females and a mass of white, powdery wax is secreted around the vulva. Each female was stuck upside-down with gum arabic in the centre of a numbered glass slide (Bedford, 1968). The slides were placed in shallow glass-topped boxes with some wet cotton wool to raise the humidity. Paper trays (5.0 x 3.8cm) were inserted into the boxes underneath each glass slide. Each female was suspended on the slide with the 'brood chamber' facing downwards so that, as the eggs were laid, they fell onto the paper tray. Both the paper tray and slide were given the same number. The boxes were kept in an incubator at 27 ^{0}C and 60±5% RH, and were checked every day at 16:00h. A total of 88 females of varying body-sizes from *C. reticulata* and 44 females from *S. malaccensis* oviposited successfully.

Once oviposition had started, the slides were collected and tapped gently to dislodge the eggs from the 'brood chamber'. All the eggs that dropped onto the paper trays beneath were transferred onto moist filter paper and counted under a stereomicroscope. The slides were put back into the boxes and the assessment continued until no further eggs were laid. This provided information on the

oviposition periods of individual female collected from each of the four farms and on the correlation between female body-size and fecundity.

II. *Total egg production.* This was studied using the following two procedures: the first involved a similar method to the one described above for daily oviposition except that egg collection and counting the eggs was performed only when females ceased oviposition. In the second method, four to five females were stuck upside-down on a numbered glass plate with gum arabic and kept in shallow glass-topped boxes with the 'brood chamber' facing upwards, so that when the eggs were laid they accumulated in the 'brood chamber'. Once oviposition had ceased, the glass plates were overturned with a quick motion onto numbered moist paper trays placed below each female. The glass plates were tapped gently to dislodge all the eggs from the 'brood chamber' onto the paper tray. The eggs on the paper trays were counted under a stereomicroscope. Any eggs left entangled by the massive powdery waxes of the multilocular disc pores inside the 'brood chamber' were also counted by placing the dead females under a stereomicroscope. In both methods, a total of 116 and 108 adult females of varying body-sizes from *C. reticulata* and 44 and 34 females from *S. malaccensis* oviposited successfully in 1997 and 1998, respectively.

The length and width of the female body denuded of wax by placing infested twigs and leaves in glass dishes containing equal volumes of 90% alcohol and xylene (Sands, 1984) was measured under a stereomicroscope fitted with a micrometer eyepiece (for details see Chapter 2, Section 2.3).

2.3. Fertility

Egg viability and crawler emergence were investigated by placing a specified number of eggs of the same age in 10 x 5cm vials with a cotton wool stopper. The vials were laid horizontally in an incubator at 27 ^{0}C and 60±5% RH, with the stopper facing a light source (emerging crawlers were positively phototropic). The eggs were observed daily to determine whether they had hatched and whether viable crawlers had emerged. Once egg hatch or crawler emergence was noted, the contents of the vials were emptied onto dry filter paper and the number of crawlers counted. This procedure was repeated until no further hatching was observed (thus giving the incubation period). The number of infertile eggs was also recorded.

2.4. Phenology

Twenty trees from each of the study orchards were marked subject to the presence of an identifiable number of scales. The sample population included all developmental stages: three nymphal stages designated as LI, LII and LIII; preovipositing females (POF); ovipositing females (OF) and eggs (E). LI consisted of crawlers and first instar nymphs. Sampling units comprised of 4-6 infested twigs, 20 cm long and 3-5 mm in diameter, each bearing at least 10 leaves, from each sample tree. The sample universe included the peripheries of the middle to top canopy of each sample tree from all four compass points. The twigs with their leaves were sampled at bimonthly intervals and taken to the laboratory for population census. From each twig 10 leaves were assessed giving a total of 40-60 leaves per tree and an overall average of 1000 leaves per farm per sampling occasion.

Each insect from the sample units (twigs and leaves) was carefully overturned with dissecting needles and examined under a stereomicroscope to establish whether

or not it was alive. For the first and second instars (ray stages), the twigs as well as the abaxial and adaxial leaf surfaces were examined. Scale stages were identified as described by Wakgari & Giliomee (1998). Adult females were dissected under a stereomicroscope for the presence of eggs inside the ovary to categorize them either as preovipositing or ovipositing. Data obtained from the laboratory examinations of the bimonthly field samples were used to calculate the percentage of the various stages in the total population of *C. destructor.* For both leaves and twigs, scale density was expressed as percentage of the total.

2.5. Data analysis

Fecundity data were subjected to log transformation to stabilize the variance before analysis. Differences in female fecundity between orchards and between females of different body sizes, as well as the interaction between orchards and season were analyzed with factorial analysis of variance (ANOVA) described by Zar (1984). The degree and trend of association between female body size and fecundity were analyzed using correlation and regression statistics.

3. RESULTS

3.1. Fecundity and size

Data for female fecundity, egg fertility and body sizes are presented in Table 2. Total egg production per ovipositing female of *C. destructor* did not differ significantly between orchards and between females collected from C. *reticulata* and those from *S. malaccensis* ($P < 0.05$) (Table 3). Female fecundity was also not significantly different between years for all orchards ($P > 0.05$) and for *S.*

Table 2. Mean fecundity, fertility, days to hatching and body-size of adult female *Ceroplastes destructor* infesting *Citrus reticulata* at four farms and on *Syzygium malaccensis* in the Western Cape Province, South Africa, during 1997 and 1998. WEF = Welgevallen Experimental Farm; RFF = Rhodes Fruit Farms; RUS = Rustenburg Estate; WFT = WhiteHall Farming Trust; STL = Stellenbosch.

	1997							1998						
	Fecundity		Fertility[1]	DTH	Body size (mm±SE)[2]			Fecundity		Fertility[1]	DTH	Body size (mm±SE)[2]		
Farm	(range)	n*	(n**)	(range)	Length	Width	n*	(range)	n*	(n**)	(range)	Length	Width	n*
WEF†	1935(14-5542)	74	97.8 (1100)	16-17	4.20(0.38)	2.52(0.10)	133	1353 (19-5091)	42	99.3 (2560)	14-18	4.80(0.19)	2.90(0.14)	42
RFF†	1720 (125-4199)	84	97.6 (5055)	16-19	4.33(0.13)	2.52(0.08)	110	1579 (38-3865)	84	98. 0 (2530)	15-18	5.15(0.09)	2.98(0.09)	84
RUS†	1838 (87-6355)	74	96.1 (2550)	16-19	4.16(0.11)	2.50(0.08)	80	1564 (173-3243)	32	98.9 (1190)	13-17	5.26(0.12)	3.03(0.16)	32
WFT†	-	-	-	-	-	-	-	1413 (197-4007)	74	98.8 (7630)	15-21	4.76(0.17)	2.68(0.12)	74
STL‡	1602 (14-4514)	74	98.6 (2660)	16-17	4.50(0.10)	2.63(0.07)	80	1505 (23-4497)	105	95.4 (3400)	12-16	4.95(0.18)	2.83(0.12)	64
MEAN	1774 (60-5153)	77	97.5 (2841)	17	4.30(0.18)	2.54(0.08)	96	1483 (90-4141)	67	98.06 (3462)	16	4.98(0.14)	2.88(0.11)	59
ANOVA	n.s.		n.s.	n.s.	0.05	0.05		n.s.		n.s.	n.s.	0.05	0.05	

DTH = Days to hatching; [1]% Crawler emergence for eggs incubated at 27^{0}C and 60% RH; [2]Dewaxed adult female; n* = sample size; n** = no. of eggs incubated; SE = Standard error of mean; † host = *Citrus reticulata*; ‡ host = *Syzygium malaccensis*; ANOVA, significant differences between farms ($P < 0.05$); n.s. = not significant ($P > 0.05$).

malaccensis. No significant interaction was found between years and farms ($P < 0.05$). However, individual females from the same orchard varied in their fecundity, ranging from 14 - 6355 eggs/female on *C. reticulata* and 13 - 4514 eggs/female on *S. malaccensis* in 1997, and 19 - 5091 eggs/female on *C. reticulata* and 23 - 4497 eggs/female on *S. malaccensis* in 1998. The frequency distribution curve presented in Fig. 5a shows that the majority of the ovipositing females laid from 1000 to 2500 eggs in a generation. Rarely did they lay more than 5000 eggs. More than three-quarters of the females had a body-width of 2.0 to 3.5 cm (Fig. 5b) and a body length of 3.5 to 5.5 cm (Fig. 5c).

Table 3. Analysis of variance for data presented in Table 2.

Source	df	MS	F	P
		a. Log Fecundity		
Year (Y)	1	0.24346	1.7640	0.1850
Farm (F)	4	0.29968	2.1713	0.0718
Y * F	3	0.07967	0.5773	0.6303
Error	351	0.13802		
		b. Body Width (cm)		
Year (Y)	1	0.04883	0.117	0.7324
Farm (F)	4	1.08003	2.590	0.0366*
Y * F	3	0.07602	0.1823	0.9084
Error	351	0.13802		

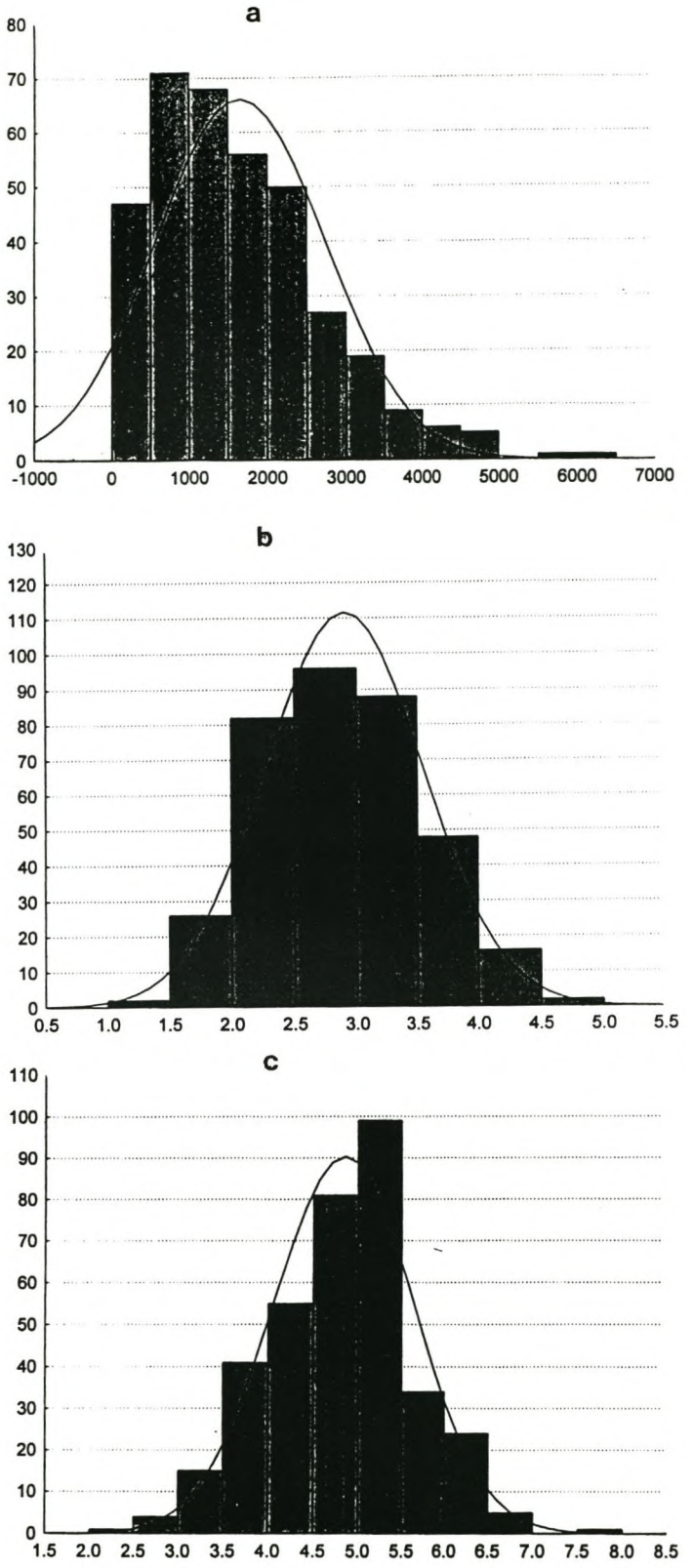

Figure 5. Frequency distribution for the fecundity (a), body width (b) and body length (c) of 260 females *Ceroplastes destructor* shown in Table 2.

The body width of *C. destructor* varied significantly between farms ($P < 0.05$), but not between years ($P > 0.05$) (Table 3). Body width and length were significantly positively correlated both for scales from *C. reticulata* and *S. malaccensis* (Table 4) during both years ($P < 0.01$). Size and fecundity also were positively correlated for females from both hosts in both years ($P < 0.01$).

Table 4. Correlation coefficients (r) showing the relationship between female fecundity and body sizes computed for two scale generations at four citrus orchards and on *S. malaccensis* (Abbreviations as in Table 2).

		1997		1998	
Farm	**Parameter**	**Length**	**Width**	**Length**	**Width**
WEF	Fecundity	0.89*	0.92*	0.80*	0.84*
	Length	-	0.88*	-	0.86*
RFF	Fecundity	0.52	0.70**	0.60**	0.71**
	Length	-	0.83*	-	0.77*
RUS	Fecundity	0.84*	0.89*	0.34	0.89*
	Length	-	0.88*	-	0.61**
STL	Fecundity	0.77*	0.75*	0.68**	0.85*
	Length	-	0.74*	-	0.82*
WFT	Fecundity	-	-	0.80*	0.92*
	Length	-	-	-	0.80*

* significantly correlated ($P < 0.01$); ** ($P < 0.05$).

Linear regression analyses indicated that fecundity and size were significantly associated in both years (Table 5). The slopes for width and length were positive and significantly greater than zero for females collected from all farms during both years,

Table 5. Linear regression coefficients and F-values showing the relationship between fecundity and body size based on data presented in Table 2. WEF = Welgevallen Experimental Farm; RFF = Rhodes Fruit Farms; RUS = Rustenburg Estate; WFT = WhiteHall Farming Trust; STL = Stellenbosch.

		Length				Width			
Year	**Farm**	**a**	**b**	**r^2**	**F**	**a**	**b**	**r^2**	**F**
1997	WEF†	-3662	1188	0.80	152.10**	-2786	1621	0.84	205.87**
	RFF†	-1710	710	0.27	15.00*	-1807	1180	0.50	39.15**
	RUS†	-4912	1477	0.70	81.56**	-2791	1560	0.79	130.84**
	STL‡	-4203	1311	0.59	49.68**	-2311	1446	0.56	44.45**
1998	WEF†	-2903	888	0.65	34.64**	-2192	1222	0.71	47.17**
	RFF†	-3295	946	0.36	22.75**	-1695	1099	0.51	40.73**
	RUS†	-1934	665	0.12	1.86	-2274	1265	0.79	52.01**
	WFT†	-3163	959	0.65	47.49**	-2694	1528	0.85	147.77**
	STL‡	-2132	746	0.46	25.35**	-2309	1376	0.72	76.04**

† host = *Citrus reticulata*; ‡ host = *Syzygium malaccensis* **significant linear relationship among the three variables ($P < 0.01$); * ($P < 0.05$).

indicating that female fecundity increased as female body width and length increased. However, the slopes for width were steeper than those for length, indicating that variation in female fecundity is explained more by differences in female body-width than by body-length.

The average number of eggs laid by various size groups is presented in Table 6. This average is significantly different between size groups for females from both hosts ($P < 0.001$), and the differences are more pronounced for females from *S. malaccensis* than for those from *C. reticulata.*

The oviposition period was also affected by body-size, with large females from both hosts taking 14 days to complete egg laying; medium-sized females from *C. reticulata* taking 12 days (Fig. 6), those from *S. malaccensis* 11 days (Fig. 7) and

Table 6. Effect of host-plant species and body size on the fecundity for *Ceroplastes destructor.*

Host	Size	Size ranges (mm)	No. females	Mean no. eggs/Φ	Oviposition period (days)
Citrus	Small	2.20 - 3.45	32	574	10
	Medium	3.46 - 4.61	30	1304	12
	Large	4.62 - 5.60	26	1970	14
Syzygium	Small	2.20 - 3.45	12	303	10
	Medium	3.46 - 4.61	12	567	11
	Large	4.62 - 5.60	20	2176	14

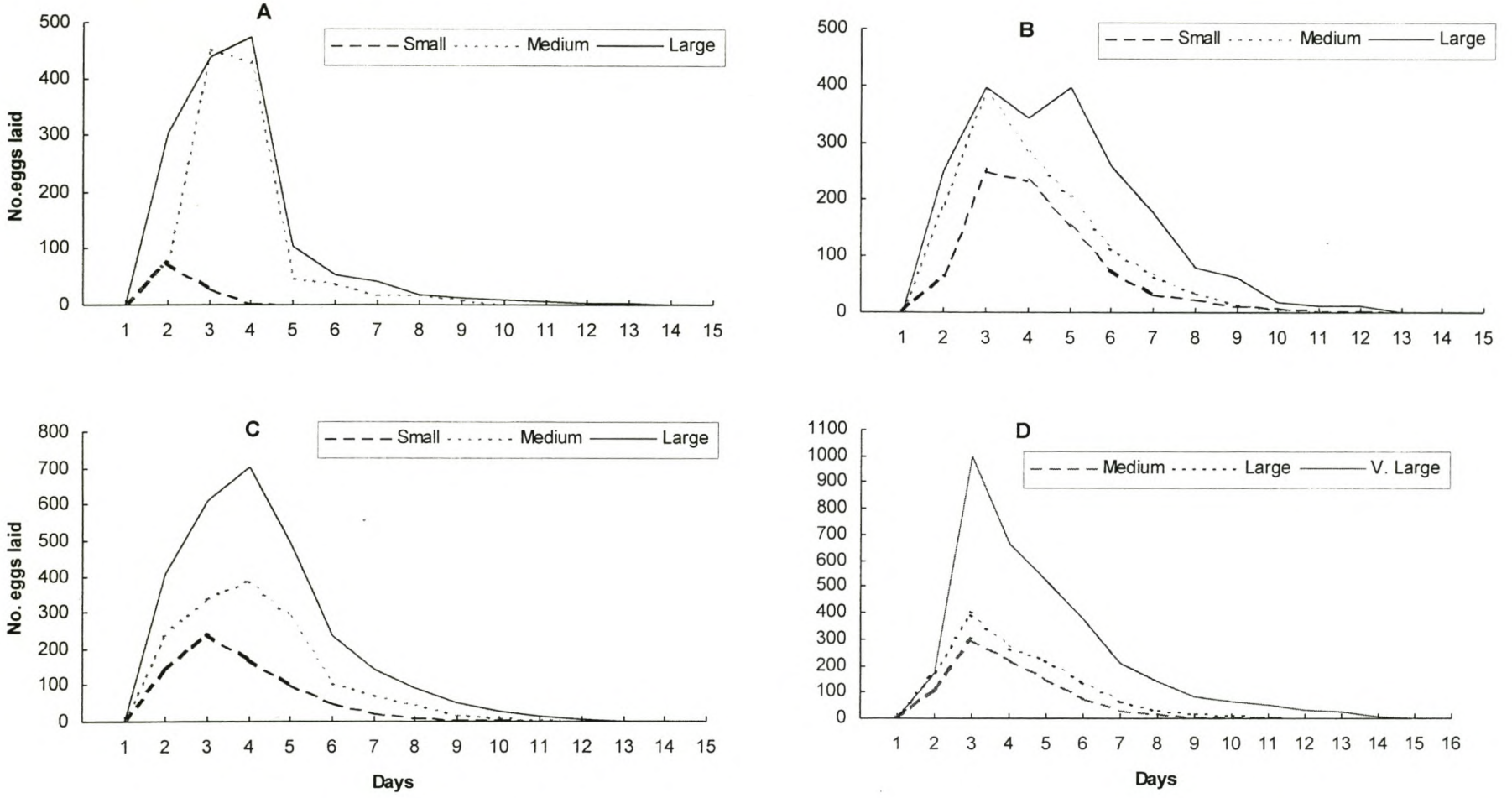

Figure 6. Effects of body size on the duration and pattern of egg laying for *Ceroplastes destructor* infesting *Citrus reticulata.* WEF = **A**. Welgevallen Experimental Farm; **B**. RFF = Rhodes Fruit Farms; **C**. RUS = Rustenburg Estate; **D**. WFT = WhiteHall Farming Trust; STL = Stellenbosch.

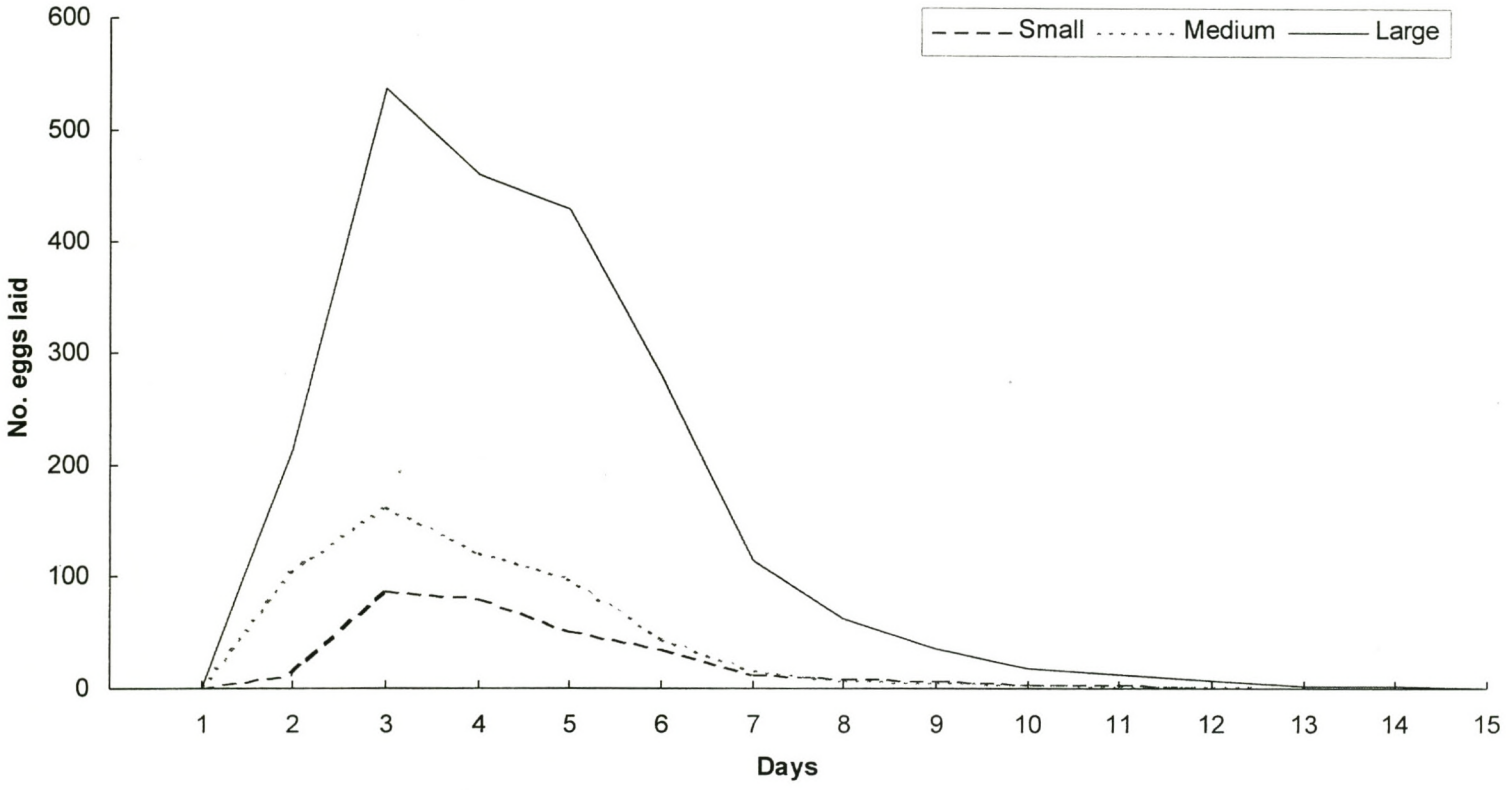

Figure 7. Effects of body size on the duration and pattern of egg laying for *Ceroplastes destructor* infesting *Syzygium malaccensis.*

small *C. destructor* 10 days. The average number of eggs laid/female/day varied from a maximum of 701 eggs on the 3rd day of oviposition to a minimum of 1 on the last (14th) day for large females from *C. reticulata*; on *S. malaccensis*, a maximum of 537 eggs was laid on the 2nd day and 1 on the 14th day. Egg laying by large and medium-sized females from *C. reticulata* peaked on the 4th day whereas for medium-sized females from *S. malaccensis*, peak oviposition was on the 3rd day. Small females from both hosts laid peak numbers of eggs on the 3rd day. The average duration of oviposition by females from both hosts for all size categories was 11 days.

3.2. Fertility

Mean percentage egg fertility during 1997 and 1998 for females collected from *C. reticulata* and *S. malaccensis* is indicated in Table 2. The level of infertility was negligible and no significant differences were found between years and between eggs laid by females from both hosts ($P > 0.05$).

3.3. Phenology

Total and partial population curves for females from *C. reticulata* and *S. malaccensis* presented in Figs 8-12 show the total and relative abundance of first, second, third instars, pre-ovipositing and ovipositing females in the live population of *C. destructor*. Oviposition by adult females commenced in November and continued until the end of December with a few ovipositing until mid January. The naked, six-legged crawlers emerged 15 to 21 days after the eggs were laid, their emergence coincided with the formation of new flushes of host plant growth. The first moult took place 30-36 days after settling depending on temperature. The oval second instar emerged from end of January to mid February during which the dry dorsal wax pad and lateral rays became distinct and separated into individual rays. The star-shaped LI

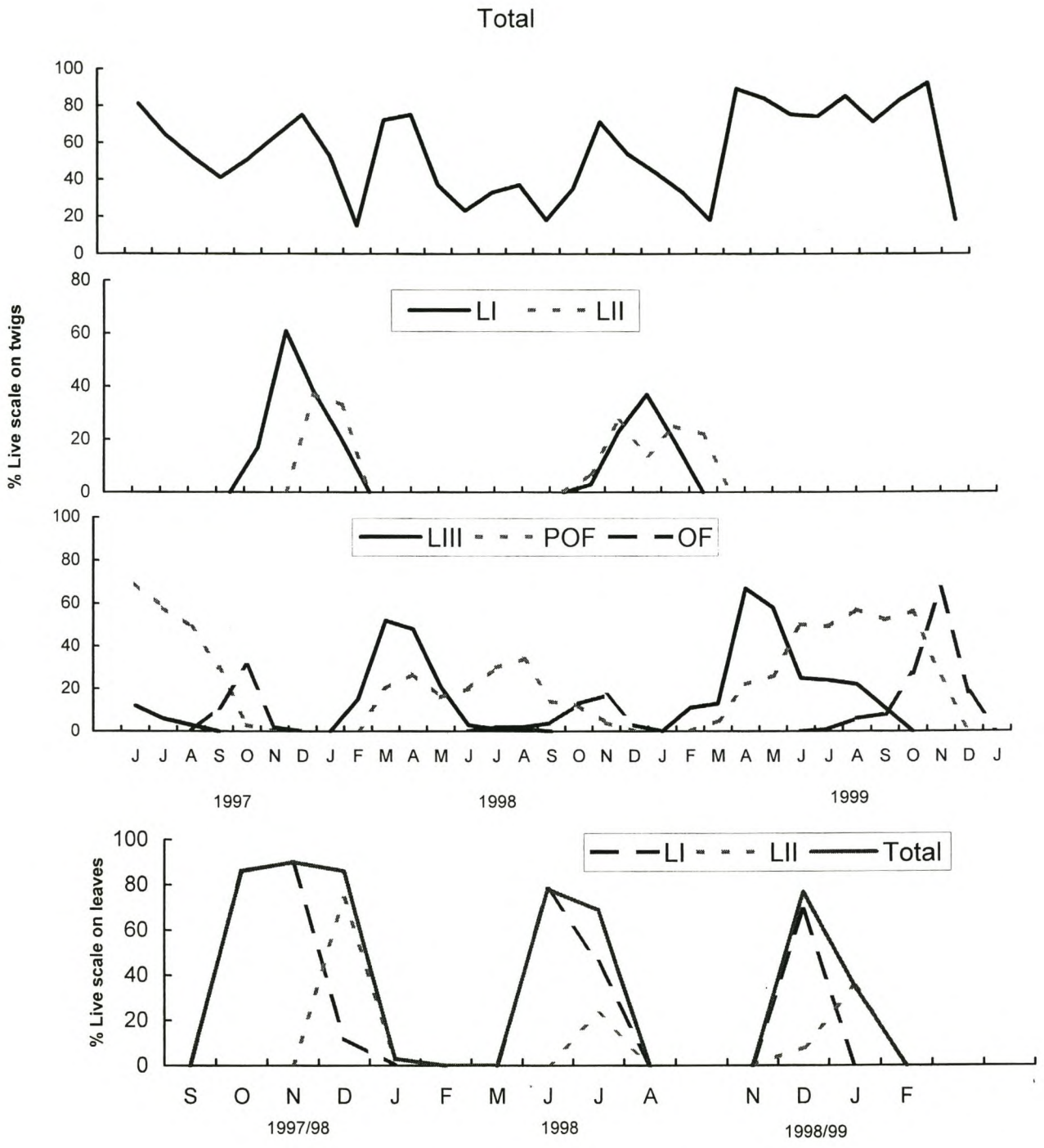

Figure 8. Total and partial population curves for *Ceroplastes destructor* infesting *Citrus reticulata* at Welgevallen Experimental Farm (June 1997 – January 2000).

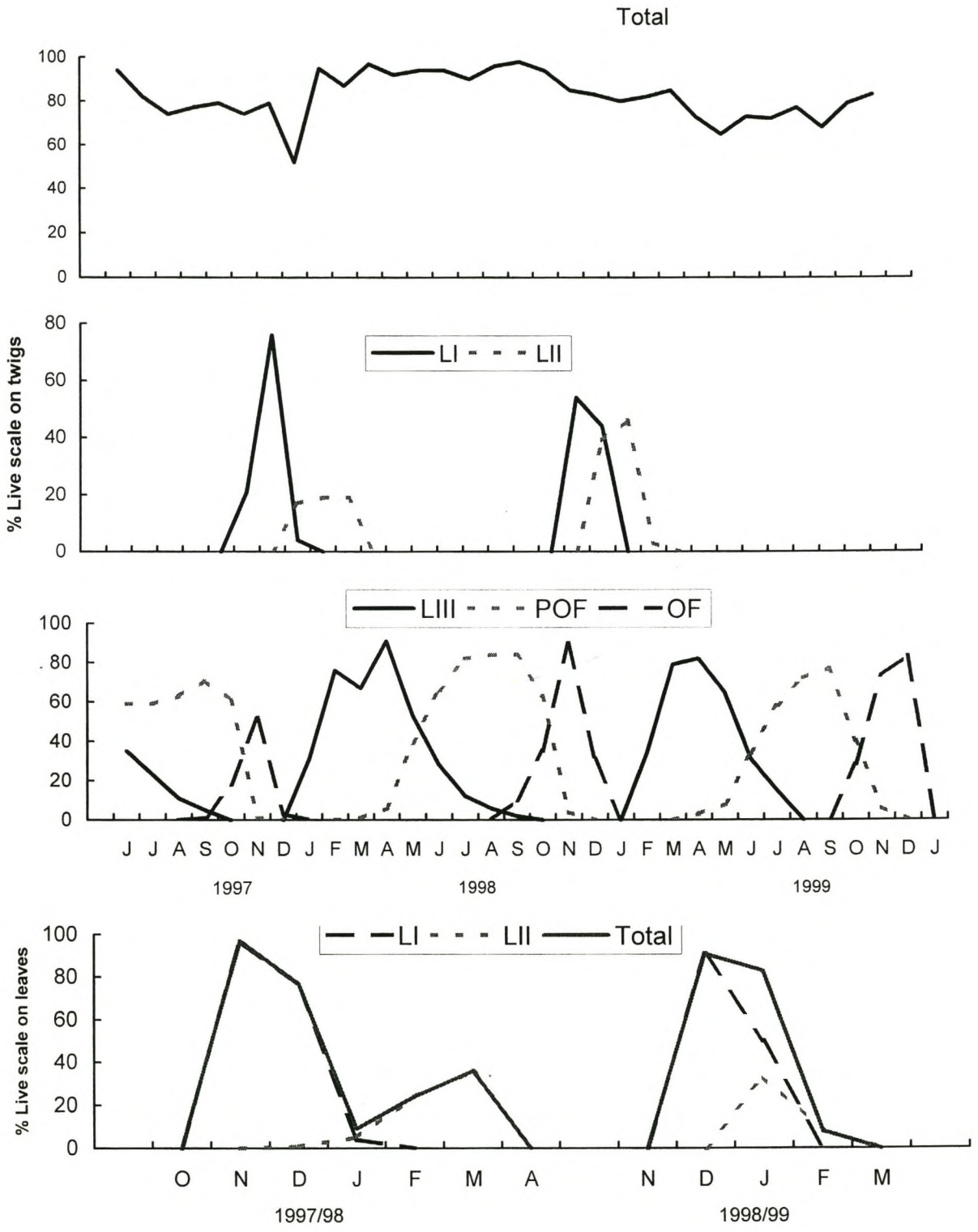

Figure 9. Total and partial population curves for *Ceroplastes destructor* infesting *Citrus reticulata* at Rhodes Fruit Farms (June 1997 – January 2000).

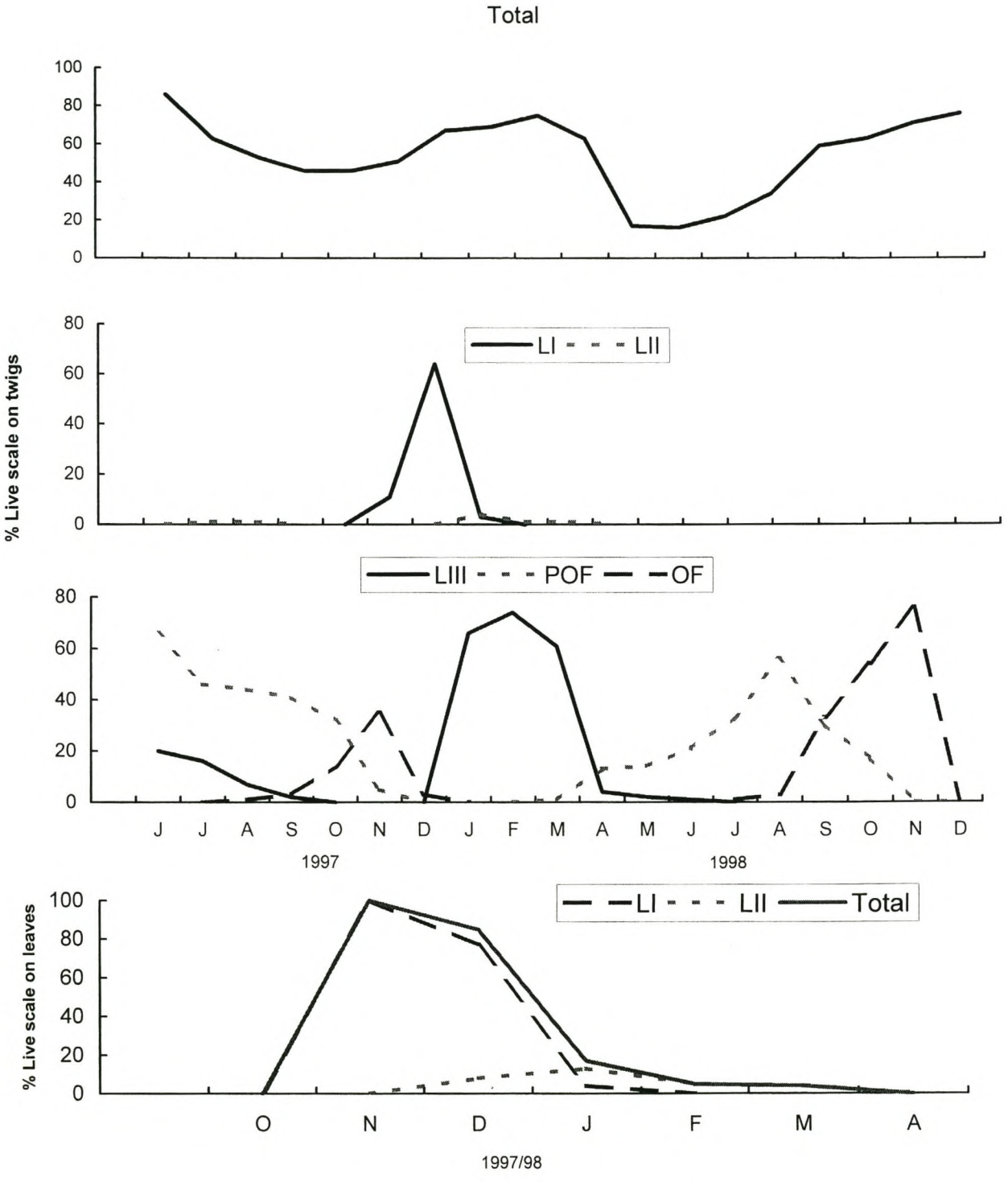

Figure 10. Total and partial population curves for *Ceroplastes destructor* infesting *Citrus reticulata* at Rustenburg Estate (June 1997 – December 1998).

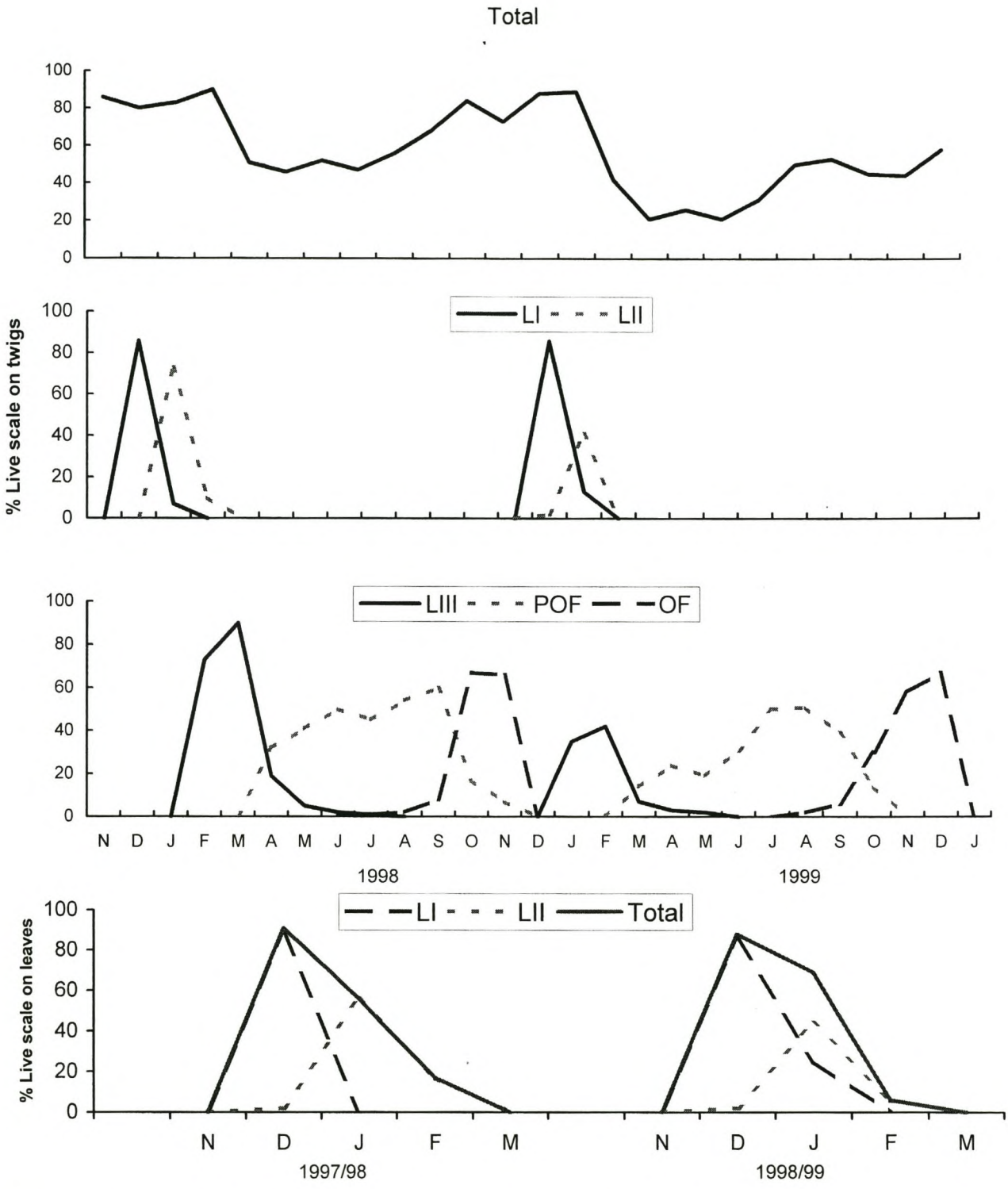

Figure 11. Total and partial population curves for *Ceroplastes destructor* infesting *Citrus reticulata* at WhiteHall Farming Trust (November 1997 – January 2000).

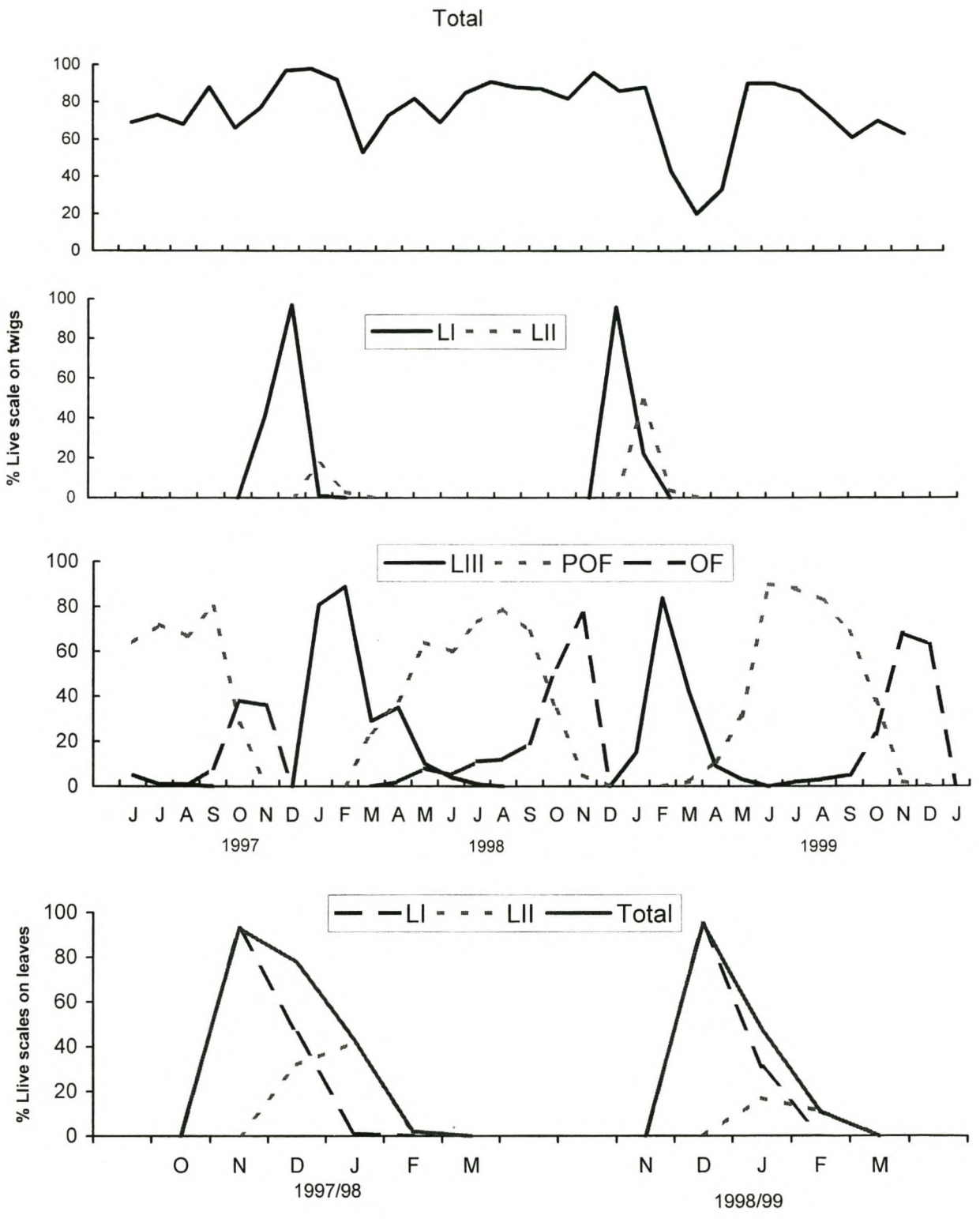

Figure 12. Total and partial population curves for *Ceroplastes destructor* infesting *Syzygium malaccensis* at Stellenbosch (June 1997 – January 2000).

and LII (rosettes) were mainly confined to the leaves (Figs 8-11) and leaf petioles, with a few settling on young twigs when the population density was high. The second moult took place about one month after the first, i.e. from the end of February to the middle of March. The oval-shaped third and last instar (= peak stage) moved to the twigs during last week of February and remained feeding on the nutritious sap of the host plant. The peak stage (LIII) extended from early March to end of July while the pre- ovipositional stage (POF) lasted from mid April to end of September.

A considerable swelling of the body of gravid females took place from September to November due to the accumulation of eggs inside the body. The abdomen of the female contracted until the ventral membrane butted against the dorsal wall. This marked the end of the ovipositional period. As contraction of the venter continued, the entire cavity thus formed between the host plant and the scale (= 'brood chamber') was filled with eggs that accumulated there until hatching. No generation overlap was observed, although a considerable overlap of stages was apparent. This was particularly true for the LIII and POF stages. *Ceroplastes destructor* overwintered mainly as POF but a few also as LIII.

4. DISCUSSION

Ceroplastes destructor can be a copiously fecund species. However, fecundity varied considerably among individual females of various body sizes from the same orchard and to a lesser extent among females of comparable sizes from different orchards. The range in fecundity reported here is similar to that found by Lo (1995) of 12-5214 for *C. destructor* infesting citrus in New Zealand. However, the maximum number of eggs laid by an individual female of *C. destructor* collected from citrus in 1997 (6355) exceeded previously reported maxima of 3000 (Smith, 1970) and 5214

(Lo, 1995). The mean fecundity for *C. destructor* during the first year of the present study (1774), was less than the 3000 reported by Zeck (1934) but slightly more than the 1750 reported by Olson *et al.* (1993) and 1233 by Lo (1995). The mean in the second year of 1483 was less than that reported by Zeck (1934) and Olson *et al.* (1993) but slightly more than that given by Lo (1995). This variation in realized fecundity between countries may be due to differences in citricultural practices and/or due to variation in climatic factors.

Female fecundity was significantly positively correlated to female body sizes. Both the regression and correlation coefficients indicated that width accounted for most of the variability in fecundity. This finding corroborated results reported by Bedford (1968), Yardeni & Rosen (1995) and Lo (1995) who demonstrated a significant correlation between female fecundity and body size for *Ceroplasstes sinoiae* Hall, *Ceroplastes floridensis* Comstock and *C. destructor,* respectively. Although size and fecundity of *C. destructor* were correlated, the regression coefficients obtained were variable between orchards and generations. Consequently, other factors affecting female fecundity, e.g. scale density, must be taken into account when constructing descriptive models. Fecundity data could help in estimating the numbers entering a new generation and in predicting subsequent survival and population changes. The variation in female fecundity between orchards may consequently have implications for the size of the succeeding scale populations and thus in the forecast of likely epidemic developments.

The variation in female body size among orchards and between females from *C. reticulata* and *S. malaccensis* could probably be associated with differences in citricultural practices between the orchards and between the *Citrus* and *Syzygium* trees. The size of *C. destructor* is, for example, known to be positively correlated with

the nitrogen levels of citrus trees (McClure, 1980; Beattie *et al.* 1990). Thus, the regular application of synthetic fertilizers in citrus orchards can affect the body size and oviposition rate of *C. destructor*.

The incubation period for eggs of *C. destructor* at 27 °C and 65 ± 5% RH in the current study ranged from 16 to 19 days with a mean of 17 days in 1997 and 12 to 21 days with a mean of 16 days in 1998. This was shorter than the 24-35 days reported by Cilliers (1967) for *C. brevicauda* Hall at 27 °C and 38% RH, the difference being probably due to the inherent species differences and also due to differences in the humidity levels used. In field populations of *C. destructor* in the present experiments, eggs laid by the same generation of females hatched over a period of two months as a result of asynchronous egg laying or possibly due to differences in rate of individual development. After hatching, the crawlers remained within the 'brood chamber' for about two days before moving onto leaves or young twigs.

The percentage of infertile eggs was very small and comparable for eggs from females on *C. reticulata* and *S. malaccensis*. Although some predatory and phytophagous mites ventured underneath dead females, they were not seen specifically feeding on the eggs, and no other egg predators were found. Infertile eggs are pale in colour upon eclosion but turn whitish and brittle with time. Furthermore, they are smaller in size than fertile eggs when laid.

The phenology of *C. destructor* was shown to be similar in successive seasons for three of the citrus orchards and *S. malaccensis* (Figs 9-12), but recruitment of the LI and LII stages was observed at Welgevallen Experimental Farm in June/July of 1998 on leaves (Fig. 8). It was also noticed that this was the only evidence of a possible occurrence of more than one generation per year as was found by Smith

(1970) and Smith & Ironside (1974) in Australia. However, none of the recruits reached the adult stage, probably because of the cold winter. The oviposition period of adult females found in this study (i.e. November/December) coincided with that reported by Olson *et al.* (1993) and Lo (1995) in New Zealand, but was one month later than that reported by Jenkins *et al.* (1953) in Australia. The variation between orchards and countries in stage intervals and phenology could be attributed to differences in climatic and soil nutrient conditions. It is essential to take such variations into account in devising specific control strategies.

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CHAPTER 4

NATURAL ENEMIES ASSOCIATED WITH WHITE WAX SCALE, *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE), ON *CITRUS* AND *SYZYGIUM*.

ABSTRACT

Parasitoids and predators associated with *Ceroplastes destructor* Newstead were reared or collected from field-sampled scale stage categories susceptible to parasitism and predation from four easy-peel citrus (*Citrus reticulata* (Blanco)) orchards and on *Syzygium (= Eugenia) malaccensis* (L.) in the Western Cape Province of South Africa from June 1997 to December 1999. Seven primary and three secondary parasitoids, as well as four predator species were identified. *Aprostocetus (= Tetrastichus) ceroplastae* (Girault) (Hymenoptera: Eulophidae) was the predominant parasitoid species, accounting for 78.87% of the total primary parasitoids reared. It occurred throughout the months during which active parasitization by other parasitoids was low. Peak numbers of parasitoids and predators were synchronized with peak emergence of scale stage categories susceptible to parasitism and predation, indicating that the scale-parasitoid/predator association contained a density-dependent regulatory mechanism. However, this density-dependent association fluctuated between generations, indicating that the regulatory effects of parasitoids and predators may not be strong enough to provide long term suppression of scales under the current

citricultural practices. Body-length of *A. ceroplastae* varied significantly between sampling periods, parasitoid sex and scale stage from which it was reared ($P < 0.001$).

1. INTRODUCTION

The population density of noxious pests tends to increase exponentially but various endogenous and exogenous factors often impede such increase. One of the major extrinsic factors that can maintain the population of insect pests at the 'steady state' level is a density dependent mortality factor. Most of the early ecological models were developed around the scenario that successful biological control of insect pests can only result from density dependent actions of natural enemies (e.g. Harcourt, 1971; Hassell & May, 1974). These models purport that a density dependent relationship is regulatory in nature in that a greater proportion of the host population is annihilated at higher host densities and mortality eases when host density falls below the equilibrium density. This type of population regulation therefore involves co-existence of both the host/prey and parasitoids/predators, i.e. a 'negative feedback' mechanism (see Geier, 1966; Harcourt, 1971). However, some studies on host-parasitoid interactions have revealed that parasitization can result in inverse density dependent (positive-feedback) relationships (e.g. Walde & Murdoch, 1988; Loch & Zalucki, 1998; Lo & Chapman, 1998) or even in a density-independent (no-feedback) relationships (e.g. Loch & Zalucki, 1998). Such relations do not fit into the classical biological control theory because pest densities are not maintained at a low stable level. A mortality factor that acts in an inverse density dependent manner, for instance, destabilizes the population rather than stabilizing it (Luck, 1971; Royama, 1977).

The destruction of a large proportion of pests by natural enemies may not necessarily affect pest survival since it may simply replace some other cause without materially altering the number of pests that survive (DeBach & Bartlett, 1964). There should ideally be functional as well as numerical responses to changes in pest populations in order for natural enemies to provide regulatory effects. In most instances natural enemies provide regulatory effects by directly killing their host/prey, thereby reducing their reproductive potential or by making them susceptible to death from some other causes.

Ceroplastes destructor Newstead was an important pest of citrus in Australia until the early 1970s (Smith, 1970; Snowball, 1969; Smith & Ironside, 1974; Hely *et al.*, 1982; Sands *et al.*, 1986; Qin & Gullan, 1994) and lately in New Zealand (Olson *et al.*, 1993; Lo, 1995; Lo & Chapman, 1998). However, it was effectively controlled during the mid 1970s in Australia by parasitoids imported from South Africa (Sands *et al.*, 1986). *C. destructor* has only been considered as a minor yet potential pest of citrus and deciduous fruit orchards in South Africa in the past (Cilliers, 1967). A complex of natural enemies have effectively regulated its population densities for a long time (Cilliers, 1967). However, its population density has surged in certain *Citrus reticulata* (Blanco) orchards in the Western Cape Province, South Africa, since 1994. This upsurge may be the result of changes in citricultural and/or pest control practices that had taken place in the recent past, causing a shift in faunistic complexes in orchards. The seasonal dynamics and the effectiveness of natural enemies in regulating populations of *C. destructor* in South African orchards remain unstudied, although Cilliers (1967) and Snowball (1969) gave a list of indigenous parasitoid and predator species. In this Chapter I assessed the present species composition of natural enemies of *C. destructor* and their temporal variation in abundance in order to

contribute towards more rational orchard spraying schedules and an effective IPM system for *C. destructor*. The effects of host stages of *C. destructor* on the body size and proportion of male and females of the parasitoid *Aprostocetus (= Tetrastichus) ceroplastae* (Girault) were assessed in order to establish which host stage is suitable for rearing parasitoids if and when augmentative releases are required.

2. MATERIALS AND METHODS

2.1. Study sites

Field sampling was carried out in four commercial groves of easy-peel citrus (*Citrus reticulata (*Blanco)) and on rows of *Syzygium (= Eugenia) malaccensis* (L.) in the Western Cape, South Africa, from June 1997 to December 1999 (see Chapter 3, Section 2.1. for detailed descriptions of study sites).

2.2. Parasitoid rearing

Two methods were employed to rear parasitoids from field-sampled materials. Firstly, twigs infested with susceptible scale stages were enclosed in emergence boxes constructed from corrugated cartons similar to those described by Bedford (1968). The boxes were maintained in an incubator at 27 °C and 60 ± 5% RH. In the second method, scales were overturned from infested twigs with needles and sorted into stage categories before placing each stage category separately into glass tubes of varying sizes. The tubes were then covered with cotton wool and maintained in an incubator at the same temperature and RH mentioned above. In both methods bee honey was smeared onto the wall of the collection tubes, serving as a source of food for emerging parasitoids. The emerging adult parasitoids were recorded daily and stored in 70% ethyl alcohol until identification. The proportion of each in the total reared was

determined. A parasitoid was classified as secondary (one whose host is a primary parasitoid) only when it emerged from a living or dead bodies of a primary parasitoid (one whose host is not a parasitoid) from scales placed in glass tubes or during dissections (see below). Dead scales in the glass tubes from which secondary parasitoids had emerged were also examined to trace the presence of any remains of nymphal or adult bodies of a primary parasitoid. Predators were collected directly from the field and identified.

2.3. Temporal variations in parasitism and predation

External appearance is often a poor indicator of whether *C. destructor* is alive or dead and, when dead, the cause of mortality may not be easily recognizable. Percent parasitism and diseased scales were therefore determined from serially sampled field material by dissecting about 250 hosts susceptible to parasitism, i.e. third instar (LIII) and preovipositing female (POF) (young and mature females), under a stereomicroscope at bimonthly intervals. This provided data on the rate of active parasitism. Percentage predation was determined from direct counts of the white remains of the spiracular bands, and scale covers with chewed edges or ragged holes in them in each sample unit at each sampling period. Detailed analyses of the host (*C. destructor*)-parasitoids/predators relationships are given in Chapter 5.

2.4.Effects of scale stages on body sizes of Aprostocetus ceroplastae

Sample units bearing early third instar, late third instar, young and mature adult stages were separately enclosed in emergence boxes or tubes and emerging parasitoids were separately stored in 70% ethyl alcohol. The body length of *A. ceroplastae*, reared from the different host stages at different times of the year was

measured under a stereomicroscope equipped with a micrometer eyepiece. *A. ceroplastae* was used as an indicator species because of its predominance. Sexing was based on descriptions given by Ben-Dov (1972) and Prinsloo (1984). Factorial analysis of variance described by Zar (1984) was used to examine the effects of host stages, sampling periods and parasitoid sexes on body length of *A. ceroplastae*.

3. RESULTS

Seven primary and three secondary parasitoid species as well as four predator species were reared from LIII and POF scales (Table 1). *A. ceroplastae* was the dominant species, accounting for 78.9% of the total number of the primary parasitoids reared, followed by *Anicetus nyasicus* (Compere) (Table 1). *Aprostocetus ceroplastae* was active during every sampling occasion almost all year round, attacking LIII (Fig. 1) and POF. Of the three secondary parasitoids, *Marietta leopardina* Motschulsky (= *M. exitiosa* Compere) was the dominant species followed by *Cheiloneurus* sp. The total number of primary and secondary parasitoids reared from scales from both *C. reticulata* and *S. malaccensis* varied considerably between years (Table 2).

A single parasitoid to a host was found for all the primary parasitoids. The secondary parasitoid *Cheiloneurus* sp., on the other hand, occurred gregariously in up to ten to a host. Among the predator species *Cydonia runata* F. *and Coccidophaga (= Eublemma) scitula* (Rambur) were predominant. The Cape white-eye bird (*Zosterops pallidus* Swainson) was observed feeding on scales while the honeybee (*Apis mellifera* L.) removed the wax cover in their corbiculae and exposed scales to desiccation. It was noticed that scales whose wax cover had been removed would either die after a few days or go into premature oviposition if they were in the mature

Table. 1. Primary and secondary parasitoids and predator species reared from susceptible stages of *Ceroplastes destructor* and the percentage of each in the total reared (June.1997 - December 1999).

Species name	Family	% of total
Primary		
Aprostocetus ceroplastae (Girault)	Eulophidae	78.87
*Anicetus nyasicus (*Compere*)*	Encyrtidae	8.84
Anicetus sp.	Encyrtidae	1.56
Metaphycus sp.	Encyrtidae	4.47
Coccophagus atratus Compere	Aphelinidae	1.78
Coccophagus catherinae Annecke	Aphelinidae	1.64
Euxanthellus sp.	Aphelinidae	1.60
Others	-	1.24
Secondary		
Marietta leopardina Motschulsky	Aphelinidae	55.84
Marietta connecta Compere	Aphelinidae	5.50
Cheiloneurus sp.	Encyrtidae	38.66
Predators		
Coccidophaga scitula (Rambur)	Noctuidae	-
Exochomus flavipes Thunb.	Coccinellidae	-
Cydonia runata F.	Coccinellidae	-
Nephus sp.	Coccinellidae	-

Figure 1. *Aprostocetus ceroplastae* ovipositing in third instar *Ceroplastes destructor* on citrus.

adult stage when the wax cover was removed. Parasitism, predation and diseased scales, expressed as a percentage of live susceptible scale stages on twigs and plotted for each orchard as a monthly average, are shown in Figs 2-6. Since most parasitoids acted concurrently, it was difficult to determine the specific parasitoid species responsible for scale mortality. Therefore, mortality due to all parasitoids was lumped together for each scale generation. Mortality due to predation was also lumped together in a similar manner. Parasitoids and predators showed a response that was synchronized with age intervals of susceptible host stages (*cf.* Figs 2-6 in this Chapter and Figs 8-12 of Chapter 3). Mortality due to disease was negligible, averaging about 2% for scales from *C. reticulata* and 5% for scales from *S. malaccensis,* and its effects were inconsistent throughout the study periods (Figs 2-6).

Table 2. Number of primary and secondary parasitoids reared from *Ceroplastes destructor* on *Citrus reticulata* and *Syzygium malaccensis* from June 1997 to December 1999 in the Western Cape Province, South Africa.

Year	No. of scales examined	Primary parasitoids (%)	Secondary parasitoids
1997	7329	3199 (43.65)	86
1998	6383	2398 (37.57)	141
1999	18666	5609 (30.05)	176
Total	32378	11206 (34.61)	403

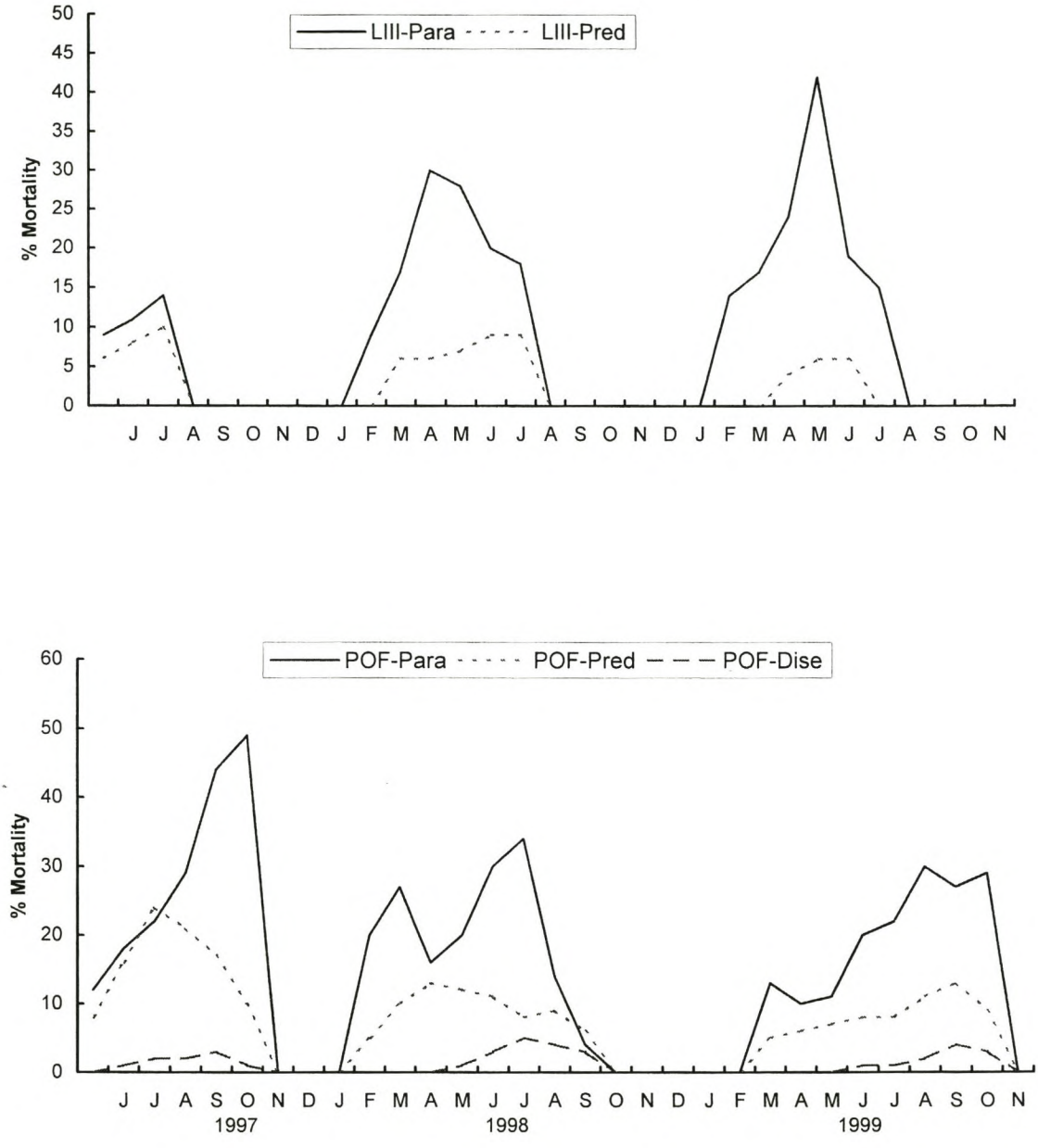

Figure 2. Percentage parasitism (Para), predation (Pred) and diseased (Dise) LIII and POF stages of *Ceroplastes destructor* infesting *Citrus reticulata* at Welgevallen Experimental Farm (June 1997 – December 1999).

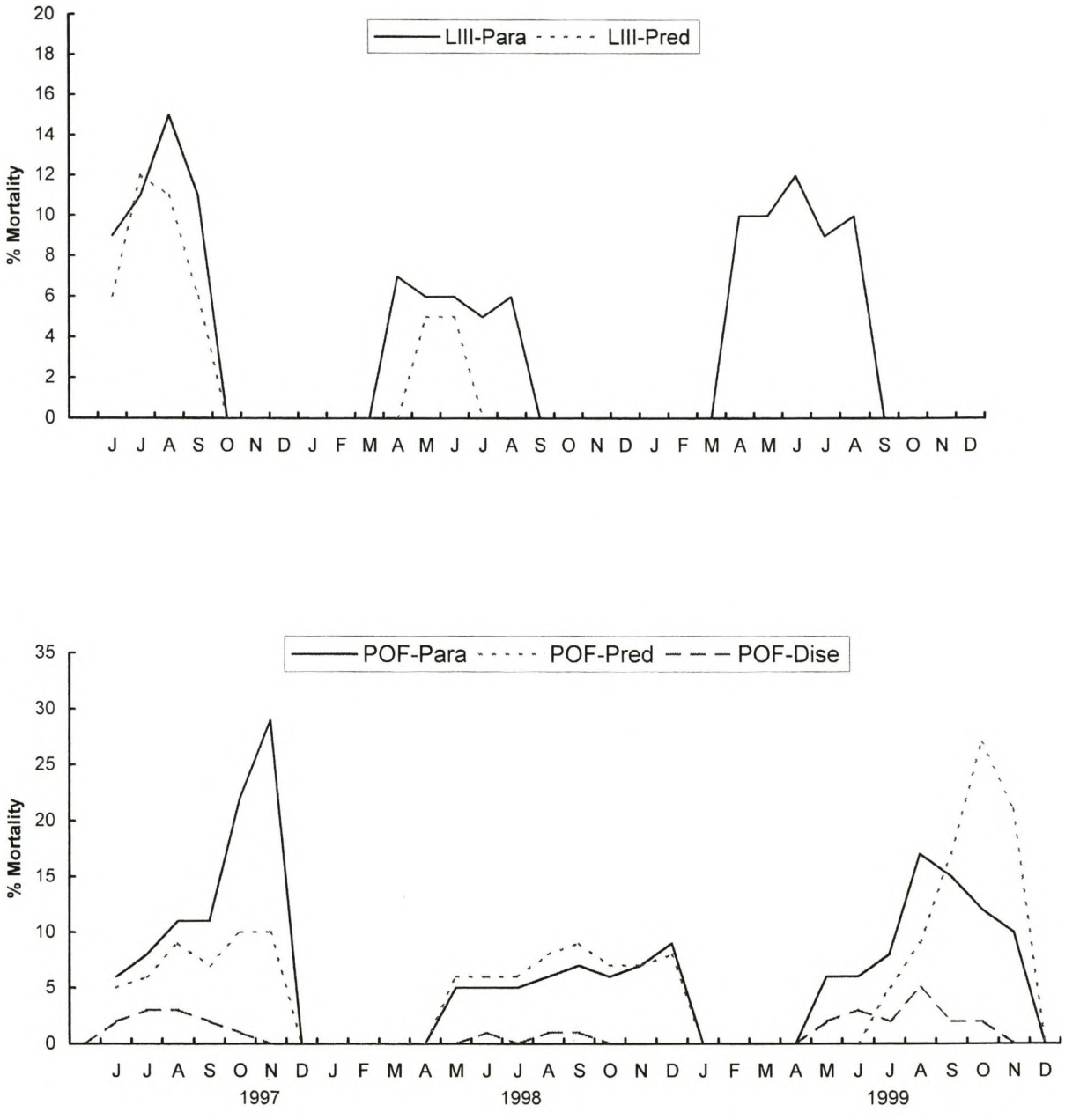

Figure 3 Percentage parasitism (Para), predation (Pred) and diseased (Dise) LIII and POF stages of *Ceroplastes destructor* infesting *Citrus reticulata* at Rhodes Fruit Farms (June 1997 – December 1999).

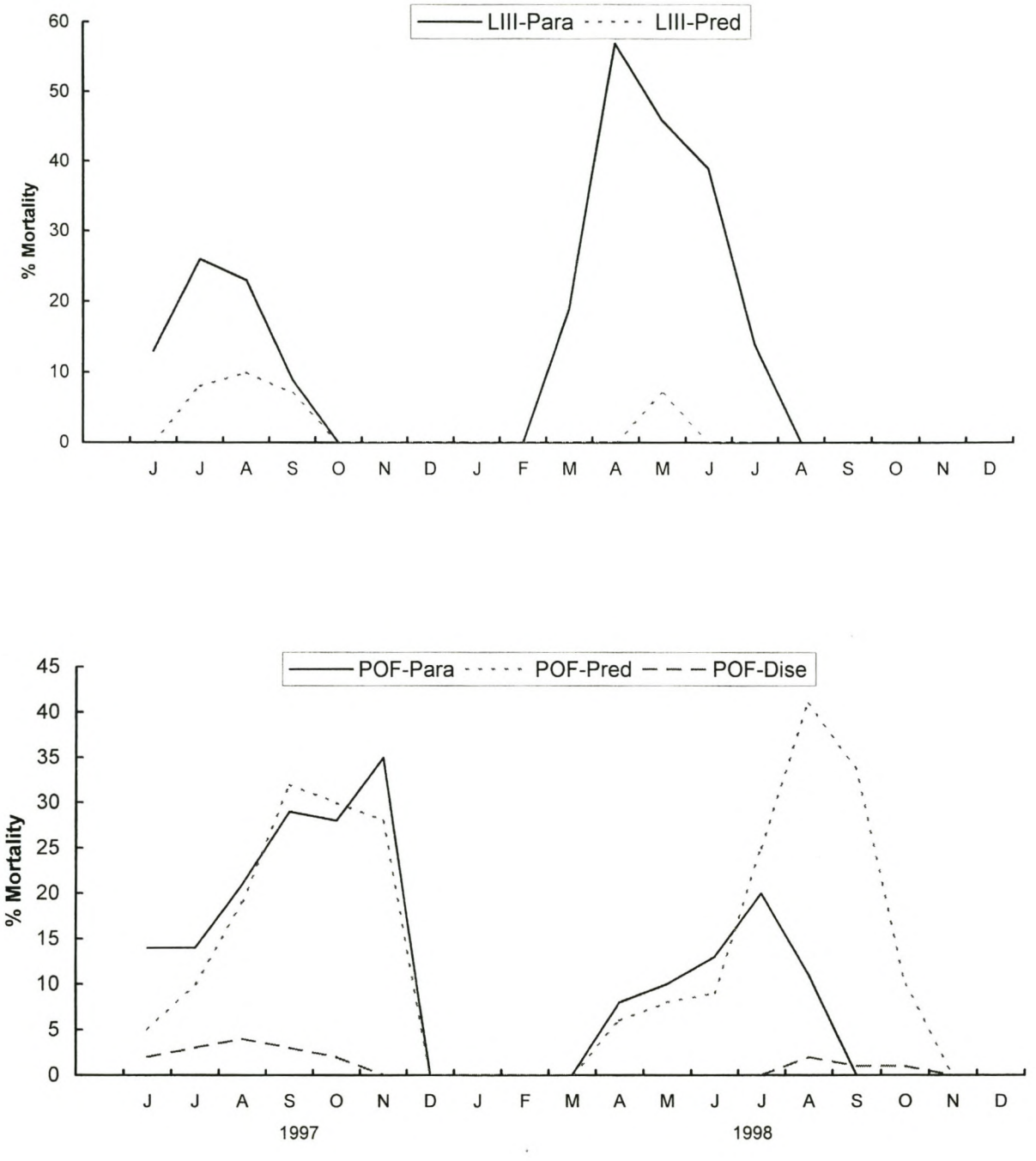

Figure 4. Percentage parasitism (Para), predation (Pred) and diseased (Dise) LIII and POF stages of *Ceroplastes destructor* infesting *Citrus reticulata* at Rustenburg Estate (June 1997 – December 1998).

Both LIII and POF were more or less equally susceptible to parasitism in all citrus orchards and on *S. malaccensis.* However, adult females were more susceptible to predation than LIII scales in all orchards and on *S. malaccensis* (Figs 2-6).

The monthly population curves for the three main primary parasitoids and all the secondary parasitoid species are presented in Fig. 7 a & b. *Aprostocetus ceroplastae* was the dominant species throughout the susceptible host stages whereas *A. nyasicus* and the other parasitoids seemed to be more active for only a limited period during the year. *Anicetus nyasicus* attacked mostly the adult stage rather than other developmental stages. On the contrary, both *Coccophagus* spp. and *Euxanthellus* sp. were active during the LIII and young adult host stages. *Marietta leopardina and M. connecta* were found as secondary parasitoids only at the third instar scale stage whereas *Cheiloneurus* sp. was active during the adult scale stage. *Apanteles* sp. was recorded from July to November of 1998 and 1999 as a parasitoid

Table. 3. Mean body length (mm) of male and female *Aprostocetus ceroplastae* reared from susceptible stages of *Ceroplastes destructor* during different times of the year. N = 15/sampling period; *Ac* = *A. ceroplastae.*

Scale stage	LIII				POF			
Ac Sex	M		F		M		F	
Time	Feb/Mar	Aug/Sept	Feb/Mar	Aug/Sept	Aug/Sept	Oct/Nov	Aug/Sept	Oct/Nov
Length	0.71	0.88	0.92	1.20	0.93	1.06	1.32	1.38
SE	0.03	0.02	0.02	0.03	0.03	0.02	0.03	0.04

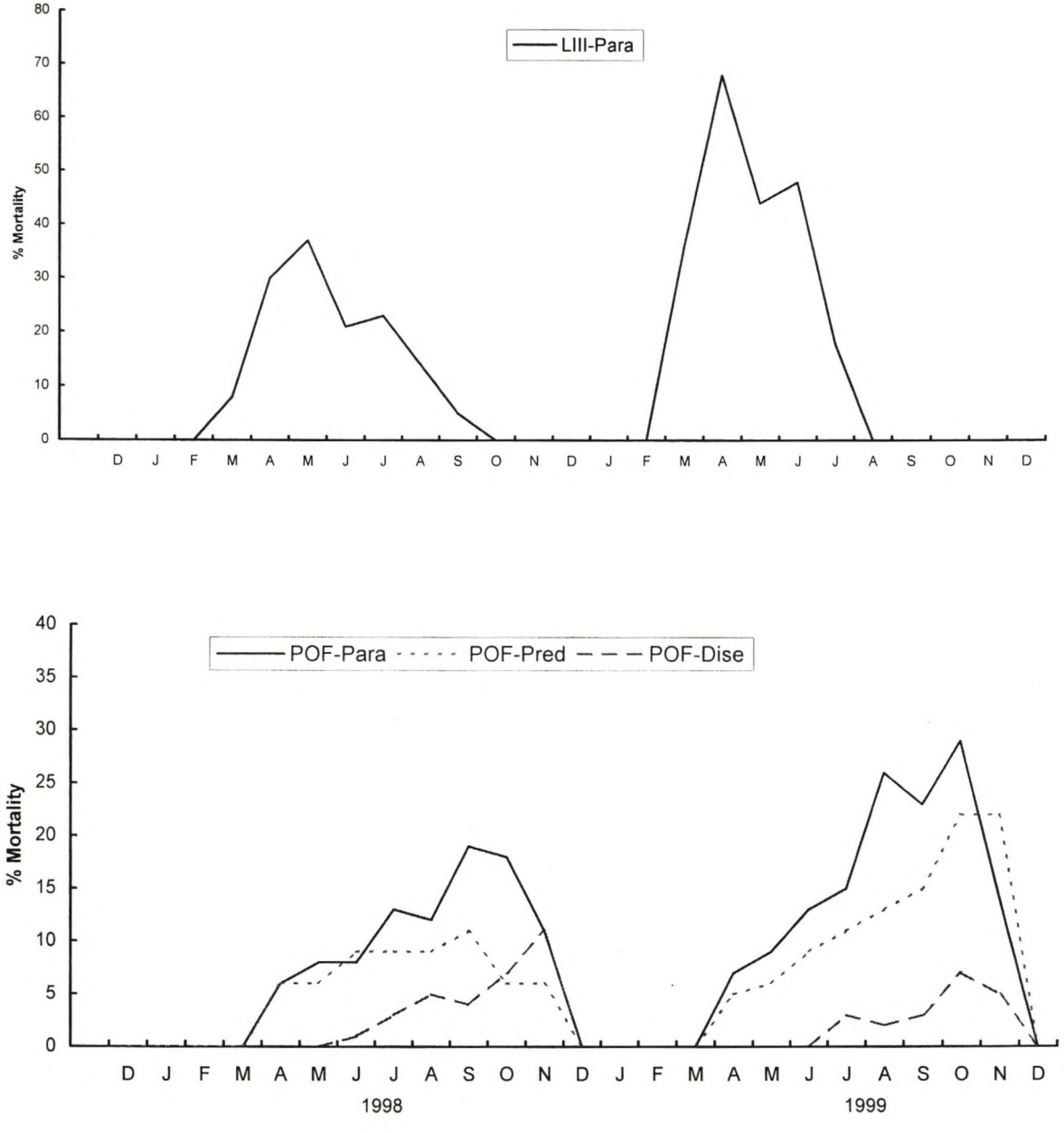

Figure 5 Percentage parasitism (Para), predation (Pred) and diseased (Dise) LIII and POF stages of *Ceroplastes destructor* infesting *Citrus reticulata* at WhiteHall Farming Trust (November 1997 – December 1999).

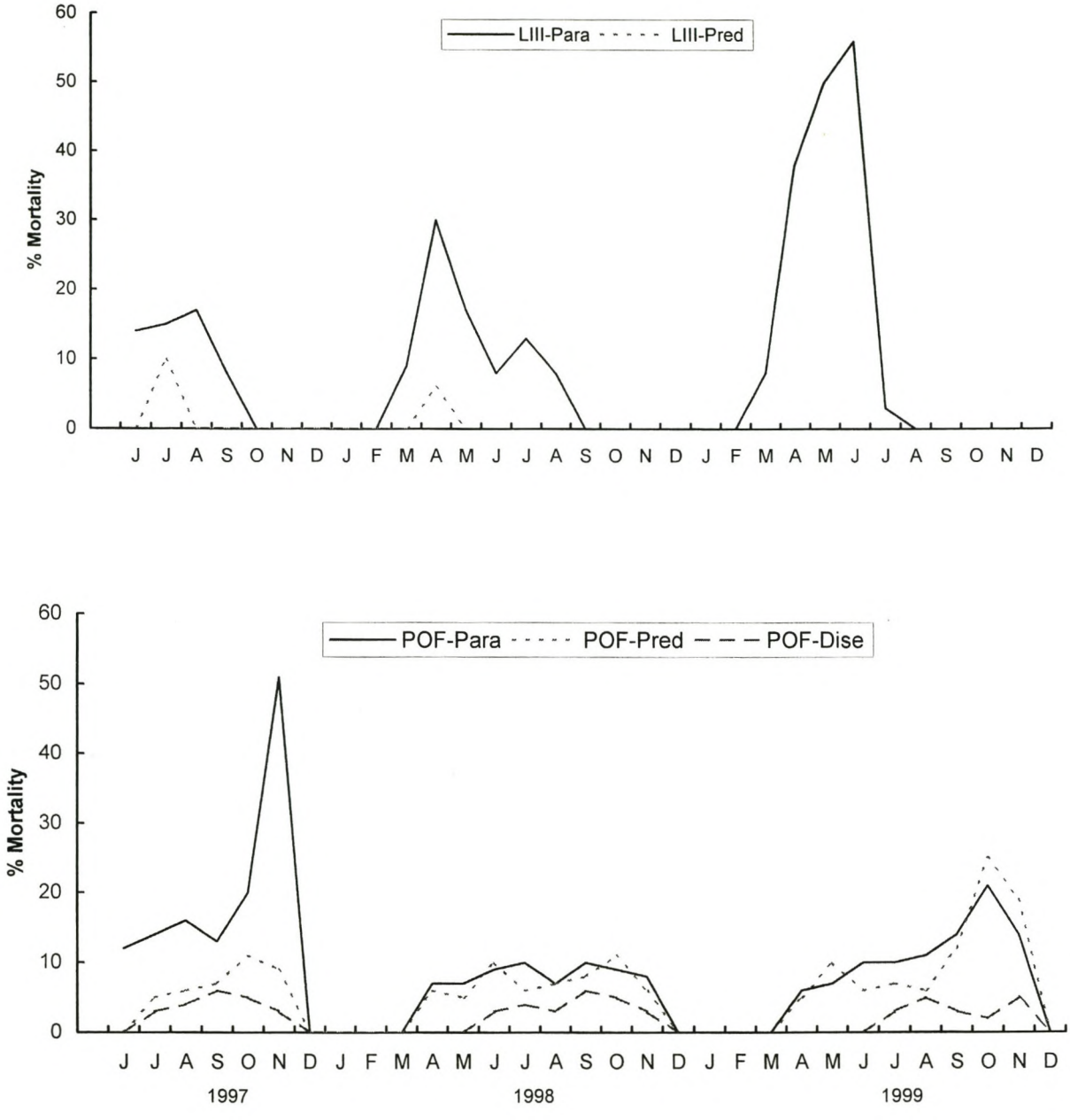

Figure 6. Percentage parasitism (Para), predation (Pred) and diseased (Dise) LIII and POF stages of *Ceroplastes destructor* infesting *Syzygium malaccensis* at Stellenbosch (June 1997 – December 1999).

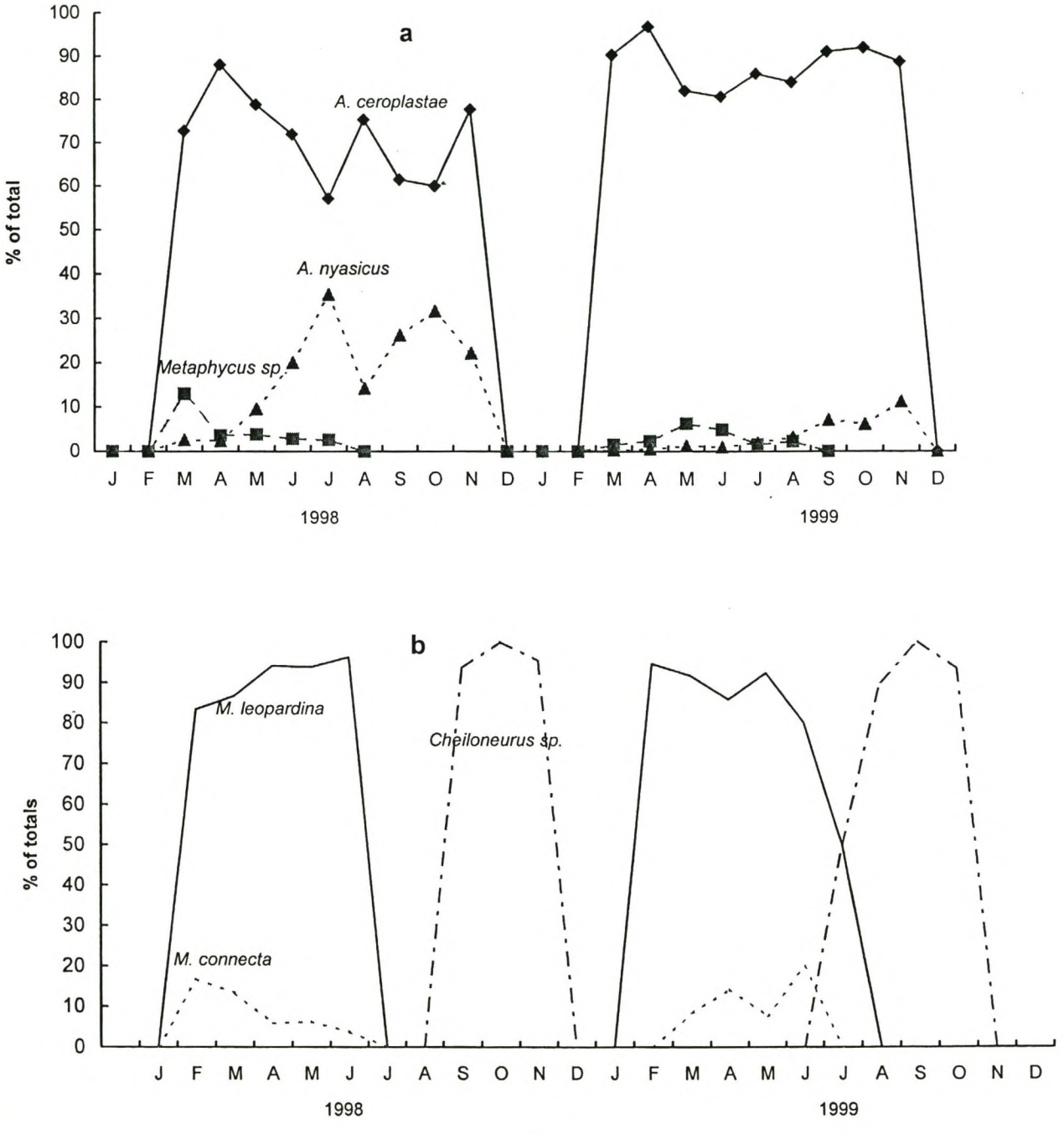

Figure 7. Temporal variations in abundance of three major primary parasitoids and all secondary parasitoids reared from *Ceroplastes destructor;* **a** = Primary parasitoids, **b** = Secondary parasitoids.

of *C. scitula* whereas *Elasmus* sp. was reared only in 1999 (June – October). The latter was probably a secondary parasitoid of *Apanteles* sp. (Prinsloo, personal communication). Only adult scales were prone to disease. No parasitism or predation was noted during the rosette (LI and LII) stages of *C. destructor*, i.e. December to February (see Fig. 7a & b).

The body length of *A. ceroplastae,* reared during different times of the year from the LIII and POF scale stages is presented in Table 3. It varied significantly between scale stages, parasitoid sexes and sampling periods (Table 4). The interaction between host stages and sampling period indicated that the differences in the size of the parasitoid reared from different host stages varied according to the time of the year. In addition, the interaction between host stages and parasitoid sex indicated that the difference in the size of the parasitoid reared from the two host stages was not the

Table 4. Analysis of variance computed on data presented in Table 3.

Factor	Df	MS	F	P-level
Host stage (HS)	1	1.7017	122.0628	0.0000
Parasitoid sex (PS)	1	2.9610	212.3937	0.0000
Sampling time (ST)	1	0.9594	68.8206	0.0000
HS X PS	1	0.0848	6.0828	0.0151
HS X ST	1	0.1421	10.1957	0.0018
PS X ST	1	0.0075	0.5395	0.4642
HS X PS X ST	1	0.0460	3.3011	0.0719
Error	112	0.0139	___	___

same for the two sexes. This is apparent from Table 3 in which the size of parasitoids reared from the same host stage during different times of the year varied. The Table also shows that the size of the parasitoids reared from the two host stages during different times of the year varied significantly.

The host stage also had a significant effect on the proportion of emergent male and female *A. ceroplastae*. The number of female *A. ceroplastae* reared from the early LIII scales was less than 25% of the total number of parasitoids reared from this stage. At the late LIII and POF scale stages, however, males and females of *A. ceroplastae* emerged in almost equal proportion.

4. DISCUSSION

The variation between generations in the number of parasitoids reared from both LIII and POF *C. destructor* from *C. reticulata* and *S. malaccensis* could probably be attributed to differences in orchard protection programmes during different years (see below). Of the eight primary parasitoids identified, *A. ceroplastae* was the dominant one, occurring throughout the months during which the percentage of active parasitization by the other parasitoids was low. *A. ceroplastae* is a solitary endoparasite of *C. destructor* during the third instar and adult stages. This species had also been identified as a dominant parasitoid of the Florida wax scale (*Ceroplastes floridenssis* Comstock) in Israel where it accounted for 90 to 100% of the primary parasitoids (Rosen, 1967; Ben-Dov, 1972; Agrov *et al.*, 1992). It has for long been noted as a primary parasitoid of *Ceroplastes* in the Mediterranean countries (Ben-Dov, 1972). Lo & Chapman (1998) reported *Euxanthellus philippiae* Silvestri as a dominant parasitoid of *C. destructor* in New Zealand. *Euxanthellus* sp. was not a major parasitoid of *C. destructor* in the current study, accounting for only 1.56% of

the primary parasitoids. Scales parasitized by *A. ceroplastae* appeared normal until about 10 days after parasitization when their body fluid turned brownish, followed by darkening of the venter as the parasitoid developed to the prepupal and pupal stages. Eventually parasitized scales turned black and brittle. The emerging adult wasp, measuring 1-2 mm long, chewed its way out for a free-living habit.

The predator species that contributed most to total generation mortality was the noctuid *C. scitula.* Cilliers (1967) has reported that *C. scitula* was a major predator of *Ceroplastes mimosae* Sign., *C. brevicauda* Hall and *C. destructor* while Agrov *et al.* (1992) found that the coccinellid *Chilocorous bipustulatis* (L.) was the major predator of *C. floridensis* in Israel. The latter was not observed during the present study. Disease was found to be unimportant as a mortality factor in this study. This differs from the finding of Lo & Chapman (1998), who reported that disease was a major mortality factor of *C. destructor* populations. This difference could probably be related to differences in climatic conditions, where the more humid and moist weather in New Zealand tends to favour prodigious growth of disease causing agents.

No parasitoid was reared from the second instar *C. destructor* during the current study, although Cilliers (1967) reported rearing parasitoids from the second instar of *C. mimosae* and *C. destructor*. Observations revealed that parasitization commenced only 3-4 weeks after emergence of the third instar and continued to the adult stage. Ben-Dov (1972) has also reared parasitoids only from the third instar and adult females of *C. floridensis* in Israel. According to Lo & Chapman (1998) parasitism of *C. destructor* was restricted to the third instar. This differs from the current results, where third instar *C. destructor* was almost as susceptible to parasitism as the adult females.

Peak numbers of parasitoids and predators were synchronized with peak numbers of hosts susceptible to parasitoids and predators, although a lag period of about one-month in appearance of parasitoids and predators was evident. Evidently, such a lag period signifies the lapse in some time between the events that lead to birth and appearance of a parasitoid or a predator as an active agent. The average scale mortality due to parasitism over the three generations ranged from 12-22% per month at the LIII stage and 19-29% at the POF stage for scales from *C. reticulata*. For scales from *S. malaccensis* the corresponding figure was 13-23% and 9-21% at the LIII and POF stages, respectively. The level of parasitism and predation found here was far greater than that reported by Lo & Chapman (1998). This variation is probably attributable to the larger diversity of parasitoid and predator species that are associated with the indigenous *C. destructor* in South Africa.

The variation in parasitism and predation obtained between orchards was probably due to differences in citricultural and/or pest control practices. Scale mortality due to parasitism, for instance, dwindled at RFF in 1998 probably because of drift of dimethoate and methidathion insecticides applied against red scale (*Aonidiella aurantii* (Maskell)) on citrus trees adjacent to the experimental trees. The proportion of scale mortality due to predation at RUS appeared rather high. Here the population density of *C. destructor* per sample unit was low compared to other orchards. The apparent high percent predation in this orchard was conceivably due to the high 'searching efficiency' of predators when the density of available hosts was low. Moreover, the population density of the Cape white-eye bird was generally higher at RUS than at the other study orchards and may have contributed more to this higher apparent predation. Nevertheless, the number of both parasitoids and predators generally increased with scale density during the season in all orchards, demonstrating

a density-dependent response to pest populations (see Chapter 5 for details). However, parasitism and predation appeared to be unstable over generations. Both fluctuated between scale generations, with predation being less variable. This apparent variation in parasitism and predation between generations indicated that the regulatory effects of parasitoids and predators might not be strong enough to provide long term suppression of scales under the current citricultural practices. For instance, although trees in the experimental rows were not sprayed throughout this study, the number of scales did not decline significantly. The fact that adjacent blocks had been receiving regular insecticide sprays might have contributed to the instability of the system by reducing the overall population of natural enemies in the orchards. Furthermore, even if spraying of an orchard with insecticides ceases, stability in a population of scale insects does not take place until some years after the cessation of spraying (e.g. DeBach & Huffaker, 1971). It is conceivable that the parasitoids can render a better regulatory effect if interference by frequent spraying of orchards with broad-spectrum insecticides is limited (see Chapter 8 for effects of insecticides on *A. ceroplastae*).

There appeared to be a relationship between the size of the host and the sex of the parasitoid *A. ceroplastae*. The majority (> 75 %) of the emergent *A. ceroplastae* from the smaller early third instar scale was males. Ben-Dov (1972) reared only male A. *ceroplastae* from third instar *C. floridensis*. This could be because *C. floridensis,* being a bivoltine species, is smaller in body size than *C. destructor,* which is univoltine in the Western Cape (Wakgari & Giliomee, 1998). Moreover, both male and female *A. ceroplastae* reared from the early third instar scales were significantly smaller in body size than their counterparts reared from adult scales. The emergence of only a few, small-sized female *A. ceroplastae* from early third instar nymphs makes this stage of *C. destructor* unsuitable for a large scale rearing of *A. ceroplastae.*

However, the late third instar and young adult would be ideal stages because a comparable proportion of both male and female *A. ceroplastae* emerged from these stages.

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CHAPTER 5

POPULATION DYNAMICS OF THE WHITE WAX SCALE, *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE), ON CITRUS.

ABSTRACT

The population dynamics of the white wax scale, *Ceroplastes destructor* Newstead, was studied in four easy-peel citrus orchards in the Western Cape Province of South Africa for three consecutive years (1997 – 1999). *Ceroplastes destructor* has one generation per annum in South Africa with no generation overlap but with a considerable overlap of phenological stages. No differences in time of occurrence of phenological stages were found between generations, although key mortality factors varied slightly between two of the orchards. Key stage mortality determined from a cohort life table was generally in the third instar (LIII) and pre-ovipositional (POF) stages. A significant density-dependent mortality factor was demonstrated during the first instar (LI) and POF stages.

1. INTRODUCTION

The white wax scale, *Ceroplastes destructor* Newstead, is an endemic and univoltine species with three nymphal instars and an adult female that colonizes various trees, shrubs, ornamentals and citrus in Southern Africa. Although this species has only

been regarded as a potential pest of citrus and deciduous orchards in the past, its population density in certain orchards, particularly on *Citrus reticulata* (Blanco) in the Western Cape Province of South Africa has reached very high levels since 1993/94 (Wakgari & Giliomee, 1998). There is no empirical information on the population dynamics of *C. destructor* and the environmental factors responsible for the variation in its population density.

The variation in population density from generation to generation provides the frame of reference against which the roles of various mortality factors can be analyzed (Southwood, 1978). A number of interacting intrinsic and extrinsic factors inherent in natural and agro-ecosystems govern this variation. Population density and structure are the outcome of four interacting primary processes: natality, mortality, immigration and emigration (Krebs, 1978). DeBach & Smith (1947) argued that population changes are associated with host nutrition, weather, competition, inherent changes in fecundity, incidence of disease, parasites and predators. Of the primary processes, mortality operates continuously in insect generation development whereas natality and dispersal occur over a relatively short periods of time. For instance, natality and dispersal occur once a year, during November/December for *C. destructor* in the Western Cape (Wakgari & Giliomee, 1998; 2000). Changes in population density are therefore often interpreted in terms of changes in mortality during particular stages of the life cycle (Podoler & Rogers, 1975).

Understanding the population structure and dynamics of any pest species and the underlying biological and/or physical reasons for the population fluctuations are important prerequisites for devising a sound and cost effective management plan. The construction and analysis of life tables have been recognized for long as a suitable method for studying the population dynamics of insects with discrete generations (e.g.

Schneider *et al.*, 1987). The life table is a summary of survival, in terms of the number of individuals surviving to a given age x (l_x) or time t (l_t) from an initial number at age zero (l_0) or time zero (t_0). However, the methods for construction and analysis of biologically meaningful field life tables have been a subject of intense debate in the past.

In this study the population dynamics of *C. destructor* was investigated to provide information on the extent of temporal variations in population density and to determine the biological processes causing changes, so that these processes could be taken into account in developing descriptive models and control strategies. The relative contribution of each mortality factor (k_i) to the total generation mortality (K) and to changes in population densities was determined through analysis of key factors, a concept introduced by Morris (1959) as a useful tool to quantify population processes. Key factors enable us to make predictions about future population trends or the response of populations to changes in mortality factors (Southwood, 1978). Regular field observations of the same sample units from permanent census trees for three consecutive generations (1997-1999) provided a good estimate of changes in population density and the biological processes responsible for the changes. Varley & Gradwell (1970) aptly argue the importance of sampling the same sample universe in population studies for construction and analyses of biologically meaningful life tables.

2. MATERIALS AND METHODS

2.1. Study orchards

Field sampling was carried out in four commercial easy-peel citrus (*C. reticulata*) orchards in the Western Cape Province of South Africa. Two were near

Stellenbosch (34°S 19°E), 230 meters above sea level. These were the Welgevallen Experimental Farm (WEF) and Rustenburg Estate (RUS). The third was at Rhodes Fruit Farms (RFF) (33°54'S 18°57'E) in Drakenstein, about 362 meters above sea level, and the fourth was at WhiteHall Farming Trust (WFT) (34°14'S 19°06'E) in the Grabouw region, about 340 meters above sea level. No insecticides were applied to the trees in the experimental blocks throughout the study period.

Scale developmental stages were designated as follows (see Wakgari & Giliomee, 1998):

E-C = Egg-Crawler (combined because the proportion of infertile eggs was negligible, as almost all the eggs that were laid hatched); **LI** = First instar nymph (settled crawlers); **LII** = Second instar female; **LIII** = Third instar female; **POF** = Preovipositing female (includes young and mature adult female); **OF** = Ovipositing female.

2.2. Life tables

Life tables for *C. destructor* from the four citrus orchards were constructed in the form of age-specific or cohort survivorship (l_x). *Ceroplastes destructor* is uniparental and hence the sex ratio was not considered in the analyses of life tables. Twenty trees were randomly marked as permanent census trees from each of the orchards and regularly assessed thereafter. From each tree, two twigs of 20 cm long and about 3-5 mm in diameter, each bearing at least 10 leaves, were selected from the middle canopy (*ca.* 1.5m high), giving a total of 40 sample units per orchard. A population census was carried out on these twigs (permanent sample units) at monthly intervals until the end of each generation. The census was conducted for three generations at WEF and RFF and for two generations at RUS and WFT.

The initial egg population was calculated by multiplying the number of ovipositing females in the parental generation from sample units by the average number of eggs per female and their size index. Female fecundity was determined in the laboratory from females randomly sampled from the field. Females from the sample units that had completed oviposition were taken to the laboratory to determine their body sizes (length, width, height).

One of the major difficulties in the study of population dynamics of insects with overlapping stage intervals is the estimation of the actual number of insects in a particular stage during subsequent sampling occasions. However, this was not a problem in the current study because, with continuous observation of the same sample units during subsequent assessments, the exact number of scales (live or dead) in each sample unit was known. The number of individuals that progressed from one stage to the next and those that died of various mortality factors was recorded. These were integrated at the end of that stage to give the total population that passed through the stage. Although sampling precision of 0.10 is a commonly used predetermined level for construction of life tables (Southwood, 1978), the subsequent censoring of the same sample units during a given scale generation allowed a more reliable estimate of changes in density. In determining the total population for different stage categories, survival rate was assumed constant over time for each age group.

External appearance is often a poor indicator of whether an insect is alive or dead with sessile insects like *C. destructor*. In particular, it was not possible to determine mortality due to parasitism by mere visual observations as visible changes in external appearance of parasitized females are detected only at the later developmental stages of the parasitoids. Therefore, actual age-specific mortalities

were determined by sampling scale-infested twigs from trees adjacent to the permanent census trees. These trees were presumed to have a similar infestation level as the latter. The samples were studied under a stereomicroscope in the laboratory. Random distribution of parasitoids in orchards was assumed such that every scale-infested tree had an equal chance of being subjected to parasitism.

Mortality due to parasitism could be cumulative over time within a generation because of an extended period of susceptible host stages. This may lead to an overestimation of the actual percent parasitism particularly if all parasitoid exit holes are counted during subsequent sampling occasions. On the other hand, if exit holes are ignored as indicators of parasitism and only live or dead parasitoids upon dissection of scales are considered as an index of parasitism, the rate of parasitism would be underestimated since some parasitoids may escape during the interval between two sampling dates. Therefore, the difference between number of live scales at two successive sampling dates (t and t') was used to determine the actual number that died due to different mortality factors during that time interval, i.e.

$$M_i = N_t - N_{t'}, \quad t > t'$$

where M_i is the number of individuals that died during the interval between t and t', N_t is the number of individuals alive at t; and $N_{t'}$ is the number of individuals alive at t'. M_i was then partitioned among the different mortality factors determined from samples brought to the laboratory. This proportion was used to estimate the number of scales that died during that sampling period. Proportions were then summed to give the total number that died of various factors for a given age interval. The percentage parasitism and diseased scales was determined by dissecting about 250 scales of susceptible stages (LIII, young and mature POF) under a stereomicroscope at every sampling occasion. Percentage predation was determined by a direct count of scale

remains, remains of the white marks of the spiracular bands and scale covers with chewed edges or ragged holes in them. Since most parasitoids acted concurrently, it was difficult to determine the specific parasitoid species responsible for scale mortality. Therefore, mortality due to all parasitoids was lumped together for each scale generation. Mortality due to predation was also lumped together in a similar manner.

All other mortality factors in the life tables were obtained from direct observations or dissections in the laboratory (see above), except for 'dispersal' of crawlers and the 'unknown' factors for all stages. The figure for dispersal of crawlers was derived from the difference between the number of LI and the number of E-C that died of all other mortality factors summed and subtracted from the initial total number of eggs. Mortality due to the 'unkown' factors was calculated from the difference between the number entering the next age interval and the number unaccounted for when all mortality factors were summed and subtracted from the number entering the previous age interval, as described by Nebeker (1977). The 'miscellaneous factors' represented the unexplained deaths when scales were found on sample units but the cause of death could not be determined.

2.3. Key-factor analysis and density-dependent mortality

A key factor is one that has useful predictive value (Morris, 1959) or the factor that contributes the most to changes in numbers between generations (Varley & Gradwell, 1960) or the factor that causes population change (Manly, 1977). The following four methods were used to identify key factors in two orchards for which data for three generations were available: visual inspection of k_i (= mortality due to the individual (i) mortality factors) values in relation to K (= generation mortality)

over successive generations (Varley *et al.*, 1973); the largest regression coefficient for the relationship of k_i on K (Podoler & Rogers, 1975); the largest correlation coefficient between k_i and K (Harcourt, 1971); and a significant regression coefficient for the relationship of K on k_i (Metcalfe, 1972). The 'killing power' of an individual mortality factor (k_i) was calculated as

$$k_i = \log N_{ij} - \log N_{ij+1},$$

where N_{ij} is the number of individuals of the j^{th} stage alive before the mortality factor acts, and N_{ij+1} is the number of individuals of the j^{th} stage surviving the mortality factor. The total generation mortality is the sum of mortalities due to all individual factors within a given generation,

$$K = \sum_{i=1}^{n} ki$$

Five mortality factors were identified, k_1 = Parasitoids; k_2 = Predators; k_3 = Dispersal; k_4 = Unknown; k_5 = Miscellaneous.

A mortality factor, *sensu* Luck (1971), is deemed density-dependent when the regression coefficient, b, for the relationship between k_i and the population density on which it acts is significantly greater than 0. Varley & Gradwell (1968) developed a 'proof of density dependence' which was tested by Luck (1971). It involves two regressions, the initial log density of insects on which k acts against the log density of survivors and *vice versa*. When both lines, plotted on a single graph through a single set of points, lie on the same side of a line which passes through the mean value of x and y with b = 1.0, and have slopes which differ significantly from b = 1.0, the factor is said to be proved density-dependent.

The abbreviated column headings for the life tables are,

x	age of cohort
d_x	number dying in age interval x

l_x	number alive at beginning of age interval x
d_xF	mortality factor/s
$100d_xl_x^{-1}$	percentage mortality, or d_x as a percentage of l_x
k	$\log_{10}N_{ij} - \log_{10} N_{ij+1}$ or 'killing power' of d_xF
S_x	Survival rate within x.

3. RESULTS

3.1. Life tables

Life tables for the inter-generation changes of *C. destructor* are presented in Tables 1-4 for each of the study orchards. Although a large number of scales died at the E-C to LII stage categories, the survival rate was nevertheless usually higher at these stages than at the LIII and POF stages. In other words, a greater proportion of scales died during LIII and POF stages than during the earlier immature stages. This is also apparent from the high *k*-values at the LIII and POF stages shown in Tables 1-4 and also from the survival curves illustrated in Fig. 1, in which survival rate declined sharply in the LIII-POF stage categories. However, irregularities in survival rates were observed between the same stages from different orchards. Survival rates of the LI and LII stages at RFF in 1998 were lower than the 1997 and 1999 generations in this and other orchards, apparently because of drift of insecticides (methidathion and dimethoate) sprayed on trees adjacent to the experimental trees in December 1997 that caused heavy mortality of the early developmental stages (Fig. 1, RFF). The effect of insecticide drift at RFF was also apparent from the reduction in parasitism of the LIII and POF stages during 1998 at this site compared to the other experimental orchards.

Table 1. Abbreviated life tables for *Ceroplastes destructor,* infesting easy-peel citrus (*Citrus reticulata*) at Welgevallen Experimental Farm.

1997

x	$l_x^{\dagger}$	d_xF	d_x	$100d_xl_x^{-1}$	k	S_x
E-C	71340	Infertility	2197	3.08	0.014	
		Dispersion	22770	31.92	0.173	
		Miscellaneous	20222	28.35	0.249	
		Total	45189	63.35	0.436	0.3665
LI	26151	Miscellaneous	6861	3.08	0.132	
		Unknown	5119	19.58	0.134	
		Total	11980	45.81	0.266	0.5419
LII	14171	Miscellaneous	3342	23.59	0.117	
		Unknown	5047	35.61	0.273	
		Total	8389	59.20	0.390	0.4080
LIII	5782	Parasitoids	1843	31.87	0.325	
		Predators	941	16.27	0.104	
		Miscellaneous	979	16.93	0.087	
		Unknown	367	6.35	0.028	
		Total	4130	71.42	0.544	0.2858
POF	1652	Parasitoids	876	53.03	0.963	
		Predators	478	28.93	0.172	
		Disease	16	0.97	0.004	
		Miscellaneous	152	9.20	0.043	
		Unknown	23	1.39	0.006	
		Total	1545	93.52	1.188	0.0648
OF	107	–	–	–		1.0000

Generation mortality = 99.85%.
† denotes census per 40 sampling units from 20 trees per orchard (see text for detail).

During the LIII and POF stages, parasitoids contributed more to total generation mortality (K) than any other mortality factors. However, predators were more important than parasitoids at RUS during the POF stage (Table 3).

3.2. Key-factor analysis

The correlation coefficients for the relationships between stage specific mortality (k) and total generation mortality (K) presented in Table 5 indicate that the two are significantly positively correlated during the LIII scale stage at WEF and

Table 1. Continued

1998

x	$l_x^{\dagger}$	d_xF	d_x	$100d_xl_x^{-1}$	k	S_x
E-C	96063	Infertility	2065	2.15	0.010	
		Dispersion	32524	33.86	0.184	
		Miscellaneous	27452	28.58	0.257	
		Total	62041	64.59	0.451	0.4541
LI	34022	Miscellaneous	7934	23.31	0.115	
		Unknown	8525	25.06	0.172	
		Total	16459	48.37	0.287	0.5163
LII	17563	Miscellaneous	5160	29.38	0.151	
		Unknown	6887	39.22	0.352	
		Total	12047	68.60	0.503	0.3140
LIII	5516	Parasitoids	2097	38.02	0.464	
		Predators	861	15.61	0.104	
		Miscellaneous	845	15.32	0.082	
		Unknown	617	11.80	0.052	
		Total	4420	80.13	0.702	0.1987
POF	1096	Parasitoids	608	55.47	1.200	
		Predators	356	32.48	0.190	
		Disease	6	0.56	0.003	
		Miscellaneous	53	4.83	0.022	
		Unknown	32	2.92	0.013	
		Total	1055	96.26	1.428	0.0374
OF	41	–	–	–		1.0000

Generation mortality = 99.95%.

1999

E-C	28413	Infertility	203	0.71	0.003	
		Dispersion	12480	43.92	0.254	
		Miscellaneous	5734	20.18	0.197	
		Total	18417	64.81	0.454	0.3519
LI	9996	Miscellaneous	4118	41.20	0.231	
		Unknown	3655	36.56	0.206	
		Total	7773	77.76	0.437	0.2224
LII	2223	Miscellaneous	646	29.06	0.149	
		Unknown	1241	55.83	0.671	
		Total	1887	84.89	0.820	0.1511
LIII	336	Parasitoids	109	32.44	0.276	
		Predators	11	3.27	0.020	
		Miscellaneous	77	22.92	0.120	
		Unknown	16	4.76	0.021	
		Total	213	63.39	0.437	0.2861
POF	123	Parasitoids	73	59.35	0.793	
		Predators	19	15.44	0.086	
		Disease	11	9.00	0.043	
		Miscellaneous	6	5.31	0.022	
		Total	109	89.10	0.944	0.1090
OF	14	–	–	–		1.0000

Generation mortality = 99.95%

† denotes census per 40 sampling units from 20 trees per orchard (see text for detail).

Table 2. Abbreviated life tables for *Ceroplastes destructor,* infesting easy-peel citrus (*Citrus reticulata)* at Rhodes Fruit Farms.

1997

x	$l_x^{\dagger}$	d_xF	d_x	$100d_xl_x^{-1}$	k	S_x
E-C	127437	Infertility	4741	3.72	0.017	
		Dispersion	33631	26.39	0.139	
		Miscellaneous	27450	21.54	0.160	
		Total	65822	51.65	0.316	0.4835
LI	61615	Miscellaneous	23303	37.82	0.206	
		Unknown	23646	38.38	0.417	
		Total	46949	76.20	0.623	0.2380
LII	14666	Miscellaneous	3447	23.50	0.116	
		Unknown	6658	45.40	0.391	
		Total	10105	68.90	0.507	0.3110
LIII	4561	Parasitoids	1811	39.71	0.386	
		Predators	947	20.76	0.117	
		Miscellaneous	389	8.53	0.040	
		Unknown	147	3.22	0.014	
		Total	3294	72.22	0.557	0.2778
POF	1267	Parasitoids	600	47.36	0.490	
		Predators	129	10.18	0.059	
		Disease	24	1.90	0.011	
		Miscellaneous	199	15.03	0.076	
		Unknown	28	2.21	0.010	
		Total	980	77.36	0.646	0.2264
OF	287	–	–	–		1.0000

Generation mortality = 99.77%

1998

E-C	143606	Infertility	3368	2.34	0.011	
		Dispersion	54378	37.87	0.213	
		Miscellaneous	42663	29.71	0.298	
		Total	100409	69.92	0.522	0.3008
LI	43197	Miscellaneous	10588	24.51	0.122	
		Unknown*	31132	72.07*	1.344	
		Total	41720	96.58	1.466	0.0342
LII	1477	Miscellaneous	217	14.70	0.069	
		Unknown	863	58.42	0.502	
		Total	1080	73.12*	0.571	0.2688
LIII	397	Parasitoids	74	18.64	0.098	
		Predators	3	0.76	0.004	
		Miscellaneous	19	4.80	0.022	
		Unknown	8	2.00	0.009	
		Total	104	26.20	0.133	0.7380
POF	293	Parasitoids	12	4.10	0.031	
		Predators	32	10.92	0.073	
		Miscellaneous	67	22.87	0.121	
		Unknown	18	6.14	0.028	
		Total	129	44.03	0.253	0.5597
OF	164	–	–	–		1.0000

Generation mortality = 99.88%

*Insecticide drift caused heavy mortality.

Table 2. Continued

1999

x	$l_x^{\dagger}$	d_xF	d_x	$100d_xl_x^{-1}$	k	S_x
E-C	162511	Infertility	3413	2.10	0.009	
		Dispersion	67718	41.67	0.241	
		Miscellaneous	54554	33.57	0.395	
		Total	125685	77.34	0.645	0.2266
LI	36826	Miscellaneous	6483	17.48	0.084	
		Unknown	10432	28.33	0.183	
		Total	16915	45.81	0.267	0.5419
LII	19911	Miscellaneous	4814	24.18	0.120	
		Unknown	13206	66.33	0.902	
		Total	18020	90.51	1.022	0.0949
LIII	1891	Parasitoids	156	8.25	0.398	
		Predators	7	0.37	0.012	
		Miscellaneous	863	45.64	0.627	
		Unknown	761	40.24	0.224	
		Total	1787	94.50	1.261	0.0550
POF	104	Parasitoids	23	22.12	0.186	
		Predators	32	30.77	0.172	
		Disease	3	2.88	0.013	
		Miscellaneous	1	1.00	0.004	
		Unknown	2	1.92	0.008	
		Total	61	58.69	0.383	0.4131
OF	43	–	–	–		1.0000

Generation mortality = 99.97%
† see Table 1.

during the E-C, LII and LIII stages at RFF.

Changes in submortalities (k_i) and generation mortalities (K) for two of the study orchards (WEF and RFF) are presented in Fig. 2. Inspection of changes in submortalities shown in these graphs indicated that the values for k_1 and k_2 at WEF and for k_5 at RFF changed in the same way as the changes in the total generation mortality (K) with time (Fig. 2). In other words, both k_1 and k_2 at WEF and k_5 at RFF were key factors. Tests for the highest regression coefficients and the highest correlation coefficients for the relationship of k_i on K and for the significant regression

Table 3. Abbreviated life tables for *Ceroplastes destructor,* infesting easy-peel citrus (*Citrus reticulata*) at Rustenburg Estate.

1997

x	$l_x^{\dagger}$	d_xF	d_x	$100d_xl_x^{-1}$	k	S_x
E-C	36018	Infertility	1116	3.10	0.014	
		Dispersion	9107	25.28	0.131	
		Miscellaneous	6544	18.17	0.127	
		Total	16767	46.55	0.272	0 5345
LI	19251	Miscellaneous	6475	33.64	0.178	
		Unknown	7701	40.00	0.401	
		Total	14176	73.64	0.579	0.2636
LII	5075	Miscellaneous	921	18.15	0.087	
		Unknown	747	14.72	0.086	
		Total	1668	32.87	0.173	0.6713
LIII	3407	Parasitoids	1834	53.83	0.889	
		Predators	152	4.46	0.029	
		Miscellaneous	616	18.08	0.100	
		Unknown	418	14.12	0.057	
		Total	3020	90.49	1.075	0.0951
POF	387	Parasitoids	141	36.43	0.733	
		Predators	188	48.58	0.340	
		Disease	8	2.07	0.010	
		Miscellaneous	13	4.00	0.015	
		Unknown	5	1.30	0.006	
		Total	355	91.78	1.104	0.0822
OF	32	–	–	–		1.0000

Generation mortality = 99.91%

1998

E-C	21896	Infertility	823	3.76	0.017	
		Dispersion	6225	28.43	0.152	
		Miscellaneous	4008	18.30	0.137	
		Total	11056	50.49	0.306	0.4951
LI	10840	Miscellaneous	3576	33.00	0.174	
		Unknown	4918	45.37	0.491	
		Total	8494	78.37	0.665	0.2163
LII	2346	Miscellaneous	249	10.61	0.049	
		Unknown	497	21.19	0.117	
		Total	746	31.80	0.166	0.6820
LIII	1600	Parasitoids	942	58.87	0.905	
		Predators	18	1.13	0.007	
		Miscellaneous	337	21.06	0.117	
		Unknown	169	10.56	0.048	
		Total	1466	91.62	1.077	0.0838
POF	134	Parasitoids	52	38.81	0.242	
		Predators	66	49.25	1.243	
		Miscellaneous	12	8.95	0.041	
		Total	130	97.01	1.526	0.0299
OF	4	–	–	–		1.0000

Generation mortality = 99.98%

† see Table 1.

Table 4. Abbreviated life tables for *Ceroplastes destructor,* infesting easy-peel citrus (*Citrus reticulata*) at WhiteHall Farming Trust.

1998

x	$l_x^{\dagger}$	d_xF	d_x	$100d_xl_x^{-1}$	k	S_x
E-C	8394	Infertility	103	1.22	0.006	
		Dispersion	3624	43.17	0.250	
		Miscellaneous	1716	20.44	0.199	
		Total	5443	64.83	0.455	0.3517
LI	2951	Miscellaneous	860	29.14	0.150	
		Unknown	443	15.02	0.103	
		Total	1303	44.16	0.253	0.5584
LII	1648	Miscellaneous	87	5.28	0.024	
		Unknown	525	31.86	0.178	
		Total	612	37.14	0.202	0.6286
LII	1036	Parasitoids	584	56.37	0.507	
		Predators	14	1.35	0.007	
		Miscellaneous	161	15.54	0.074	
		Unknown	13	1.25	0.006	
		Total	772	74.51	0.594	0.2549
POF	264	Parasitoids	80	30.30	0.281	
		Predators	90	34.10	0.186	
		Miscellaneous	6	2.30	0.010	
		Total	176	66.70	0.577	0.3330
OF	88	–	–	–		1.0000

Generation mortality = 98.95%

1999

E-C	36738	Infertility	456	1.24	0.005	
		Dispersion	15735	42.83	0.247	
		Miscellaneous	6743	18.35	0.173	
		Total	22934	62.42	0.425	0.3758
LI	13804	Miscellaneous	6542	47.39	0.279	
		Unknown	3528	25.56	0.289	
		Total	10070	72.95	0.568	0.2705
LII	3734	Miscellaneous	501	13.42	0.063	
		Unknown	653	27.49	0.098	
		Total	1154	40.91	0.161	0.5909
LIII	2580	Parasitoids	1067	41.36	0.479	
		Predators	27	1.05	0.007	
		Miscellaneous	572	22.17	0.131	
		Unknown	384	14.88	0.070	
		Total	2050	79.45	0.687	0.2055
POF	530	Parasitoids	181	34.15	0.383	
		Predators	89	16.79	0.110	
		Disease	27	5.10	0.029	
		Miscellaneous	84	15.85	0.078	
		Unknown	21	3.96	0.018	
		Total	402	75.85	0.618	0.2415
OF	128	–	–	–		1.0000

Generation mortality = 99.65%

† see Table 1

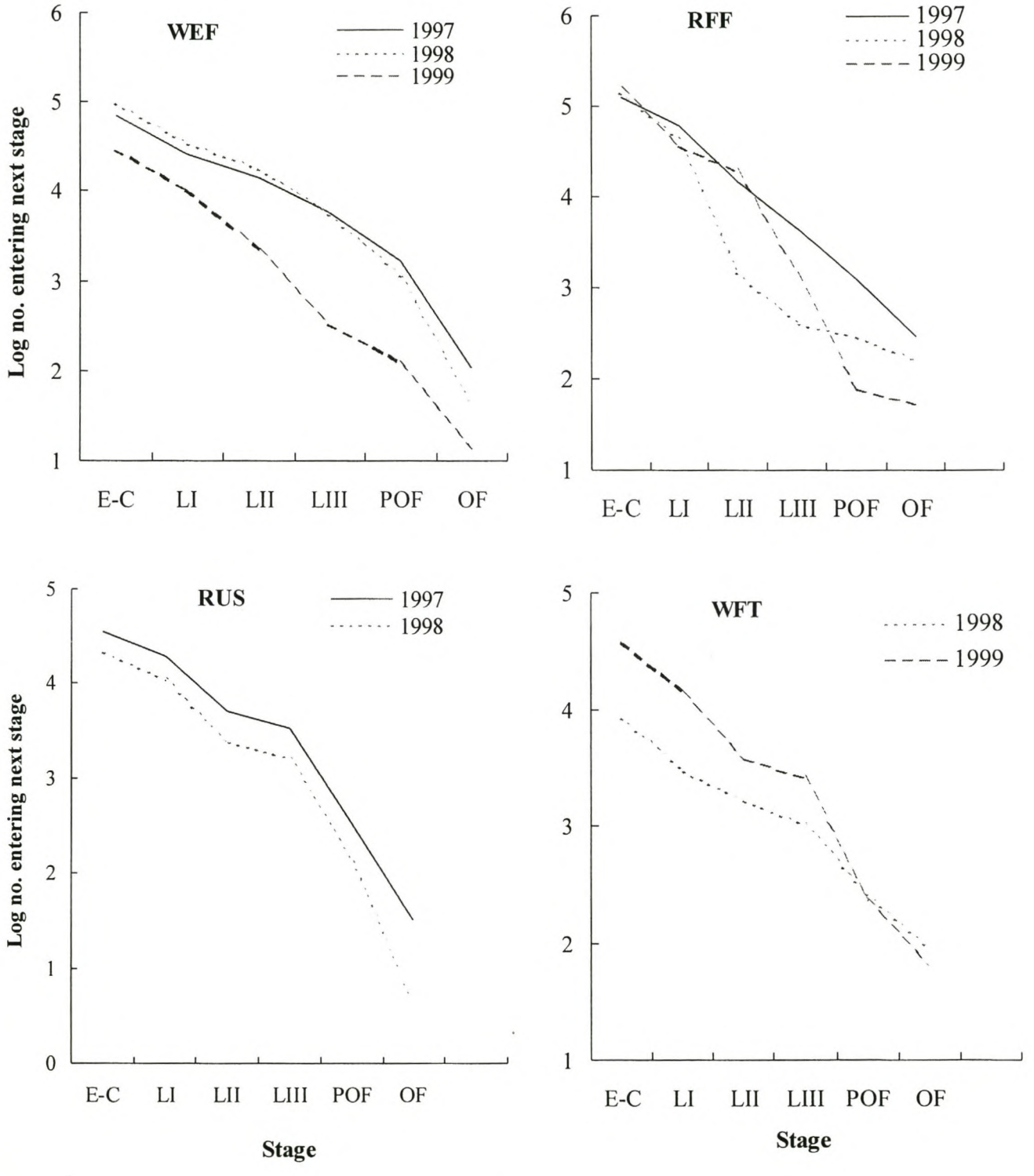

Figure 1. Survival curves for *Ceroplastes destructor* population at four citrus orchards: **WEF** (Welgevallen Experimental Farm), **RFF** (Rhodes Fruit Farms), **RUS** (Rustenburg Estate) and **WFT** (WhiteHall Farming Trust).

coefficients for the relationship of K on k_i are presented in Table 6. Key factors determined by these methods were generally consistent with the results obtained by the graphic method.

Table 5. Correlation coefficients (r) for the relationship of stage mortalities (k) on total generation mortality (K).

	Orchard	
Stage of cohort	**WEF**	**RFF**
E-C	0.666	0.896*
LI	-0.049	-0.289
LII	0.094	0.995*
LIII	0.834*	0.843*
POF	0.629	-0.390

* significant correlation ($P < 0.05$).

3.3. Analysis of density-dependent mortality

At WEF only k_1, acting on POF scales, resulted in a slope significantly greater than 0 ($P < 0.01$) (Fig. 3a). Some of the regression coefficients obtained for the other mortality factors at all scale stages were negative, indicating an inverse density-dependence, and some yielded positive slopes of less than 0.05. At RFF, the slopes for k_5 at the LI stage, k_3 at the E-C stage and k_1 at the POF stage were found to be significantly greater than 0 ($P < 0.01$), implying density-dependent mortality (Figs 3b-d).

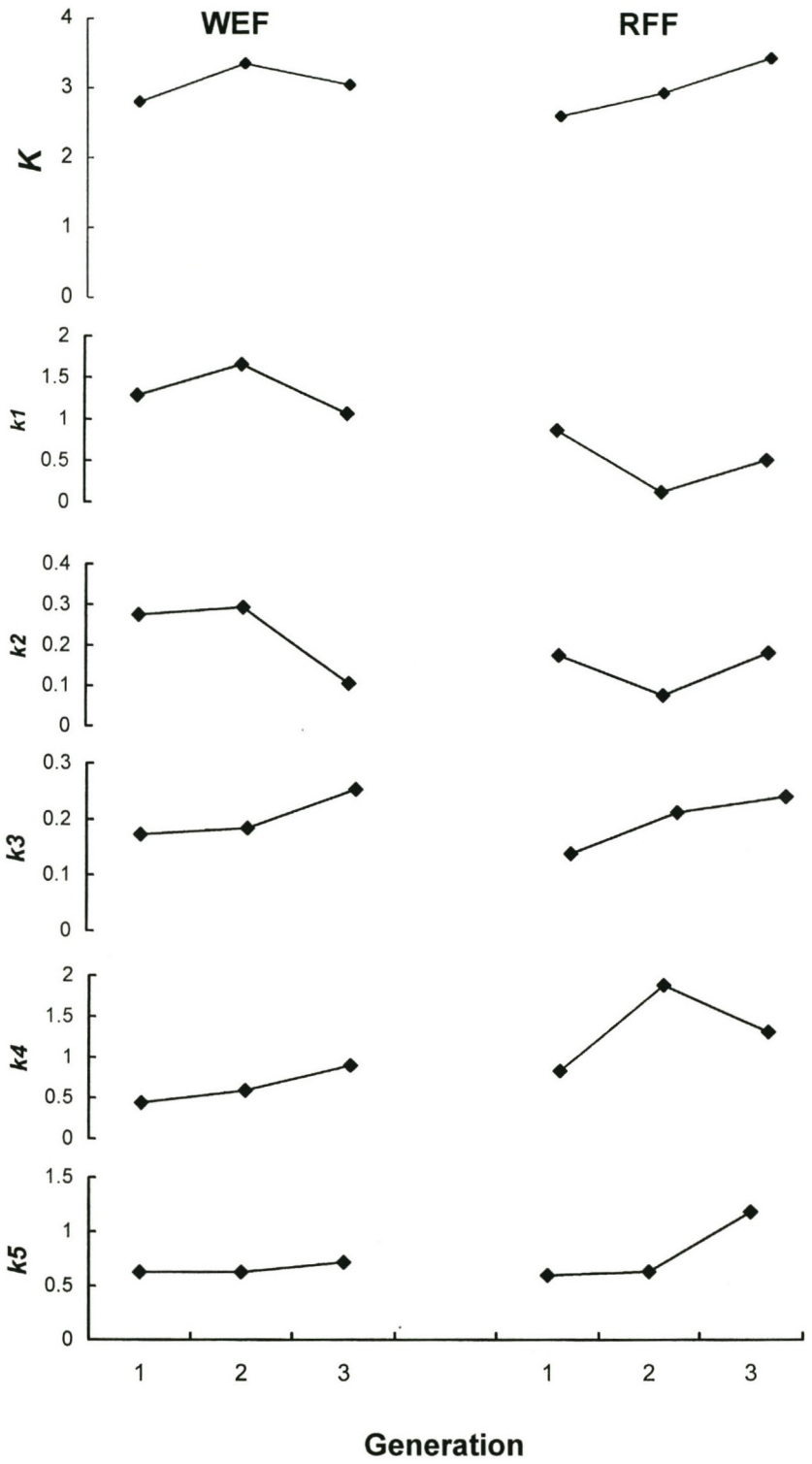

Figure 2. Graphic key-factor analysis for *Ceroplastes destructor* populations on citrus at Welgevallen Experimental Farm (WEF) and Rhodes Fruit Farms (RFF), South Africa.

Table 6. Three methods of key factor analysis for *Ceroplastes destructor* populations on citrus in South Africa: regression coefficients of *k* on *K* and *K* on *k*, correlation coefficients of *k* on *K* (r) and t-values for regression of *K* on *k* with the corresponding probability (P) levels.

		Regression coefficients (b)		r		
Orchard	*ki*	*k* on *K*	*K on k*	*k* on *K*	*t-test*	P
WEF	k_1	0.74	0.63	0.68	2.43	< 0.05
	k_2	0.06	0.43	0.16	4.69	< 0.01
	k_3	0.01	0.32	0.05	2.31	n.s.
	k_4	0.21	0.29	0.24	3.74	< 0.05
	k_5	-0.02	-0.44	-0.08	0.97	n.s.
RFF	k_1	-0.34	-0.40	-0.37	5.32	< 0.01
	k_2	0.03	1.25	0.18	2.70	< 0.05
	k_3	0.12	7.18	0.93	2.67	< 0.05
	k_4	0.43	0.26	0.34	2.57	< 0.05
	k_5	0.76	1.17	0.94	5.81	< 0.01

n.s. = not significant (P > 0.05)

The regression coefficients for log initial density of POF on which k_1 acted against log density of survivors and for log density of survivors against log initial density of POF at WEF were 1.51 and 0.45 respectively, and differed significantly from b = 1.0 (P < 0.01). This was the only indication of the presence of a density-dependent mortality factor operating at this orchard. At RFF, the regression coefficients for log initial density of the LI stage on which k_5 acted against log density

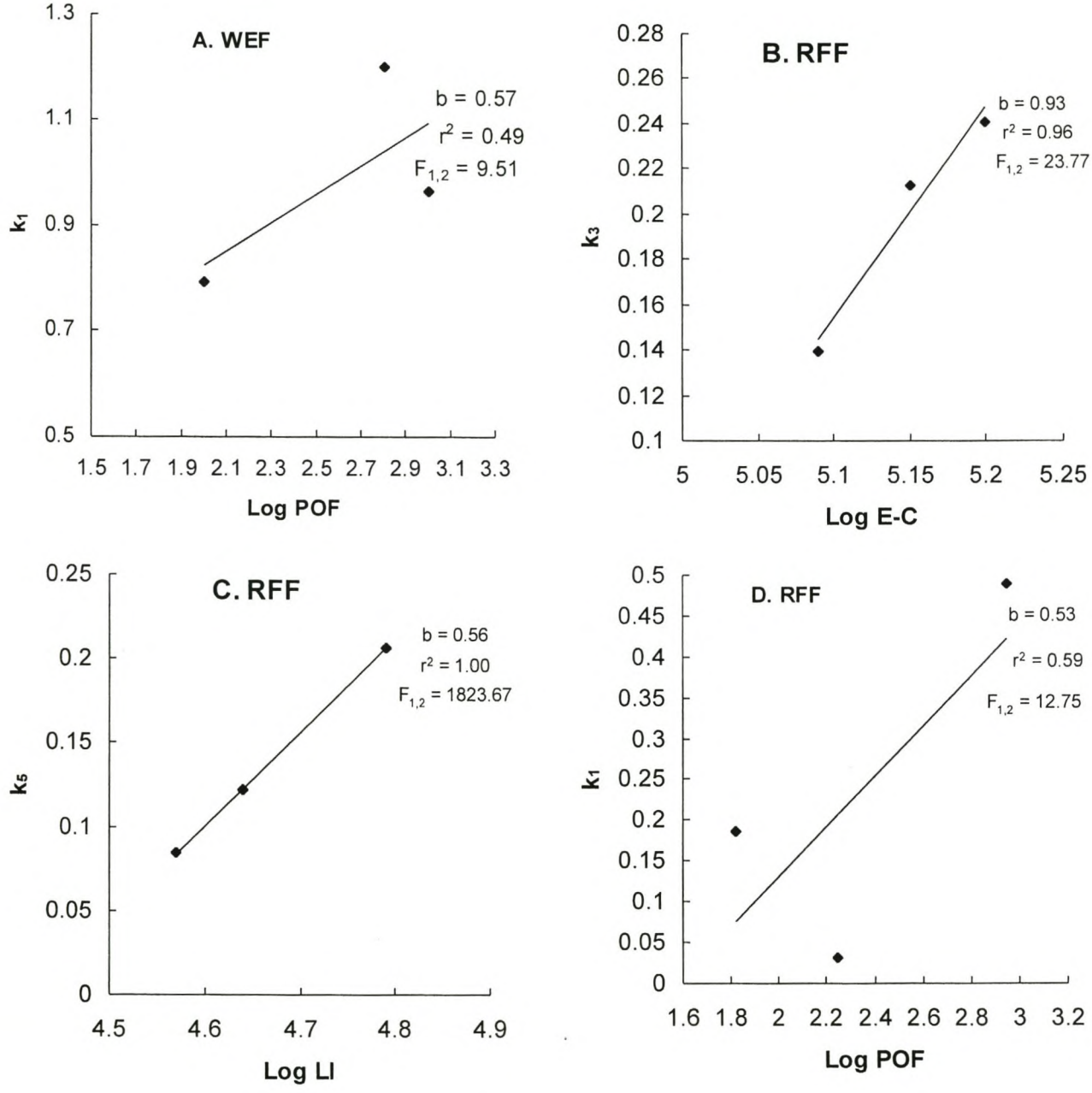

Figure 3. Test for density relationship for *Ceroplastes destructor* populations on citrus at Welgevallen Experimental Farm (A. WEF) and Rhodes Fruit Farms (B-D. RFF), South Africa: regression of k-values against log density on which they act. The slopes are significantly different from b = 0 in both orchards.

of survivors and for log density of survivors on log initial density were respectively 2.19 and 0.46, and differed significantly from b = 1.0 ($P < 0.01$). The regression coefficients for log initial density of POF on which k_1 acted against log density of survivors and *vice versa* were respectively 1.45 and 0.59, and differed significantly from b = 1.0 ($P < 0.01$). The test did not prove that k_3 was a density-dependent mortality factor at RFF, although this factor was found to be density-dependent based on the test for density-dependence above.

4. DISCUSSION

Although more of the early immature instars had died than the more mature instars or the young and mature adult females, the proportion of scale insects that died in relation to the number entering each stage was higher at the LIII-POF stages than at the earlier immature stages. In other words, the LIII and POF were the key stages for mortality or the critical stages that contributed most to total generation mortality (*K*). Podoler *et al.* (1981) and Schneider *et al.* (1987) demonstrated that key stage mortality of *Ceroplastes floridensis* Comstock was in the POF stage. Variation in survival rates between orchards in the current study was related to the differential actions of various mortality factors and differences in citricultural practices.

The proportion of infertile eggs was negligible while mortality of the E-C stage from miscellaneous factors was high. A great proportion of the E-C stage at all orchards had also disappeared through wind dispersal and failure to find suitable settling sites. No predators or parasitoids were observed that contributed to egg or crawler mortality, although *Anicetus nyasicus* (Compere) (Encyrtidae: Hymenoptera), was occasionally observed parasitizing ovipositing females. Mortality factors at the LI

and LII stages were similar and constituted the 'miscellaneous' and 'unknown' factors, both having induced very high mortality at these stages. At the LIII and POF stage categories, parasitoids (mainly *Aprostocetus ceroplastae* (Girault)) (Hymenoptera: Eulophidae) and predators (mainly *Coccidophaga* (=*Eublemma*) *scitula* (Rambur)) (Lepidoptera: Noctuidae) contributed most to total generation mortality. Disease contributed very little to the total mortality but its potential as a mortality factor should not be overlooked.

Although analysis of key factor/s requires several successive life tables (e.g. Schneider *et al.*, 1987), reasonably consistent results were obtained here with the different methods of analysis in three successive generations. A key factor analysis was used because of variability in mortalities between orchards and because most of the non-key mortality factors appeared to have a considerable importance in contributing to the total generation mortality in each orchard. At WEF, k_1 acting on the POF stage was demonstrated as a key factor. Further, k_2 had also acted as a weak key factor at WEF and k_5 as a strong key factor at RFF. Podoler *et al.* (1981) have found predation to be the main mortality factor of *C. floridensis* during the spring generation in Israel. Parasitoids and predators constituted the key mortality factors of populations of *Aonidiella aurantii* (Maskell) in the lowlands of Swaziland (Atkinson, 1983) and of *Ctenarytaina thysanura* Ferris in Australia (Mensah & Madden, 1994). However, Atkinson (1983) found variations in key mortality factors of *A. aurantii* infesting twigs and fruits of orange trees. The variation in key factors between WEF and RFF in the current study could probably be due to differences in orchard protection practices. Insecticide drift at the latter orchard had, for instance, impaired the roles of parasitoids and predators and reduced scale mortality at the key stage category in 1998.

A significant density-dependent mortality factor was demonstrated during the LI and POF stages. Only k_1 acting on POF scales at WEF and both k_1 and k_5 at the POF and LI stages respectively at RFF, proved density-dependent. Both k_3 and k_4 (unknown factors) at WEF and k_4 at RFF appeared to be compensating for the key factors in the respective orchards. The slope (*k*-values on log density) during some scale stages were negative, indicating the presence of inverse density-dependent mortality factors that act to destabilize the population. The slopes for some of the *k*-values on log density were very small in value and with random pattern of distribution, particularly at the early immature stages, showing that their contribution to changes in population density was small. Nevertheless, the overall generation mortality in all orchards was extremely high, probably due to additive effects of these mortality factors. The additive effects of a number of weak density-dependent mortality factors acting in each of a number of age intervals can, when combined, give an important total effect (Varley & Gradwell, 1970). The regression coefficient (b) of the density-dependent factor/s in the two orchards ranged from 0 to 1.0, indicating that these factors operate to stabilize generation survival and do not as such contribute much to variance in generation survival. According to Varley & Gradwell (1970) and Schneider *et al.* (1987), only direct density-dependent factors with b between 1.0 and 2.0 are overcompensating and cause variation in generation survival. It has also been accentuated that variance in generation survival can be caused by both density-dependent and density-independent mortality factors (Luck, 1971).

In general, the results of the present study indicated that some of the mortality factors were operating randomly and had no density-dependent regulatory effects. Some were acting as weak density-dependent factors at some stages of scale development, having no significant effects on their own in inducing change in

population densities over generations. However, parasitoids in general demonstrated a density-dependent effect at the POF stage. The 'miscellaneous' factors also had a density-dependent effect at the LI stage in RFF. Interestingly, the key factors in both orchards also acted as density-dependent mortality factors and this has positive implications for biological and integrated management of *C. destructor*. It is essential that future management plans for *C. destructor* take these factors into account in order to maximize their efficacy by avoiding harmful agricultural practices. It was demonstrated that an extremely high generation mortality of *C. destructor* by natural agents is possible if the use of conventional insecticides or insect growth regulators is avoided or their application properly scheduled. However, each orchard should be considered independently because key factors may vary between orchards as found in the current study. This was also demonstrated by Podoler *et al* (1981) and Schneider *et al.* (1987) for *C. floridensis* in Israel.

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CHAPTER 6

DISPERSAL OF THE WHITE WAX SCALE, *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE)[†].

ABSTRACT

The dispersal of *Ceroplastes destructor* Newstead and the effect of crawler density at the source on the number dispersed and distance traveled was studied using rectangular, yellow sticky traps in an open and level field. Dispersal is by first instar nymphs, mainly on air currents, and the numbers caught on a series of sticky traps up to 4 m from the source were very similar, suggesting that wind dispersal was very efficient. The number of crawlers captured on the yellow sticky traps varied significantly between crawler densities at the source ($P < 0.001$), trap distances ($P < 0.001$) and trap directions from the source plant ($P < 0.001$). The observed and expected numbers of crawlers caught were significantly positively correlated to the initial crawler density at the source ($P < 0.01$), suggesting that dispersal was density dependent. The actual and expected numbers of crawlers caught per cm^2 of trap area and trap distances were significantly negatively correlated ($P < 0.001$). However, the reduction in the expected number of crawlers on the traps was more rapid with increasing distance from the source than what was observed, indicating that a number of crawlers dropped out of the air currents during wind dispersal. After six weeks the population of the second instar nymphs was smaller on source seedlings initially

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heavily infested than on those which were initially more lightly infested, probably due to a crowding effect. This supports the contention that dispersal was density dependent.

1. INTRODUCTION

The white wax scale, *Ceroplastes destructor* Newstead (Hemiptera: Coccidae), is among the complex of insects for which citrus is a suitable host. It was first described by Newstead in 1910 (Newstead, 1917) and some 50 years later briefly studied by Cilliers (1967). Cilliers commented that *C. destructor* was a potential pest that required detailed studies of its biology and ecology. The population density of *C. destructor* has increased in certain citrus growing areas of the Western and parts of Eastern Cape Provinces, South Africa, and particularly on easy-peel citrus, *Citrus reticulata* (Blanco) (Wakgari & Giliomee, 1998). This surge in population density could probably be because of colonization by crawlers from infested trees within the same orchard or recruitment from distant sources.

Dispersal of insects is often by winged and adult individuals (Moran *et al.* 1982). However, the highly mobile first instar nymphs, or crawlers, in many sessile and wingless insects may also accomplish dispersal (see Brown, 1958; Greathead, 1972; Washburn & Frankie, 1981; Washburn & Washburn, 1984; Yardeni, 1987; Wakgari & Giliomee, 2000). Dispersal increases the availability of resources and space for the subsequent generations and is also a means to evade adverse environmental conditions. Scale insects can be distributed over a long distance through the interchange of nursery stock, by birds, by actively flying insects or by people (Quayle, 1916; Greathead, 1997). Greathead (1997) reviewed the dispersal of scale insects and concluded that spread on

wind currents was the major means of dispersal both within and between host plants (see also Washburn & Frankie, 1981; 1985; Washburn & Washburn, 1984; Yardeni; 1987). However, the effect of crawler density on the number and distance of dispersal has not been studied in detail. Observations in the field revealed that crawlers moved considerable distances between trees. On several occasions, it was noticed that citrus trees that had been free of scales during one generation had become heavily infested during the next. These trees were up to 4 m away from any infested trees. This colonization was presumed to have been due to crawlers being carried on wind currents, since the role of humans and animals in dispersing crawlers in established orchards is thought to be minimal. Experiments were therefore designed to assess whether or not crawlers could be dispersed on air currents up to 4 m, and how initial crawler density affected the rate of emigration.

2. MATERIALS AND METHODS

2.1. Dispersion

Dispersal distance and effects of crawler density on the rate of emigration were evaluated in an open and level field at the Botanical Garden of the University of Stellenbosch (34°E 19°S), 230 meters above sea level.

The experiment consisted of four densities of *C. destructor* crawlers, 400, 600, 800 and 1000 per seedling. Each crawler was transferred individually with a camel's hair brush onto 64 easy-peel citrus (*C. reticulata)* seedlings less than 1 year old, about 1.2m tall and planted in a 20 liter pot. The seedlings were placed approximately 10m apart on a level field. The experiment was laid out in a factorial design with the four density levels, the four distances and four compass points as main effects. The trial

had four replications. Four vertical, rectangular yellow sticky traps 30 cm high and 10 cm wide were placed around each seedling, one each at a distances of 1, 2, 3, and 4 m from the source plant along each of the four compass points (N, S, E and W). Each trap was tied to a stake 1m above the ground. The height of the trap from the ground was meant to correspond with take-off height. The traps were collected after six weeks, the maximum duration for the first instar and the number of crawlers caught counted under a stereomicroscope.

2.2. Data analysis

Factorial analysis of variance was used to determine the effect of crawler density at the source on the observed number of crawlers caught on the yellow traps. It was necessary to calculate the expected number of crawlers at each trap distance and compass point in order to account for the relative reduction in surface area taken up by the traps as distance from the source increased and to make comparison possible. The expected number of crawlers per cm^2 of trap area was, therefore, calculated by using the number of crawlers caught at the 1m distance as a reference for the various densities, distances and compass directions. One meter was used as a reference distance since it was the smallest distance examined in this experiment. The expected number of crawlers/cm^2 of trap area was calculated as follows. At 1m trap distance the height of the trap from the source seedling = 100 cm (= the distance); trap area was 10cm x 30cm = 300 cm^2; a straight line passing through the trap from the source would divide the trap into two equal parts of 5cm wide. Thus,

At 1m

$\text{Sin } \theta = 5\text{cm}/100\text{cm}; \theta = 0.05; \theta = 2.88598^0$

$\text{Sin } \theta = x/100\text{cm}; x = 0.05\ (100\text{cm}) = 5\text{cm}$

Thus, trap width at 1m distance is expected to be 5cm x 2 = 10cm and trap area would be 10cm x 30cm = 300cm^2. Similarly, traps at a distance of 2, 3 and 4 m would cover an area of 600, 900 and 1200 cm^2, respectively.

Suppose 29 crawlers were caught at 1m at a density of 1000 crawlers at the source; this means that the observed number of crawlers at this distance would be 29 crawlers/300cm^2 = 0.097 crawler/cm^2. Suppose also that 7 crawlers were caught at the 4m distance at this density level. Thus, at 4m the expected number would be 29 crawlers/1200cm^2 = 0.02417 crawler/cm^2, whereas the observed number would be 7 crawlers/300cm^2 = 0.02333 crawler/cm^2. The observed and expected numbers of crawlers caught per cm^2 of the yellow traps for the various crawler densities and trap distances were subjected to multiple regression. The effects of trap direction on the observed and expected number of crawlers caught/cm^2 of the yellow traps were examined using dummy variables (Rawlings, 1988). The full model consisted of separate intercepts and separate slopes for both density and distance assigned to the four compass points. The degrees of freedom associated with the residual sum of squares in the full model were n-p, where n is number of observations and p is number of parameters. In the reduced model common intercepts and slopes for both density and distance were assumed for the four compass points. The residual sum of squares of the reduced model had n- (p-k) degrees of freedom, where n and p are as defined above and k is the number of linear functions.

3. RESULTS AND DISCUSSION

Wind current was an efficient dispersal agent for *C. destructor* crawlers within the range of distances studied here (Tables 1 and 2). The number of crawlers caught on the yellow sticky traps varied significantly between crawler densities ($P < 0.001$), trap

distances from the source ($P < 0.001$) and compass points ($P < 0.001$) (Table 3). There was a significant interaction between crawler density, trap distance and trap directions (Table 3).

In the current study, the number of crawlers caught on traps was high in proportion to the size of the traps used, confirming that wind is indeed an effective dispersal agent. This corroborated earlier reports by Quayle (1916), Jenkens *et al.* (1953), Hulley (1962), Washburn & Frankie (1985) and Yardeni (1987) who showed that wind was the principal dispersal agent for the crawlers of scale insects. Previous work on the wind dispersal of *C. destructor* (Hely, 1960) showed that they could be carried up to 6m. Distances recorded for other scale insects were 135m for the black scale, *Saissetia oleae* (Bernard) (Quayle, 1916), 54m for the soft brown scale, *Coccus hesperidum* L. (Hoelscher, 1967) and 3.5 km for *Icerya seychellarum* (Westwood) trapped 6 m above surrounding vegetation (Hill, 1980). Dispersal distance has also been shown to be affected by height of take-off and wind speed (Greathead, 1972; Wainhouse, 1980; Moran *et al.*, 1982) and by the temperature and humidity (Greathead, 1972). Total daily wind speed during the course of this experiment is presented in Figure 1. Wind speed was generally high in November and December and varied considerably between days, months and years. This high wind speed may have been responsible for the disappearance of more than 92% of crawlers at all density levels.

In the case of some sessile insects, crawler dispersal is aided by various behavioral and morphological adaptations. For example, Washburn & Frankie (1981), Washburn & Washburn (1984) and Yardeni (1987) argued that the positive phototactic and negative geotactic responses combined with some active aerial dispersal behavioural

Table. 1. Effects of crawler density, trap-distance and wind direction on the number of crawlers caught (± standard error) for the different crawler densities at and trap distances from the source.

Density	Distance (m)	Direction			
		N	S	E	W
400	1	10.75±0.85	5.25±0.85	8.0±0.71	8.75±0.49
	2	6.75± 0.48	9.25±0.48	10.75±0.48	9.50±1.04
	3	4.75±0.48	6.25±0.48	3.00±0.41	5.50±0.65
	4	2.75±0.63	2.25±0.25	1.25±0.25	1.25±0.25
600	1	18.75±0.85	13.50±0.85	23.00±1.08	19.75±1.11
	2	14.00±0.91	10.50±0.64	11.75±1.11	8.00±0.91
	3	13.25±0.85	13.00±0.41	10.50±0.29	12.25±0.85
	4	5.25±0.48	2.00±0.41	3.75±0.48	6.50±0.65
800	1	18.75±0.86	18.00±0.41	21.00±0.91	14.00±1.08
	2	16.00±0.71	12.00±0.91	19.75±1.11	17.00±0.71
	3	22.75±1.49	20.25±0.75	20.25±0.86	21.25±2.39
	4	5.25±0.85	3.00±0.41	12.75±1.11	7.25±0.48
1000	1	32.75±1.03	27.00±2.97	25.75±1.55	29.25±1.70
	2	22.25±1.75	14.25±0.75	16.75±1.11	18.75±0.85
	3	17.25±0.85	15.75±1.18	12.75±0.48	18.00±0.71
	4	7.25±0.48	8.25±1.11	5.00±0.41	9.00±0.71

Table 2. Effects of crawler density, trap-distance and trap direction on the number of observed and expected crawlers caught/cm^2 of trap area (± standard error). Den. = Density.

Den.	Distance (m)	Observed/cm^2 Direction N	S	E	W	Expected/cm^2 Direction N	S	E	W
400	1	0.036±0.0028	0.018±0.0028	0.027±0.0024	0.029±0.0014	0.036±0.0028	0.018±0.0028	0.027±0.0024	0.029±0.0014
	2	0.023± 0.0017	0.031±0.0014	0.036±0.0017	0.031±0.0035	0.011±0.0008	0.016±0.0010	0.018±0.0007	0.016±0.0017
	3	0.016±0.0017	0.021±0.0014	0.010±0.0012	0.019±0.0014	0.005±0.0008	0.007±0.0005	0.003±0.0004	0.006±0.0009
	4	0.009±0.0021	0.008±0.0008	0.004±0.0010	0.004±0.0010	0.003±0.0006	0.002±0.0003	0.001±0.0003	0.001±0.0003
600	1	0.063±0.0028	0.045±0.0039	0.077±0.0037	0.066±0.0036	0.063±0.0028	0.045±0.0039	0.077±0.0037	0.066±0.0036
	2	0.047±0.0030	0.035±0.0022	0.039±0.0035	0.027±0.0030	0.024±0.0016	0.018±0.0010	0.020±0.0018	0.014±0.0016
	3	0.044±0.0028	0.043±0.0014	0.035±0.0012	0.041±0.0030	0.014±0.0011	0.014±0.0006	0.012±0.0003	0.014±0.0010
	4	0.018±0.0017	0.007±0.0014	0.013±0.0016	0.022±0.0021	0.004±0.0005	0.002±0.0005	0.003±0.0004	0.006±0.0006
800	1	0.063±0.0028	0.060±0.0012	0.070±0.0031	0.047±0.0037	0.063±0.0028	0.060±0.0012	0.070±0.0031	0.047±0.0037
	2	0.054±0.0024	0.040±0.0031	0.066±0.0036	0.067±0.0024	0.027±0.0012	0.020±0.0015	0.033±0.0020	0.028±0.0012
	3	0.076±0.0051	0.067±0.0025	0.069±0.0030	0.071±0.0079	0.025±0.0018	0.022±0.0008	0.023±0.0011	0.021±0.0009
	4	0.018±0.0028	0.010±0.0012	0.043±0.0038	0.024±0.0017	0.005±0.0006	0.003±0.0003	0.012±0.0011	0.006±0.0005
1000	1	0.109±0.0036	0.090±0.0098	0.086±0.0051	0.098±0.0056	0.109±0.0036	0.090±0.0098	0.086±0.0051	0.098±0.0056
	2	0.074±0.0059	0.047±0.0025	0.056±0.0036	0.063±0.0028	0.037±0.0029	0.024±0.0012	0.028±0.0020	0.031±0.0015
	3	0.050±0.0028	0.053±0.0038	0.043±0.0017	0.060±0.0024	0.019±0.0009	0.018±0.0012	0.014±0.0007	0.020±0.0007
	4	0.025±0.0018	0.028±0.0038	0.017±0.0014	0.031±0.0023	0.006±0.0005	0.007±0.0009	0.004±0.0004	0.008±0.0005

patterns, such as orienting downwind and standing on the hind legs with antennae and fore legs outstretched have developed during Coccoid evolution. These dispersal behavioural patterns were clearly demonstrated by crawlers of *C. destructor* in the current study. Moran *et al.* (1982) have also demonstrated that wind-dispersal in *Dactylopius austrinus* De Lotto is aided by the presence of long wax filaments.

Table 3. Analysis of variance computed on data presented in Table 1.

Factor	**Df**	**MS**	**F**	**P**
Density (De)	3	1655.089	445.066	< 0.001
Distance (Di)	3	1932.724	519.724	< 0.001
Direction (Dr)	3	63.974	17.203	< 0.001
De * Di	9	204.589	55.015	< 0.001
De * Dr	9	40.297	10.836	< 0.001
Di * Dr	9	23.557	6.335	< 0.001
De * Di * Dr	27	17.940	4.824	< 0.01
Error	192	3.719		

Although such morphological adaptation is not present in *C. destructor,* the fact that crawlers are small in size, dorsoventrally flat and have a pair of long apical setae on the anal plates might give them a greater potential for take-off and long-distance dispersal.

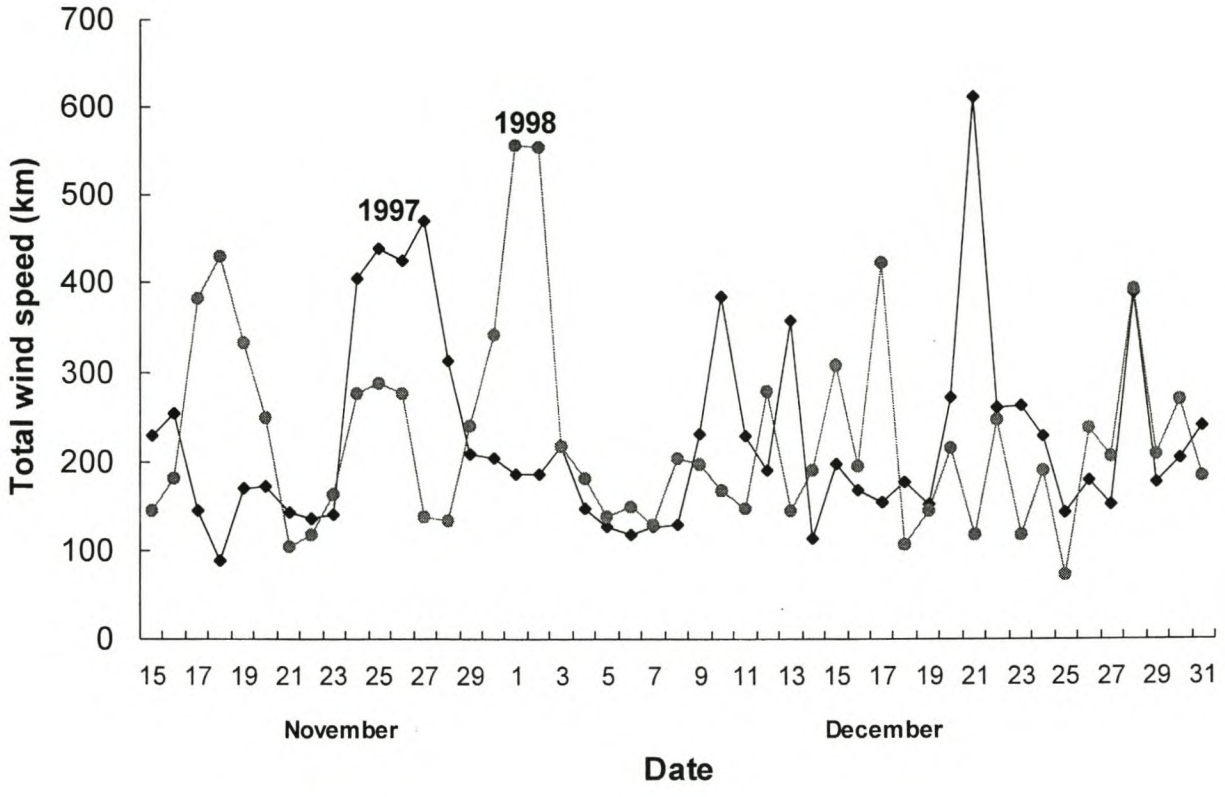

Figure 1. Total daily wind run (Km) at Stellenbosch during the course of the experiment.

The effects of direction on the number of observed and expected crawlers/cm^2 of trap size were tested using both reduced and full models of dummy variables. The reduced model differed from the full model for the observed density ($F_{9,\ 253} = 2.09$; $P = 0.03$), but not for the expected density ($F_{9,\ 253} = 1.26$, $P = 0.26$). However, none of the coefficients for the dummy variables were significant ($P > 0.05$) for both observed and expected density, indicating that a common intercept and common slopes for both distance and density could be assigned to the four compass directions (Table 4).

Table 4. Regression coefficients with their 95% confidence intervals and the corresponding coefficient of determination for the observed and expected crawlers/cm^2 on density and distance.

Data	**Intercept**	**95% c. i.**	**b_1 (Density)**	**95% c. i.**	**b_2 (Distance)**	**95% c.i.**	**R^2**
Observed	0.030	0.022 to 0.378	0.571	0.501 to 0.642	-0.587	-0.658 to -0.517	0.672
Expected	0.040	0.033 to 0.047	0.343	0.277 to 0.409	-0.771	-0.837 to –0.705	0.713

The slopes of the regression, b_1 and b_2, for density and distance respectively were smaller for the expected data than for the observed (Table 4). The regressions were highly significant both for the observed ($F_{2, 253} = 258.9$; $P < 0.001$) and expected ($F_{2, 253} = 314$; $P < 0.001$) numbers. The slopes for density were positive and significantly greater than zero both for the observed ($t_{253} = 15.9$; $P < 0.001$) and expected ($t_{253} = 10.22$; $P < 0.001$) numbers, indicating that the observed and expected density of crawlers on the traps increased as the density at the source increased. However, the slope coefficient for the expected data was lower than that for the observed (Table 4). In addition, there was no overlap between the 95% confidence intervals, indicating that this difference was significant. The slope coefficients for distance were negative (Table 4) and differed from

Table 5. The mean number of second instar nymphs remaining on each seedling at the original site of release and the number elsewhere on the plant, six weeks after release.

Crawler density	**No. on seedlings after dispersal (% of original density)**	**nearby branches**
400	31 (7.8)	2
600	34 (5.6)	2
800	9 (1.1)	2
1000	8 (0.8)	0

zero both for the observed ($t_{253} = -16.3$; $P < 0.001$) and expected ($t_{253} = -22.9$; $P < 0.001$) numbers, indicating that both the observed and expected density of crawlers on the traps decreased as the distance from the source increased. The slope coefficient for the observed data was steeper than that for the expected (Table 4) and there was no overlap between the 95% confidence intervals, suggesting that this difference was significant. The reduction in the expected density of crawlers on the traps was more rapid with increasing distance from the source than what was observed, indicating that a number of crawlers dropped out of the air currents during wind dispersal.

The number of second instar nymphs which were still present on the seedlings, six weeks after release is presented in Table 5. More remained on the seedlings with an original crawler density of 400 and 600 than on those with an original density of 800 and 1000, suggesting that there may have been some effect of crowding on dispersal.

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CHAPTER 7

EFFECTS OF SCALE DENSITY ON FEMALE FECUNDITY, FERTILITY AND BODY SIZE OF *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE), AND ITS HOST PLANT.

ABSTRACT

Field evaluation of the effects of different densities of *Ceroplastes destructor* Newstead on growth, survivorship and reproduction of scales was carried out at Stellenbosch on naturally infested *Syzygium (=Eugenia) malaccensis* (L.) plants. The effects of scale density on leaf bearing ability and on area of leaf surface covered with sooty mould fungus of *Syzygium* plants were also examined. Scale body size and fecundity were inversely related to scale density ($P < 0.001$), suggesting density-dependent intraspecific competition. Female fecundity and body sizes were significantly positively correlated ($P < 0.05$). Scale survivorship was also density related in that it declined with increasing density ($P < 0.05$). Scale parasitism and predation were positively correlated with scale density ($P < 0.05$), suggesting that with increase in host density the searching and oviposition efficiency of the parasitoids and predators increased. The number of leaves was negatively correlated with scale density ($r_s = -0.73$; $P < 0.01$), indicating that with increase in scale density the production of new leaves was reduced thereby reducing the

resource base for subsequent generations of scale. Scale density and leaf area covered with sooty mould fungus were significantly positively correlated ($r^2 = 0.49$; $P < 0.01$).

1. INTRODUCTION

The population density of insect pests is affected by various interacting abiotic and biotic processes. One of these processes is intraspecific competition that may result in a decrease in the rate of population increase. Intraspecific competition increases with increasing density and often results in increased mortality, decreased natality due to limited space for living and breeding and depletion of food (Price, 1997). The spatial and temporal aggregation of insects is one of the direct density dependent factors that regulate insect populations (Washburn *et al.*, 1985). McClure (1979) and Washburn *et al.* (1985) have, for instance, demonstrated that heavy spatial aggregation of nymphs of the elongate hemlock scale, *Fiorinia externa* Ferris, and the soft scale, *Pulvinariella mesembryanthemi* (Vallot), respectively, lead to reduced fecundity. In sedentary insects like *C. destructor* Newstead, intraspecific competition and the resulting density-dependent regulation could be severe owing to the restricted ability to move from areas of high density. Such competition is often surmounted through dispersal by adults in most alate species and by active crawlers in sessile insects. Dispersal permits individuals to spread and escape crowding as the population increases and the environment becomes untenable, hence allowing the colonization of new habitats. In the case of *C. destructor* active dispersal takes place during the first instar (see Chapter 6) and movement to permanent settlement sites (young twigs) after the second instar (see Chapter 3).

The effects of soft scale insects on their host plants were reviewed by Vranjic (1997). Soft scales are known to cause both direct damage through removal of resources needed for plant growth and penetration and damage of plant tissues as well as indirect damage through contamination of plant surfaces with honeydew and sooty moulds and through transmission of arthropod-borne pathogens (Vranjic, 1997). Washburn *et al.* (1985) noted a significant reduction in wet weight of ice plants at higher densities of *P. mesembryanthemi*, which was attributed to loss of leaves and shoots. Schaffer & Mason (1990) and Vranjic & Gullan (1990) reported more than 50% reduction in the shoot biomass of heavily infested *Guaiacum sanctum* L. and *Eucalyptus blakelyi* Maiden trees respectively.

Furthermore, intense and continuous stylet penetration deep into phloem tissues at high scale density may cause disruption of phloem continuity due to callose accumulation (Wood *et al.*, 1985; Vranjic, 1997). Washburn *et al.* (1985) examined the effects of different densities of the soft scale, *P. mesembryanthemi*, on growth of ice plant and found that plant growth was negatively correlated with initial scale density, and that plants infested with higher scale densities stopped producing new leaves and shoots. Newbery (1980a, b) also reported a negative correlation between the growth of *Euphorbia pyrifolia* Lam. and the size of infestation by *Icerya seychellarum* (Westwood). In some cases, complete mortality of plants infested with high scale densities is possible. For example, Washburn *et al.* (1985) found that none of the ice plants artificially infested with 500 crawlers of *P. mesembryanthemi* were alive at the end of the first scale generation. The effect of increasing sizes of infestation by *C. destructor* on its host plants has not been previously investigated.

The aims of this study were firstly to determine the effects of different densities of *C. destructor* on female fecundity, egg fertility and body size. Secondly, to assess the effects of different densities of *C. destructor* on leaf bearing ability and area of leaf surface covered with black sooty mould fungus of infested *Syzygium (=Eugenia) malaccensis* (L) trees. The latter, an ornamental of Australian origin, was used due to the dispersal of extremely large numbers of crawlers artificially transferred to citrus, the commercially more important host of *C. destructor.* However, the results would add to our understanding of the effects of this insect on its host plants.

2. MATERIALS AND METHODS

2.1. Sampling

Data pertaining to female fecundity, egg fertility and body sizes and area of leaf surface covered with black sooty mould fungus were obtained from samples collected directly from naturally infested *S. malaccensis* plants at Welgevallen, Stellenbosch (34°54'S 18 °54'E). Fifteen twigs of 60 cm long and about 2-4 mm diameter were marked and tagged depending on the presence of different numbers of third instar nymphs (LIII). Five levels of infestation were used. These were 500, 250, 100, 25 and 0 per twig. For each density level, three twigs (replicates), one to a tree, were selected and marked.

2.2. Effects of density on fecundity, fertility and body size

Female fecundity, egg fertility and female body size (length, width, height) were determined by taking gravid females from sample twigs described above to the laboratory just before oviposition commenced, using procedures described in Chapter 3, Sections 2.2 and 2.3 and Chapter 2, Section 2.3.

2.3. Effects of density on number of leaves and leaf area covered with sooty mould

The effect of varying scale densities on leaf bearing ability of infested plants was determined by counting the number of leaves on 60 cm long twigs selected at random from plants infested with different number of scales. In order to determine area of leaf surface covered with black sooty mould fungus, ten leaves from each of the marked sample units were sampled at random and taken to the laboratory. Total leaf area and leaf area covered by sooty mould fungus was measured using a leaf area meter (LI-COR: LAMBDA Instruments Corp).

The effect of scale density on scale survival was assessed by overturning gravid females from sample units with a dissecting needle and checking if they were alive or dead using a stereomicroscope. Parasitism and predation of scales at the varying densities were determined from these units by employing procedures described in Chapter 4, Section 2.3.

2.4. Data analysis

The effect of density on female fecundity, egg fertility and body size and the relationship between fecundity and body size (length, width, height) were analyzed using regression analysis. The effect of density on scale survival, parasitism and predation were

also subjected to regression analysis. Since the number of leaves per sample unit is not ordinal data, the relationship between scale density and number of leaves was analyzed using Spearman correlation (r_s) for nonparametric analysis (Zar, 1984). The relationship between scale density and area of leaf surface covered with sooty moulds was examined using regression analysis.

3. RESULTS AND DISCUSSION

Scale body size (length, width, height) and fecundity were inversely related to density (Fig. 1), indicating intraspecific competition. Mean fecundity of females from twigs supporting 25 scales was nearly 2.5 times higher than that of females from 500 scales per twig. Washburn *et al.* (1985) recorded a 6-fold increase in fecundity of females from ice plants initially infested with 25 crawlers of *P. mesembryanthemi* compared to those infested with 1500 crawlers. Egg fertility was not affected by density, as fertility was not significantly correlated with density ($P > 0.05$ – Fig. 2a).

The decline in female fecundity with increasing density was probably due to crowding which resulted in a reduction of scale body size and hence of fecundity, since size and fecundity were strongly positively correlated (Fig. 2b-d). The decrease in female fecundity with increasing density on sample units suggested that scales were numerically self-limiting to some extent. In other words, with the decline in female fecundity in one given generation the reproductive fitness of females in the following generation increased since more space and resources were available.

Scale density and survival rate were inversely related (Fig. 3a), indicating that intraspecific competition for space and food and physical crowding resulted in higher

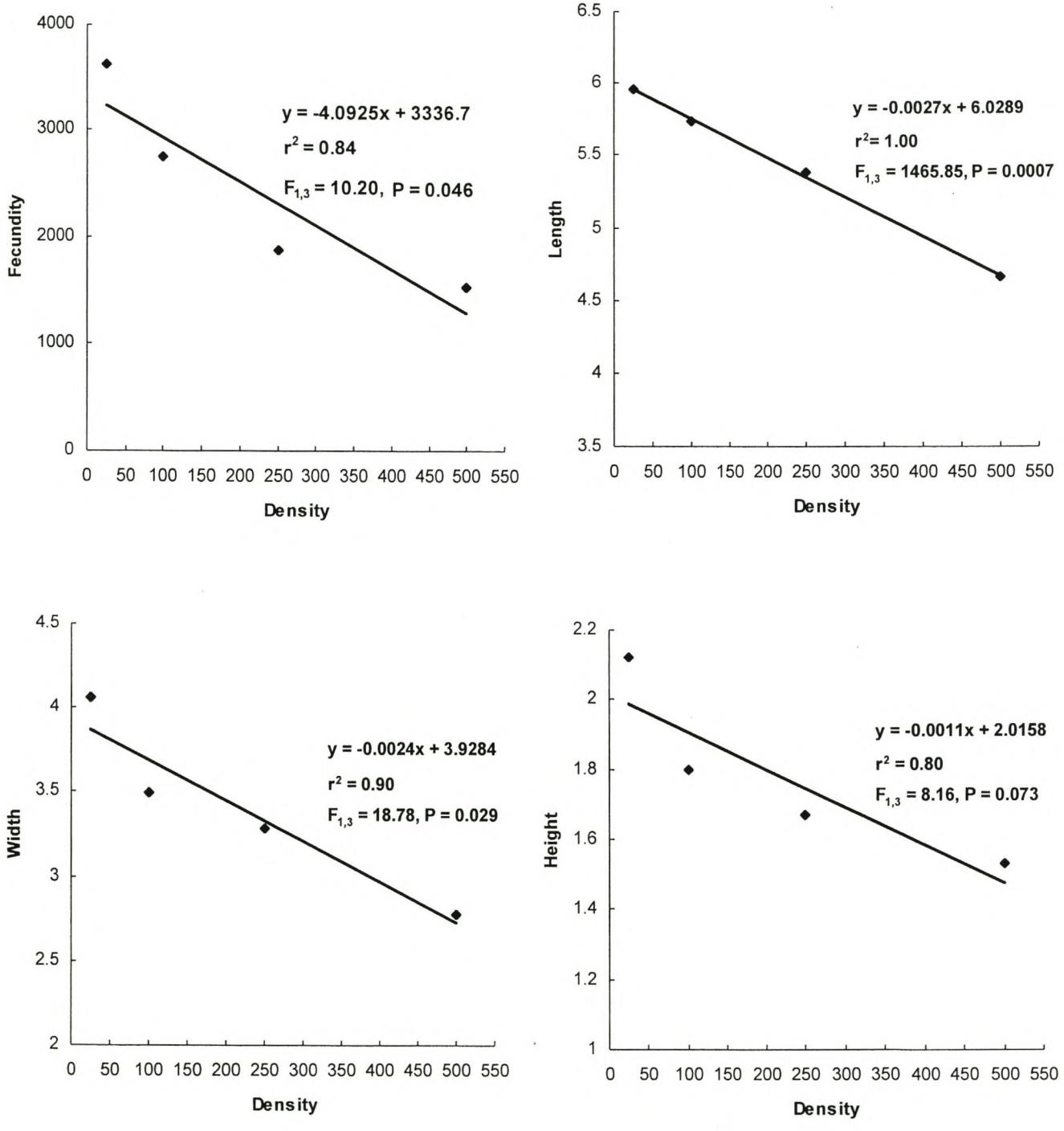

Figure 1. The relationship between mean female fecundity, body sizes (length, width, height in mm) and density of *Ceroplastes destructor* infesting *Syzygium* trees.

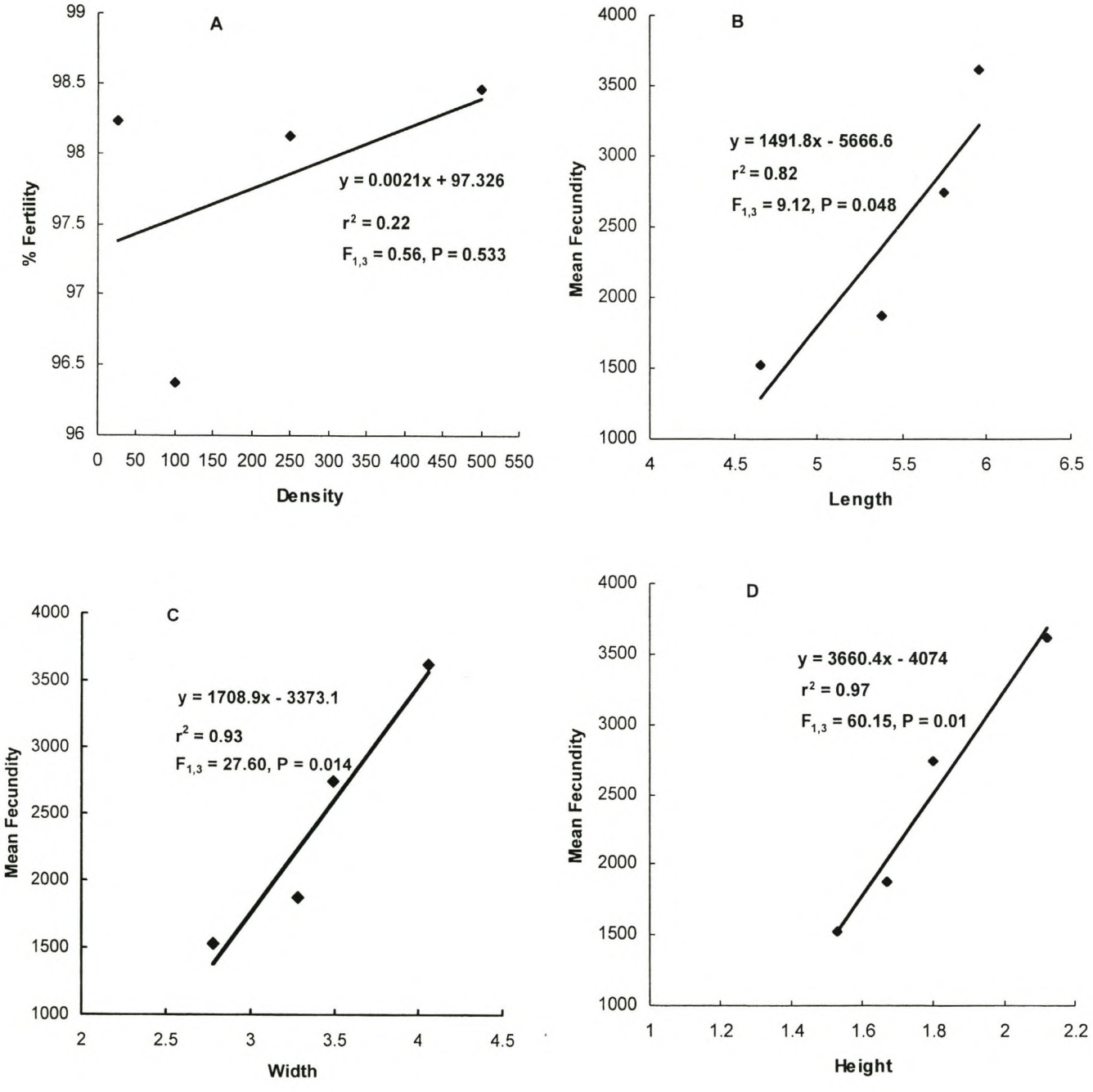

Figure 2. The relationship between egg fertility and density (A), and between body size (mm) and female fecundity (B-D) for *Ceroplastes destructor* infesting *Syzygium* trees.

scale mortality at high densities. Washburn *et al.* (1985) indicated that only three females of the initial population of 2500 insects (*P. mesembryanthemi*) on the five ice plants reached the oviposition stage. McClure (1979) has also reported that survival of nymphs of the elongate hemlock scale, *F. externa*, was negatively correlated to scale densities on host trees. At higher scale densities, inter-scale distances decrease and there is increased possibility of being the recipient of honeydew droplets, causing death either through suffocation and honeydew fouling or the subsequent growth of sooty mould. In the current study, honeydew-collecting ants (*Linepithema humile* (Mayr) and *Pheidole* sp.) (Hymenoptera: Formicidae) were present in large numbers on *Syzygium* trees in the field. Therefore, the higher scale survival in this study compared to the laboratory population of Washburn *et al.* (1985), where ants were absent, was probably due to ants harvesting honeydew droplets, hence reducing mortality from honeydew fouling.

Scale mortality from parasitism and predation were positively correlated with scale density (Fig. 3b, c). The increase in parasitism and predation with increase in scale density was probably due to reduced searching time for host feeding and oviposition, and increased oviposition efficiency of natural enemies at higher scale population levels. Scale density probably has a direct negative or positive impact on the fecundity of the parasitoid and predator species and their subsequent exploitation of available hosts (see also DeBach & Smith, 1941).

Scale density and number of leaves were negatively correlated (r_s = -0.73), the association being described by an exponential decay equation of

$$Y = 310.76e^{-0.0031x}$$ (Fig. 4a).

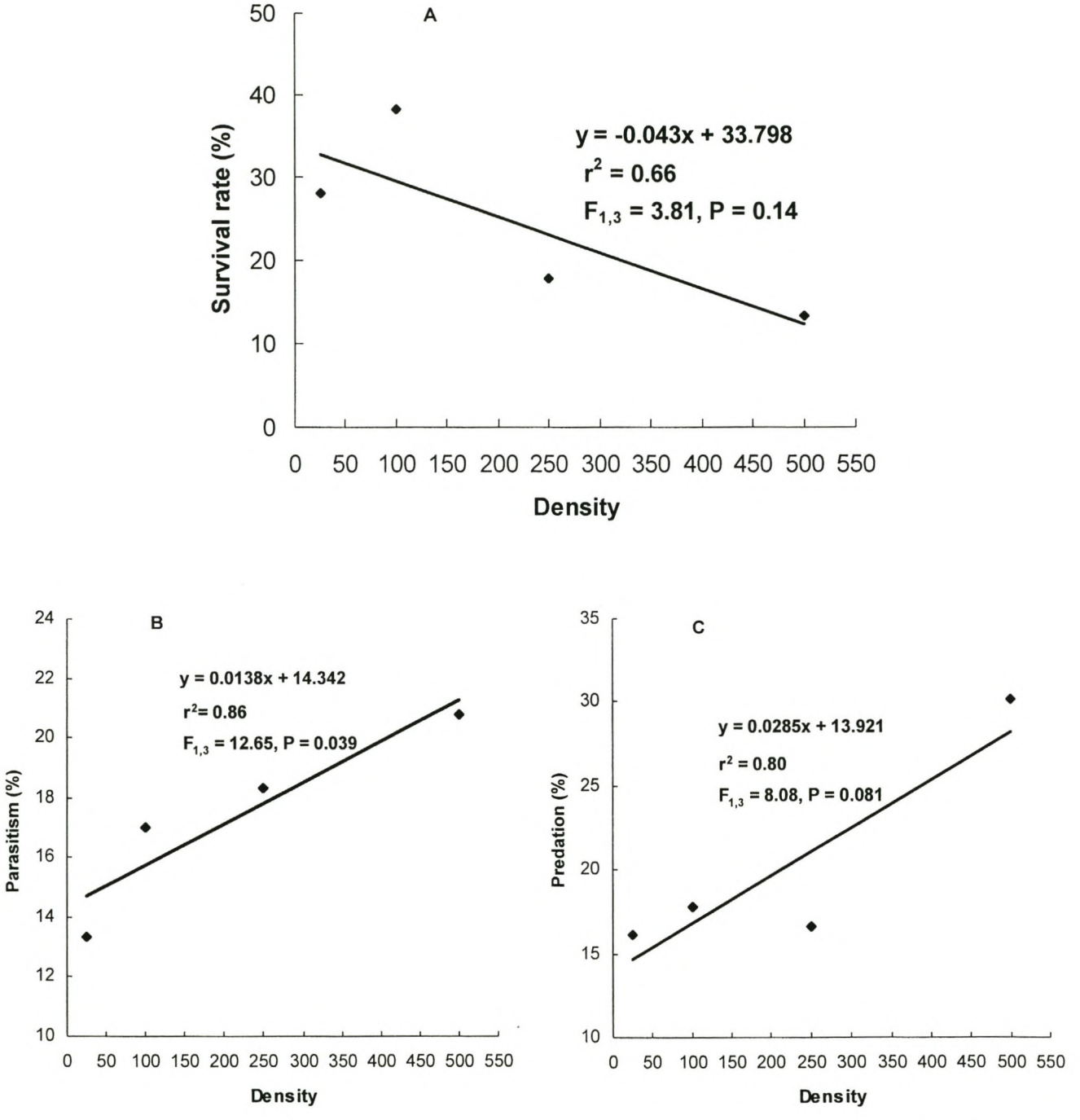

Figure 3. Effects of scale density on scale survival (A) (third instar to ovipositing female), parasitism (B) and predation (C).

The decrease in the number of leaves with increasing density indicated that twigs were probably defoliated at higher scale densities due to increased sap loss or other crowding effects. Newbery (1980a) recorded a 40% reduction in leaf production on *E. pyrifolia* heavily infested by *I. seychellarum*. Newbery (1980a) and Vranjic & Gullan (1990) have also noted a decrease in production of leaf area with increase in the level of infestation by scale insects. The scales may create a strong sink by removing large quantities of sap, thereby preventing leaf formation. If there was a deficit the plant would start to die back.

Arguably, with reduction in the formation of new leaves at high scale densities, the quality and quantity of feeding sites for the subsequent scale generation could be altered in a density dependent fashion (see Washburn *et al.*, 1985). The result could be that scale offspring may have difficulty finding a suitable settling site and may be forced to disperse to new plant patches or die.

Scale density and leaf area covered with sooty mould fungus were positively correlated (Fig. 4b). This corroborated reports by Newbery (1980b) and Brink & Hewitt (1992) who found a positive correlation between scale population density and the extent of sooty mould contamination on leaves. Various researchers have demonstrated that the deposition of sooty mould fungus reduces the rate of photosynthesis by reducing the leaf light-transmission and formation of chlorophyll (e.g. Wood *et al.*, 1988; Brink & Hewitt, 1992; Kaakeh *et al.*, 1992), often resulting in yield reduction (Kamburov, 1986). Wood *et al.* (1988) found that the presence of a lot of sooty mould on pecan foliage blocked penetration of photosynthetically active radiation to the leaf surface by up to 98% and reduced net photosynthesis of pecan leaves by 70%. They indicated that washing the

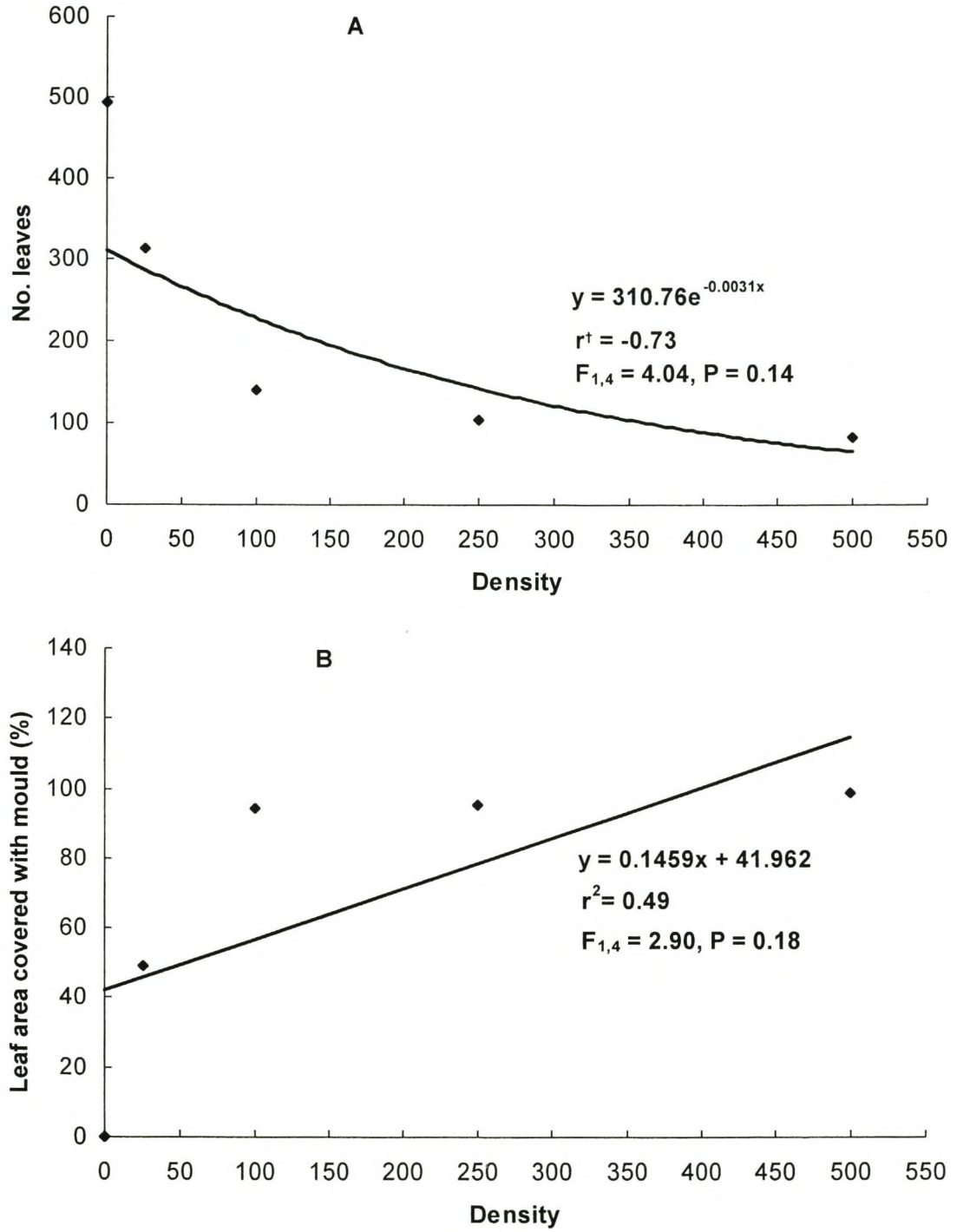

Figure 4. Effects of scale density on number of leaves (A) and percentage leaf area covered with sooty mould fungus of *Syzygium* trees infested with *Ceroplastes destructor*. † = Spearman Correlation coefficient.

sooty mould from leaflets allowed plants to recover after two days, indicating that sooty mould blocks the light and does not directly damage the leaf. Washburn *et al.* (1985) have also reported extremely heavy deposition of sooty mould on ice plants infested with high scale densities in a laboratory experiment. In the current study, despite the exposure of sooty mould to wind, rain wash off and ants collecting the honeydew on which sooty mould grew, heavy sooty mould deposition was recorded at high scale densities. This showed that once sooty mould colonizes honeydew, rains or wind currents were not likely to remove it, as was also noted by Tedders & Smith (1976). Conceivably, the heavy deposition of sooty mould on leaves, branches and fruits at higher scale densities could cause a reduction in fruit yield of citrus trees heavily infested with *C. destructor*. For example, the extent of flowering and fruiting by *Scaevola taccada* (Gaertn) was negatively correlated with the degree of infestation by *I. seychellarum* (Newbery, 1980b). The combined damage caused by sooty mould and the feeding by *C. destructor* therefore suggests that infestations of commercial citrus trees should be managed in order to maintain tree vigour and maximize productivity.

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CHAPTER 8

EFFECTS OF SOME CONVENTIONAL INSECTICIDES AND INSECT GROWTH REGULATORS ON THE DIFFERENT PHENOLOGICAL STAGES OF THE WHITE WAX SCALE, *CEROPLASTES DESTRUCTOR* NEWSTEAD (HEMIPTERA: COCCIDAE), AND ITS PRIMARY PARASITOID, *APROSTOCETUS CEROPLASTAE* (GIRAULT) (HYMENOPTERA: EULOPHIDAE)[†].

ABSTRACT

The toxicity of two juvenile hormone analogues, pyriproxyfen (Nemesis®) and fenoxycarb (Insegar®) and two contact insecticides, methomyl (Lannate) and methidathion (Ultracide) was evaluated against immature stages (LI, LII, LIII) of *Ceroplastes destructor* Newstead in the field. The effects of these chemicals and one moulting inhibitor, triflumuron (Alsystin®) and three insecticides: methyl-parathion (Penncap-M), profenofos (Selecron) and prothiofos (Tokuthion), on *Aprostocetus (= Tetrastichus) ceroplastae* (Girault) were assessed in the laboratory. Development of the first and second instar nymphs of *C. destructor* was completely arrested by the chemicals. Less than 1% of scales sprayed with pyriproxyfen at LII stage survived to adult female.

[†] *International Journal of Pest Management*, 2000 (in press).

Survival to the adult stage varied significantly between chemical treatments, and between chemicals and untreated controls ($P < 0.01$) for scales sprayed at the LIII stage. Female fecundity, fertility and body sizes of survivors of treatments applied at the LIII stage were not significantly affected by any of the chemicals ($P > 0.05$). All the chemicals exhibited high toxicity to *A. ceroplastae*. Only triflumuron was slightly harmful, while methomyl was the most toxic (harmful), causing 100% mortality in the first 30 minutes after treatment. Although all the chemicals evaluated had effectively arrested the first and second instars of *C. destructor*, none of them exhibited sufficient selectivity to *A. ceroplastae* to warrant recommendation for integrated management of *C. destructor* in citrus orchards in South Africa, where *A. ceroplastae* plays an important role.

1. INTRODUCTION

Although the synthesis and use of neurotoxic insecticides in the mid-1940s brought a radical revolution in the control of both medical and agricultural pests, their misuse not only resulted in failure of the chemicals to 'kill' but also brought upsets in the biological balance in agricultural and natural ecosystems. Natural enemies, that are the basis of biological control and many integrated pest management programmes, are often highly sensitive to synthetic insecticides and insect growth regulators (IGRs) used in the agroecosystem. DeBach (1974), for instance, argued that most disturbances of non-target pests and resurgence of target pests have been proved to be due to the adverse effects of pesticides on natural enemies. Nevertheless, many conventional insecticides, IGRs and juvenile hormone analogues (JHAs) are widely used in citrus and deciduous fruit orchards with the assumption that they are 'selective'. Empirical information on the

adverse effects of presently used insecticides and IGRs on natural enemies of citrus pests in general and of *C. destructor* in particular is scanty. In some instances, information available in published literature appears conflicting. Peleg (1988) and Darvas *et al.* (1994), for example, reported that fenoxycarb and some other JHAs are innocuous to hymenopterous parasitoids of red scale and soft scales, and that these products are compatible with citrus IPM programmes. However, the use of some IGRs and JHAs resulted in serious pest repercussions in different parts of the world. For instance, Hattingh & Tate (1995) reported that the wide scale use of triflumuron and pyriproxyfen resulted in serious repercussions of false codling moth and red scale in South Africa. Mendel *et al.* (1992; 1994) in Israel reported similar repercussions.

Ceroplastes destructor has never been regarded as a pest of major economic importance in South Africa. A complex of indigenous natural enemies provided excellent regulation for decades (Cilliers, 1967). In the recent past, however, its population has increased to pest proportions in some citrus orchards in the Western Cape Province of South Africa (Wakgari & Giliomee, 1998). The reason for this is largely unknown, although the continuous use of some IGRs (e.g. pyriproxyfen, triflumuron and fenoxycarb) and broad-spectrum insecticides (e.g. parathion, methomyl, methidathion methyl-parathion, profenofos and prothiofos) in orchards may be responsible through impairment of the important existing biological control agents. Moreover, there is no experimental evidence in published literature as to which developmental stages of *C. destructor* are susceptible to chemical control, although some authors have often suggested that the crawlers are the most susceptible. It was felt necessary, therefore, to assess the effects of these commercial products on the different phenological stages of *C.*

destructor and on *Aprostocetus ceroplastae* (Girault) (Hymenoptera: Eulophidae), a major primary endoparasitoid of *C. destructor,* and indicate their compatibility with citrus IPM programmes.

2. MATERIALS AND METHODS

2.1. Study sites

Field assessment of the effects of methomyl, methidathion, fenoxycarb and pyriproxyfen on different phenological stages of *C. destructor* was carried out at Rhodes Fruit Farms (Drakenstein), a commercial easy-peel citrus orchard located about 20 km to the north-east of Stellenbosch (33°54'S 18°57'E). No insecticide other than the experimental treatments was applied to trees in the experimental block. Bioassays using fenoxycarb, pyriproxyfen, triflumuron, methomyl, methidathion, methyl-parathion, profenofos and prothiofos against *A. ceroplastae* were conducted in the laboratory at the University of Stellenbosch, South Africa (see 2.5).

2.2 Field evaluation of chemicals against different stages of Ceroplastes destructor

Ceroplastes destructor is a univoltine species with three nymphal instars designated here as LI, LII and LIII, and an adult female designated as POF.

Seventy-five trees from two rows were marked subject to the presence of an identifiable number of scales and accessibility of branches for spray and population census. Two twigs, each 40cm long and 3-5 mm in diameter, selected at random from each tree, served as sample units. A completely randomized design with five replicates (= five trees) for each chemical was used at each scale stage. The number of live scales on

each sample unit was counted before the application of the chemicals. Each sample unit was then sprayed with either of the following products at a commercial dose to the point of run-off using a hand pump pressure spray. Fenoxycarb (Insegar®) 25 WP (25 % a.i. Insegar®)) at 0.1 % a.i.; 30 ml pyriproxyfen (Nemesis®) 100 g a.i. /*l* EC + 300 ml BP CIPRON emulsifiable oil 835 g a.i./*l* EC per 100 *l* water; 120 ml methomyl (Lannate) 200 g a.i. /*l* SL + 300 ml BP CIPRON emulsifiable oil 835 g a.i./*l* per 100 *l* water; 150 ml methidathion (Ultracide) 420 g a.i. /*l* EC per 100 *l* water. These products were sprayed on each of the LI, LII and LIII instar nymphs when they appeared. No subsequent sprays were applied to trees in the experimental block and to two guard rows on each side. Two sample units from each of five trees for every instar sprayed with water served as controls. Sprayed and control units were censused at monthly intervals for a period spanning a year. Female fecundity and egg fertility of survivors of treatments were assessed during treated generation.

2.3. Data analysis

Differences in survival rate, percentage mortality and female fecundity and fertility of scales treated with different chemicals were determined with analysis of variance (ANOVA) (Zar, 1984). Tukey's Honestly Significant Difference (HSD) Test was used for mean separation when significant F-values for treatments were recorded (Zar, 1984).

2.4. Parasitoid rearing

Aprostocetus ceroplastae was reared in the laboratory using two procedures. Firstly, twigs infested with susceptible scale stages were enclosed in emergence boxes of various dimensions in an incubator at 27 °C and 60 ± 5% RH. The boxes were made up of corrugated carton and were similar to that described by Bedford (1968). In the second method, scales from infested twigs were overturned with needles and sorted into stage categories before placing each stage separately into glass tubes of varying sizes. The tubes were then covered with cotton wool and maintained in an incubator at the temperature and RH indicated above. Emerging adult parasitoids were given bee honey smeared onto the walls of the collection tubes as a source of food. Mixed sex adults of 12-24 hrs old were used in all experiments to ensure homogeneity of their age.

2.5. Bioassay against Aprostocetus ceroplastae

Fenoxycarb, pyriproxyfen, methomyl and methidathion, at doses indicated above, and 20 ml triflumuron (Alsystin®) 480 g a.i. /*l* SC per 100 *l* water, 100 ml methyl-parathion (Penncap-M) 240 g a.i. /*l* SC per 100 *l* water, 100 ml profenofos (Selecron) 500 g a.i /*l* EC per 100 *l* water and 50 ml prothiofos (Tokuthion) 960 g a.i. /*l* EC per 100 *l* water were evaluated to determine their possible adverse effects on *A. ceroplastae* in the laboratory.

A contact bioassay of a dry film of chemicals deposited on glass plates (see below) was conducted in a series of aluminum cages constructed as follows: aluminum frame of 2 cm high and 10 x 10 cm internal dimensions (Fig. 1, VIIIb) was held between two glass plates of about 3 mm thick (Fig. 1, VIIIa). Three pairs of 7mm diameter

ventilation holes were drilled in each of two sides of the frame (Fig. 1, VIIIf). Five of the holes were covered with fine gauze. One of the central ventilation holes was fitted to a pipe extension of 2cm long and 5mm diameter to vent air through the cages (Fig. 1, VIIIe). The proximal end of the pipe extension was covered with fine gauze and its distal end connected to an aquarium pump by a plastic tube of 8mm diameter (Fig. 1, VIIId). Honey on cotton wool was supplied as a food for the parasitoids through one of the holes left open in the frame (Fig. 1, VIIIc). The glass plates were each separately sprayed with one of the test chemicals using a Potter's precision spray tower and left to dry for 15 minutes before pasting them to the frame with sticky tape and introducing *A. ceroplastae*. Cages sprayed with water served as controls. At least 60 adults were evaluated for each treatment and for the control in 6 replicates of 10 individuals to a cage. Cages were placed in an incubator at 27 ^{o}C and 70 ± 5 % RH.

Air flowed through the cages at the rate of 3309 ml per minute and was replaced at intervals of 25 seconds. The rate of airflow was measured with flowmeter (Fig. 1, II) connected to the aquarium pump (Fig. 1, I). The volume of dry air through a plastic pipe connected to a flask containing silica gel crystals (Fig.1, V) and of wet air through a pipe connected to a flask containing water (Fig.1, IV) was regulated by bolts (Fig.1, III) to obtain the required percentage humidity in the cages. Temperature and humidity probes (Fig. 1, VII) directly connected to a data logger (Fig. 1, VI) was inserted into the air pipe to monitor conditions inside cages. Parasitoid mortality in the treated and control cages was recorded at 3, 6, 12, 24, 48, and 96 hours after exposure. Corrections for parasitoid mortality in control cages was made using Abbott's formula (Abbott, 1925) (% treatment

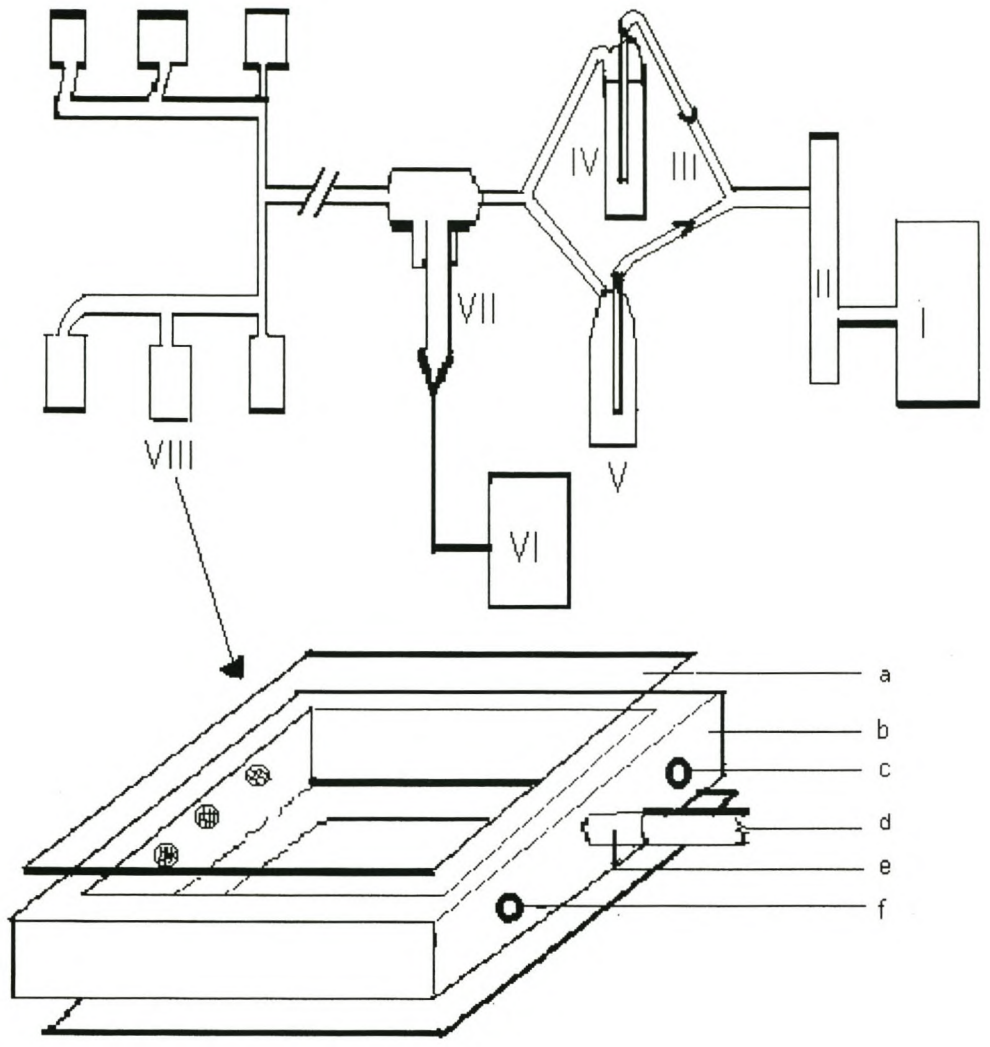

Figure 1. Diagram of the bioassay arena: **I**. Aquarium pump, **II**. Flowmeter, **III**. Bolts, **IV**. Flask containing water, **V**. Flask containing silica gel crystals, **VI**. Data logger, **VII**. Temperature and humidity probe, **VIII**. Aluminum test cage: **a**. glass plate, **b**. aluminum frame, **c**. feeding hole, **d**. plastic tube connected to the aquarium pump, **e**. aluminum pipe extension, **f**. ventilation hole.

mortality - % control mortality) / (100 - % control mortality). Mortality refers here to complete paralysis and inability of parasitoids to move.

In assessing the extent of the side effects of the products on *A. ceroplastae*, the working guideline of the IOBC/WPRS group was adopted (Hassan *et al.*, 1994). The guideline involves the testing of fresh dry spray deposits of products on leaves or glass plates against a given developmental stage of a beneficial insect. Treatment effects were classified according to toxicity categories for laboratory testing of pesticides against susceptible life stages of an insect as described by Hassan *et al.* (1994): 1 = harmless (<30% mortality); 2 = slightly harmful (30-79% mortality); 3 = moderately harmful (80-98% mortality); 4 = harmful (> 99% mortality). In this study only a direct mortality of adult *A. ceroplastae* as the result of contact with test chemicals was assessed.

3. RESULTS

3.1. Effects of chemicals on survival of Ceroplastes destructor

None of the first or second instar individuals sprayed with methomyl, methidathion and fenoxycarb survived to the third instar. Pyriproxyfen also caused 100% mortality when sprayed on the LI nymph, and the proportion surviving to the adult stage when this chemical was sprayed on LII was negligible (Table 1). Only 2.7 and 5.4% of the untreated scales (control) in the first and second instars, respectively, survived to oviposition. Mortality of *C. destructor* due to natural agents and miscellaneous factors was very high (see Chapter 5). The survival rate of scales to the mature LIII stage and to the POF when sprayed at the early LIII stage varied significantly between the treatments ($F_{4, 24} = 4.82$; $P = 0.0096$; $F_{4, 24} = 11.12$; $P = 0.00016$, respectively) (Table 1). Methomyl

Table 1. Mean survival rate of *Ceroplastes destructor* sprayed with two conventional insecticides and two IGRs at different phenological stages.

Stage		No. alive at	% Surviving to		
treated	**Treatment**	**treatment**	**LII**	**LIII**	**POF**
LI	Methomyl	282	0	0	0
	Methidathion	274	0	0	0
	Fenoxycarb	294	0	0	0
	Pyriproxyfen	276	12.0	0	0
	Control	300	19.3	4.7	2.7
LII	Methomyl	239	0	0	0
	Methidathion	241	0	0	0
	Fenoxycarb	216	43.5	0	0
	Pyriproxyfen	233	45.5	4.3	0.8
	Control	204	67.2	11.8	5.4
LIII	Methomyl	36	-	52.8a	22.2a
	Methidathion	41	-	51.2a	26.9a
	Fenoxycarb	33	-	72.7b	42.4b
	Pyriproxyfen	38	-	71.1b	39.5b
	Control	45	-	75.6b	55.5c

Mean survival rates for scales treated at LIII stage followed by different letter are significantly different ($P < 0.05$; followed by Tukey's HSD Test).

caused significantly higher scale mortality than methidathion, pyriproxyfen and fenoxycarb (Table 2). Scale mortality due to pyriproxyfen and fenoxycarb was comparable but significantly less than that caused by methidathion ($F_{3, 19} = 16.84$; $P = 0.0001$). Of the two IGRs, fenoxycarb caused relatively less scale mortality.

Table 2. Percentage mortality of *Ceroplastes destructor* sprayed with two conventional insecticides and two IGRs at different phenological stages (mortality corrected according to Abott, 1925).

	% Mortality of scales treated at		
Treatment	**LI**	**LII**	**LIII**
Methomyl	100	100	60.0a
Methidathion	100	100	51.5b
Fenoxycarb	100	100	23.6c
Pyriproxyfen	100	86	29.2c

Percentage mortality followed by different letter is significantly different ($P < 0.05$; followed by Tukey's HSD Test).

3.2. Effects of chemicals on fecundity, fertility and body sizes of surviving scales

None of the insecticides or IGRs sprayed on LIII nymphs had a significant effect on female fecundity or egg hatchability of survivors ($F_{1, 54} = 1.74$, $P = 0.156$) (Table 3). Also, no significant differences were found between body sizes (length, width, height) of females surviving the different chemical treatments.

Table 3. Mean fecundity (ranges in parenthesis), fertility and body sizes (mm) (standard errors in parenthesis) of *Ceroplastes destructor* treated with different chemicals at LIII stage and the untreated controls. Note that no females survived treatment at first and second instars (see Table 1) to assess these parameters.

	Fecundity	Percentage	Body size (SE)			
Treatment	**(range)**	**Fertility**	**Length**	**Width**	**Height**	**N**
Methomyl	720.10 (154-1218)	95.21	3.92 (0.28)	2.21 (0.20)	1.12 (0.09)	12
Methidathion	717.42 (38-1902)	95.62	4.18 (0.25)	2.35 (0.30)	1.29 (0.17)	12
Fenoxycarb	802.33 (197-1217)	96.71	4.46 (0.11)	2.94 (0.20)	1.66 (0.10)	12
Pyriproxyfen	642.25 (33-1218)	96.21	3.84 (0.22)	2.30 (0.17)	1.23 (0.15)	12
Control	1107.75 (161-2822)	97.77	4.51 (0.20)	2.90 (0.17)	1.46 (0.12)	12

3.3. Bioassay against Aprostocetus ceroplastae

All the chemicals evaluated against adult *A. ceroplastae* caused high mortality of parasitoids. Both fenoxycarb and pyriproxyfen induced mortality ranging from 80-92%, which is in the toxicity category of 'moderately harmful' (Table 4). Of the three IGRs evaluated, triflumuron was slightly less harmful than fenoxycarb and pyriproxyfen, causing 78% mortality of parasitoids. In cages sprayed with triflumuron, parasitoid

Table 4. Total and corrected percent mortality of *Aprostocetus ceroplastae* treated with different chemicals in the laboratory.

	% Mortality x hours after treatment						**%Corrected**	**Toxicity**
Treatment	3	6	12	24	48	96	**mortality**	**class**
Pyriproxyfen	0	0	88.3	88.3	88.3	90.0	88.0	3
Fenoxycarb	0	0	91.7	91.7	93.3	93.3	91.9	3
Triflumuron	0	0	0	75.9	81.7	81.7	78.0	2
Methomyl	100.0	-	-	-	-	-	100.0	4
Methidathion	58.3	100.0	-	-	-	-	100.0	4
Methyl-parathion	90.0	100.0	-	-	-	-	100.0	4
Profenofos	66.7	100.0	-	-	-	-	100.0	4
Prothiofos	93.3	100.0	-	-	-	-	100.0	4
Control	0	0	0	0	15.0	16.7	-	-

mortality was noted only 24 hours after exposure while with pyriproxyfen and fenoxycarb more than 88% of parasitoids succumbed only 12 hours after exposure. Methomyl, methidathion, methyl-parathion, profenofos and prothiofos caused 100% mortality of treated parasitoids in less than 6 hours of exposure. Methomyl was exceptionally toxic to the parasitoids, causing complete mortality within less than 30 minutes after treatment. Mortality in the control cages was about 17%, which was high but could be expected when exposing such fragile parasitoids in a confined environment.

4. DISCUSSION

The two IGRs, fenoxycarb and pyriproxyfen, induced extremely high mortality of the immature stages (LI-LII) of *C. destructor.* With fenoxycarb treatment there was no development beyond the LII stage and only a negligible proportion of those sprayed with pyriproxyfen at the LII stage survived to oviposition. Methomyl and methidathion also completely arrested development of the immature stages (LI-LII), and no individuals reached the adult stage at the end of the first generation. However, when sprayed on the LIII stage none of these chemicals induced complete mortality of treated scale, although significantly more scales survived both fenoxycarb and pyriproxyfen treatments than methomyl and methidathion. The first and second instar of *C. destructor* have their dorsum only partly covered with thin dry wax, which make them vulnerable to chemical treatments. In contrast, third instar females are embedded in a thick, translucent wet wax (Wakgari & Giliomee, 1998) that could act as a protective domicile against desiccation, adverse weather conditions, natural enemies (Takabayashi & Takahashi, 1992) and insecticides (Amitai, 1992). The results obtained here are consistent with findings of Peleg

(1982; 1988) and Eisa *et al.* (1991) for *Ceroplastes floridensis* Comstock and *Saissetia oleae* (Olivier), respectively.

The oviposition period of *C. destructor* in the field lasts for over two months due to asynchronized egg laying. This means that chemical treatment at early crawler emergence cannot provide sufficient control of that generation since late recruits can reinfest trees previously sprayed. By the time the LII starts emerging, which is about 7 to 8 weeks after egg laying, all the eggs will have hatched. The results of this study indicated that chemical treatments directed at the LII stage could provide sufficient control of this and the newly hatched crawlers without or with very minimum likelihood of reinfestation.

Female fecundity and egg fertility could be determined only for the adult females that had survived chemical treatments. Fenoxycarb and pyriproxyfen did not induce significant egg sterility or reduce the fecundity of surviving *C. destructor* females when sprayed on the LIII stage. Scale body sizes (length, width, height) were also not significantly affected by the treatments. This confirmed that chemical control at LIII stage was not effective for *C. destructor,* since scale survival was high and female reproduction was not impaired by such treatments.

All of the chemicals tested here were harmful to *A. ceroplastae,* some only 3 hours after treatment. Only triflumuron was slightly harmful. Fenoxycarb was the most harmful of the three IGRs, causing about 92% mortality of parasitoids less than 48 hours after treatment. Available information in published literature indicates that fenoxycarb has differential toxicity to beneficial arthropods. For example, Peleg (1982; 1983; 1988) reported that fenoxycarb had no adverse effects on parasitoids of *S. oleae, Chrysomphalus*

aonidum (L.) and *C. floridensis,* and according to Grenier & Grenier (1993) it is innocuous to parasitoids of *Aonidiella aurantii* (Maskell) and *Parlatoria pergandii* Comstock. On the other hand, a report by Mendel *et al.* (1994) indicated that fenoxycarb was detrimental to natural enemies of *Icerya purchasi* Maskell, *Planococcus citri* Risso and *Pseudococcus cryptus* Hempel. Rumpf *et al.* (1998) who compared the effects of 3 IGRs and 3 conventional insecticides on life-table parameters of *Micromus tasmaniae* Walker found that fenoxycarb had a more severe impact than any of the other IGRs or organophosphate insecticides tested.

Pyriproxyfen was almost as detrimental as fenoxycarb to *A. ceroplastae* in the present study. This juvenoid had been demonstrated to have a marked detrimental effect on parasitization and development of the dipterous parasitoid *Cryptochaetum iceryae* Williston (Mendel *et al.*, 1994). Its application in citrus orchards in Israel and South Africa against soft and armored scale insects resulted in outbreaks of *A. aurantii*, *I. purchasi*, *P. citri* and *P. cryptus* (Mendel *et al.*, 1994; Hattingh & Tate, 1995). Although triflumuron was only slightly harmful, the level of parasitoid mortality it induced was nonetheless too high for it to be recommended for any biological control or IPM programmes in citrus orchards. Triflumuron has also been demonstrated to have detrimental effects on natural enemies of *I. purchasi* and *A. aurantii* in South Africa (Hattingh & Tate, 1995). None of the IGRs evaluated was transient in its action, as observed effects were direct mortality of parasitoids through contact poisoning.

The effects of all the conventional insecticides tested here on *A. ceroplastae* were even more pronounced than those of the IGRs. Methomyl was the quickest in inducing complete mortality of parasitoids, indicating its incompatibility with biocontrol or IPM of

C. destructor. The detrimental effects of this insecticide against various beneficial insects have been widely documented (e.g. David & Horsburgh, 1985; Biddinger & Hull, 1995; Castane *et al.*, 1996). Methidathion also induced 100% mortality of *A. ceroplastae* within less than 6 hours after treatment, confirming its incompatibility with the *C. destructor* IPM programme. Methidathion has been demonstrated to be highly toxic to parasitoids of the citrus blackfly, *Amitus hesperidum* Silv. and to the coccinellid predator, *Delphastus pusithus* (Lec.) in the field (Fitzpatrick *et al.*, 1978). Furness (1977) found that methidathion remained toxic to parasitoids and predators of *Pseudococcus longispinus* (Targioni-Tozzetti) in the field for about a month.

Methyl-parathion, profenofos and prothiofos were all acutely toxic to *A. ceroplastae*, causing 100% mortality within less than 6 hours after treatment. Biddinger & Hull (1995) have reported that methyl-parathion caused high adult mortality of the coccinellid *Stethorus punctum* (LeConte) 24 hours after exposure. Profenofos caused extremely high mortality of the parasitoid *Apanteles marginiventris* (Cresson) and three predator species attacking *Heliothis* spp. on cotton (Wilkinson *et al.*, 1979). Bedford *et al.* (1992) indicated that profenofos at a high dosage (120 ml/100 *l* water) and prothiofos are not suitable for IPM of red scale and mealybugs.

Although all the chemicals evaluated here have completely arrested development of *C. destructor* when applied on LI and LII nymphal stages, none of them induced sufficient differential mortality of the host (*C. destructor*) and its parasitoid (*A. ceroplastae*) to be compatible with IPM of the white wax scale. However, the detrimental effects of these products require validation in the field as their effects may be affected by climatic conditions. The results also indicated that the wide-scale use of these chemicals

in South African citrus orchards may have been responsible for the recent upsurge of *C. destructor* in the Western and Eastern Cape Provinces through annihilation of *A. ceroplastae*.

Timing of chemical intervention, if used at all, is essential for effective control of *C. destructor* in the field. Conceivably, chemicals could be more effective if used at the early LII nymphal stage than at the LI for two reasons. Firstly, since all eggs of any given scale generation would have hatched by the time the LII starts emerging, action at the LII stage will avoid reinfestation. Secondly, active parasitization of *C. destructor* does not ensue at the LII stage of scale development and hence parasitoids may escape the detrimental effects of chemicals thereby achieving selectivity by timing. However, in the field various pests occur together and application of insecticides at different times in a season (early, mid, late season), often during active parasitization of *C. destructor,* appears routine. Under such conditions none of the chemicals tested here are compatible with biological or IPM programmes of *C. destructor* in citrus orchards. Furthermore, some IGRs have a long residual activity (e.g. Hattingh & Tate, 1995) and can interfere with the synchrony between pest species and their natural enemies in citrus orchards. They can lead to eradication of the entire population of the beneficial arthropods in the long term. Therefore, their persistence under field conditions must also be determined before their compatibility with citrus IPM systems can be established.

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CHAPTER 9

GENERAL CONCLUSIONS

This study was prompted by the increase in density and distribution of the population of *Ceroplastes destructor* Newstead in certain citrus orchards, particularly on easy-peel cultivars in the Western and parts of the Eastern Cape Provinces of South Africa. The study focussed on the morphology, biology, population dynamics, dispersal and survival rate at different densities of *C. destructor*. Knowledge of these aspects is a prerequisite for developing an integrated management programme.

In any biological study the correct identity of the species under consideration is of prime importance since costly mistakes in developing and executing management schemes could be made with incorrect identifications. Therefore, the different developmental stages of *C. destructor* were described and illustrated from field-collected and slide-mounted specimens. The main micro- and macro-morphological characteristics useful for identification of the different stages of *C. destructor* both in the field and laboratory were established and illustrated. Most of these characteristics are so minute and cryptic that they require special observation in the field and proper slide mounting for microscopic examination.

The most difficult stages of *C. destructor* to differentiate visually in the field are the first and second instars because of their striking morphological resemblance and concurrent colonization of both the leaves and young twigs of infested trees. Moreover,

both have a short and partially overlapping duration and are covered with dry wax. However, the first instar is smaller in body size than the second, the marginal wax rays that appear as inseparable unit during the first instar are clearly separated from one another and from the dorsal wax pad during the second instar, and the long apical setae that are clearly discernible in the first instar are absent during the second instar (Chapter 2). Differentiation of the first instar from the second on well-mounted microscopic slides is easier since most of the micromorphological characteristics of the two stages differ either in size or in number or in both. Differentiation of the third instar from the second or adult female both in the field and laboratory is relatively simple because of some distinct macro- and micro-morphological differences.

Female fecundity and body sizes of *C. destructor* varied considerably between females from different orchards and between individual females from the same orchard. Likewise, the population density of *C. destructor* differed considerably among orchards and generations. These are probably attributable to habitat heterogeneity such as variation in the edaphic or microclimatic conditions between orchards and between adjacent trees in the same orchard. Differences in microhabitat between individual trees within an orchard and the sites on the tree where the insects have settled may result in differences in body sizes and fecundity of individual scale insects. Furthermore, differences in citricultural and/or orchard protection practices at the various farms (see Chapter 3, Table1) could also be responsible for variations. Individual orchards should thus be monitored separately for decisions on control measures. Generally fecundity is very high with females laying up to 6355 eggs (Chapter 3, Table 2) and as a result populations can reach epidemic proportions under favourable conditions. No marked differences in the

period of recruitment of the different phenological stages were found between orchards (Chapter 3, Figs 8-12). In general, recruitment commenced in November and continued until late December and sometimes until middle January. The density of ray stages (LI and LII) peaked in January and February respectively. Peak population density of the LIII appeared in April and that of the adults in August. However, the phenology of *C. destructor* could vary between regions within the same country (e.g. like in Australia) depending on differences in climatic conditions. Under hot and humid conditions *C. destructor* is known to produce more than one generation a year (Smith, 1970; Smith & Ironside, 1974). Such variation should, if present, be monitored for devising proper regional management programmes.

In the current study, seven primary and three secondary parasitoids, as well as four predator species were recorded attacking *C. destructor* in the field. A eulophid wasp, *Aprostocetus ceroplastae* (Girault), accounted for more than 75% of the primary parasitoids (Chapter 4). This species occurred throughout the months in which active parasitization by other species was low. Although a considerable variation was noted between orchards in the levels of host parasitism and predation, peak percentage parasitism and predation in all orchards was synchronized with peak density of hosts susceptible to them. This implied that the host-parasitoid/predator interaction contained a density dependent regulatory mechanism. The variation in the level of parasitism and predation between generations nevertheless indicated that the regulatory effect of the natural enemies may not be strong enough to prevent substantial and long-term population fluctuations, particularly under routine insecticide spray programmes. However, census data for many successive generations are required before a definite

conclusion about the regulatory effects of the parasitoid/predator and the consequent response of the host population can be reached.

Both spatial and temporal dynamics of the population density of *C. destructor* was studied for three consecutive years in two of the study orchards and for two years in the other two. Major mortality factors responsible for the changes were identified. The critical stages for mortality were generally the third instar (LIII) and preovipositing adult female (POF), although a slight variation was found between orchards (Chapter 5). The relative importance of five mortality factors affecting the population density of *C. destructor* was analyzed using four methods of key factor analysis. These were graphic inspection of the relationship between k values (killing power of a mortality factor) and K (generation mortality) over successive generations, the largest regression coefficient for the relationship of k on K, the largest correlation coefficient between k and K, and a significant regression coefficient for the relationship of K on k. All of the methods confirmed that parasitoids, predators and miscellaneous factors were the key factors. A significant density-dependent mortality was demonstrated in the LI and POF stage categories. However, the regression coefficients for the relation between k and log density of survivors for most of the mortality factors involved was found to be either randomly scattered (causing random mortality) or negative (destabilizing the population) or too small (no significant density-dependent regulatory effect). It also appeared that k_5 (the miscellaneous factors) at RFF was a strong density-dependent factor that masked the effects of the other weak density-dependent relationships. The fact that the density of scales before and after a mortality factor acted was determined from the same sample units provided a valid proof of density-dependency since the independent variable was

free of sampling errors. Evidently, only a density-dependent factor would regulate the population density of an insect pest and provide stability. Developing a realistic population model for a given mortality factor would however require census data for several successive generations, and this aspect merits further long-term study.

Dispersal of *C. destructor* is by first instar nymphs, mainly on wind currents. This was demonstrated by surrounding citrus seedlings artificially infested with different crawler densities with rectangular, yellow sticky traps at different distances from the source (seedlings) and counting the number of crawlers trapped after six weeks (Chapter 6). The number of crawlers caught on the traps varied significantly between densities, trap distances and trap directions. Dispersal rate increased with an increase in crawler density at the source, indicating that dispersal was density-dependent. The number of crawlers caught on the yellow traps was inversely related to the distance of the traps from the source, suggesting that some crawlers were dropped off or were diverted by wind currents. Dispersal was also demonstrated to be one of the major factors responsible for the disappearances of crawlers in orchards (Chapter 5, Tables 1-4). Wind speed was high during the course of the experiment (November/ December – see Chapter 6, Fig. 1). Thus it was likely that both intra- and inter-orchard crawler recruitment on wind currents may have been responsible for the recent increase in distribution of *C. destructor* in certain easy-peel orchards.

Scale survival was negatively correlated with density, probably due to competition for resources, honeydew fouling and crowding effects. Scale body size and fecundity were inversely related to scale density, suggesting density-dependent intraspecific competition (Chapter 7). The association between female fecundity and

body size appeared to be stronger with increasing density, suggesting that at high density intense competition induced differential increments in body size. Scale survivorship declined with increasing density whereas scale parasitism and predation increased with increase in scale density.

Formation of new leaves of infested *Syzygium* trees also declined significantly with increasing density. This could be due to loss of sap as a result of scale feeding or due to sooty mould reducing the rate of leaf-light transmission and photosynthetically active leaf area. In the current study deposition of sooty mould fungus on leaves was found to be density related. The effect of sooty mould deposition on the growth and physiology of infested plants requires further investigation. If the amount of direct damage by scales on plants resulting from sap sucking and their indirect effect through encouragement of sooty mould growth can be quantified it would be possible to estimate the 'action threshold' level.

Field evaluation of efficacies of two conventional insecticides (methomyl and methidathion) and two insect growth regulators (IGRs) (fenoxycarb and pyriproxyfen) against the three immature stages of *C. destructor* (LI, LII, LIII) indicated that both the LI and LII were extremely susceptible to the chemicals while the LIII showed differential susceptibility to them. The effects of four conventional insecticides and four IGRs at doses recommended for South African orchards were evaluated against *A. ceroplastae* in laboratory bioassays. All chemicals were toxic to *A. ceroplastae* (Chapter 8). Only triflumuron was slightly less toxic. It was inferred that a single application of these insecticides during the early LII stage (early February) could render effective control of *C. destructor* since both the LI and LII stages would succumb and since all eggs would

have hatched by the time the LII emerges. This would avoid the possibility of re-infestation. Moreover, parasitoids that proved to play a key role in the regulation of populations of *C. destructor* (Chapter 5) are less active at this stage of host development and are thus likely to escape the effects of synthetic insecticides. However, since different chemicals are applied at different times in a year against different pests (see Chapter 3, Table 1), the danger of inadvertently killing most of the natural enemies of *C. destructor* is highly likely. It is essential to note that only a fraction of the broad spectrum of synthetic insecticides (conventional or otherwise) used in South African citrus orchards was evaluated in this study. It is important to assess the adverse effects on *A. ceroplastae* of as many of the commercial insecticides used in South African citrus orchards as possible in order to develop an effective IPM system for *C. destructor*. Both field and laboratory assays are warranted.

In view of the increasing abundance and distribution of *C. destructor* in certain easy-peel orchards, it is conceivable that augmentative release of *A. ceroplastae,* coupled with regular orchard monitoring and restricted spraying of selective insecticide/s, may be an effective way to curb the pest. *A. ceroplastae* is one of the parasitoids imported from South Africa to Australia in mid 1960s where it successfully established and provided effective control of *C. destructor* (Snowball, 1969; Sands *et al.,* 1986). Evidence is presented here that *A. ceroplastae* could provide better regulatory effect in its indigenous environment if interference by frequent spraying of orchards with broad-spectrum insecticides is limited. Therefore, developing a rearing technique for *A. ceroplastae* appears essential for augmentative biocontrol in places where serious upsurges in populations of *C. destructor* appear. To do this it is imperative to have a good knowledge

of which host stage is most suitable for rearing the parasitoid. In this regard, young adult *C. destructor* were found to be the most suitable since both males and females *A. ceroplastae* emerged from this stage in almost equal proportions (Chapter 4). Although the third instar *C. destructor* was susceptible to parasitism, the majority of the emergent *A. ceroplastae* were male, particularly those reared from early third instar. Thus, early third instar *C. destructor* would not be recommended as a host for a large scale laboratory rearing of *A. ceroplastae*. This also entails that for any augmentative biological control to be successful proper timing of release is essential. In a given *C. destructor* generation, the body size of the third instar could be large enough to support the emergence of equal proportion of both male and female *A. ceroplastae* from April. Therefore, augmentative release should be undertaken from April. However, the period of occurrence of the different phenological stages of *C. destructor* could vary from orchard to orchard and even more likely from region to region within a country. Hence, augmentative biological control should be based on strict monitoring of the phenology of the insect.

Finally, the results of the current study indicate that *C. destructor* can be effectively controlled using an integrated approach. In particular, the integration of orchard monitoring, orchard sanitation (e.g. thinning and destroying heavily infested plant parts), proper timing and the limited use of insecticides, leaving refugia around orchards for parasitoids and predators and augmentative release of *A. ceroplastae* are all ingredients of an effective management programme for *C. destructor*. For instance, *Syzygium* trees are widely grown around citrus orchards at Rustenburg Estate, serving as refugia for predators and parasitoids of *C. destructor*. Consequently, the population density of *C. destructor* was far lower in this orchard than in the other orchards studied.

The current study has generally attained its set objectives and contributed to the understanding of the morphology, biology, population dynamics and management techniques of *C. destructor.* It is also hoped that both the science of Coccidiology and the citrus industry at large will benefit from the results of the study.

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