INVESTIGATIONS INTO THE ECOLOGY OF A POPULATION OF CITRUS RED SCALE (*Aonidiella aurantii* MASK.) IN THE SWAZILAND LOWLANDS

by

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A thesis submitted for the degree of Doctor of Philosophy
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August, 1981.

ABSTRACT

In the Swaziland lowlands, biological control of the citrus pest red scale, *Aonidiella aurantii* (Mask.), has been consistently unsuccessful although it is successful in middle altitude regions. However, recent cases of resistance to organophosphate insecticides elsewhere in southern Africa, make it important to reconsider biological control of red scale in the lowlands. Should similar resistance be evolved in this region, the pest could be controlled only by natural means together with oils. This account attempts to answer questions about the natural control of a red scale population in the lowlands, by examining data collected between 1972 and 1975.

The population was continuously breeding with overlapped generations. It consisted of three sections, on leaves, twigs and fruit, having different rates of reproduction, development and mortality. These sections are considered separately but that on leaves, being relatively unimportant, is largely ignored. The generation mortality is estimated in the sections on twigs and fruit and related to climatic and biotic indices. The causes of seasonal and between-years variation in the sections on twigs and fruit are elucidated. The effectiveness of each kind of natural enemy is examined and the factors affecting natural enemy numbers are investigated. The question of population regulation is discussed. Differences in mean infestation levels in middle altitude and lowland regions are explained in terms of different rates of reproduction and mortality.

TABLE OF CONTENTS

CHAPTER PAGE

APPENDICES

INTRODUCTION

Background and history of the study

Red scale, *Aonidiella aurantii* (Maskell), is considered to be the most important citrus pest in the world (Ebeling, 1959). It is present almost wherever citrus is grown (Burke, 1967). Although it damages the trees only at high infestation rates, the presence of even a few scales on the fruit constitutes a blemish which is difficult to remove and which can make the fruit unsuitable for marketing; especially for exporting. The necessity for blemish-free fruit has led to the extensive use of insecticides in the industry and it is difficult to achieve the same quality by biological control.

In Southern Africa, red scale is regarded as the key pest on citrus because the methods used for its control dictate the approach which is adopted to control the whole pest complex (Georgala, 1963, 1964; Georgala *et al.*, 1972). At the time this study was undertaken there were three basic approaches to citrus pest control.

(i) Two or three preventative sprays for red scale, the first of which was applied at flowering in spring (August/September) and the second or third at more flixible dates as required. The materials were usually parathion with either oil or dimethoate. One or two preventative sprays of Abate or Delnav were also applied against citrus thrips (*Scirtothrips aurantii* Faure). Various other materials were used if necessary to control outbreaks of American bollworm (*Heliothis armigera*)or fruit flies.

This was the most common approach, particularly in the warmer areas where scale pressure was high. It was effective but expensive. For example the cost per tree for materials alone was about R1,00, while the net profit (after all expenses including marketing) from a Valencia orange tree in Swaziland might average R5-6,00.

(ii) A single preventative spray in spring for red scale and either one or two sprays for thrips. If they appeared, other pests were controlled on a corrective basis.

(iii) Biological or integrated control of red scale, with thrips controlled by materials (e.g. tartar emetic bait plus sugar) of low toxicity to natural enemies. Sporadic pests such as bollworm and fruit fly were treated on a corrective basis. Fungicides such as Dithane were used which had an acaricidal action. Many pests which could prove troublesome under a preventative approach tended to remain scarce under biological control, for example mealy bugs, and soft scales. However fruit blemish could still arise from low densities of mites or thrips.

Materials suitable for this approach were listed by Bedford (1968) and Catling (1969). Light mineral oils are of relatively low toxicity to hymenopterous parasitoids (e.g. Searle,1965) and their addition to toxic materials reduces both the initial and residual toxicity of the mixture to parasitoids (Searle,1964). Oils, either alone or mixed, have therefore formed the basis of corrective sprays for red scale in biological control orchards.

Bedford (1968 a,b; 1969; 1971) strongly advocated the use of integrated pest control on citrus, particularly in the relatively cool Western Transvaal where scale pressure was lower than in the warm Eastern Transvaal. Annecke (1969) also recommended this approach while Catling (1971 b) listed the regions in southern Africa where it had been successfully applied. The arguments in favour of integrated control were cheapness (to some extent offset by the need for better orchard surveys) and the fact that many potential pests were not troublesome under this approach. However in 1971 restrictions were placed on the use of parathion because of the low-residue requirements of some export markets. Only one application could be used, sprayed no later than eight weeks after petal-fall. There were suggestions that similar restrictions might be applied to other toxic but effective materials used for red scale control. These factors added to the arguments in favour of integrated control, at that time.

Between 1967 and 1970 in Swaziland, Catling (1971 a) had successfully applied integrated control in the cool middle altitude area (*c* 700m; the 'middleveld') of the country. He found it difficult to apply in the warm lowlands (below 460m; the 'lowveld') which constitute the main citrus growing region. The reason for this difficulty was the high infestation-rate of red scale in the lowveld climate (Catling, 1971 a). However Catling was unable to attempt the introduction of integrated control to the lowveld for longer than a year, which was considered too short a period to effect a successful transfer from chemical to biological control of red scale. By 1971 it had become apparent that the middleveld was unsuitable for commercial citriculture because of 'greening disease' which flourishes under cool climatic conditions and which is transmitted by the psyllid *Trioza erytreae* (Del Guercio). Hence by 1971 there were several good reasons for again trying to introduce biological control of red scale to selected orchards in the lowveld, this time over a longer trial period.

Between February 1972 and June 1975 I attempted to introduce biological control of red scale to an orchard at Swaziland Irrigation Scheme (altitude *c*280m). This was unsuccessful. After four years the red scale infestation was still far above a commercially acceptable level, despite the introduction of two exotic species of parasitoids and one species of predator. Similar unsuccessful attempts were made at Tambankulu Estate (altitude *c* 210m) between November 1972 and October 1973, and at Ngonini Estate (altitude *c* 380m) between December 1972 and June 1975. Detailed data were collected of the populations in all three orchards, the most extensive set being that collected at Swaziland Irrigation Scheme.

Objectives of this study

The attempts, described above, to achieve biological control of red scale in a warm region of Swaziland, were abandoned in 1975. Since then there have been several instances in South Africa of alleged resistance of red scale to organophosphate insecticides. In one instance, at Letaba in the Northern Transvaal, Nel *et al.* (1979) have proved that red scale is resistant to parathion, and also in varying degrees to a number of other organophosphates normally used on citrus. At Letaba, red scale has now been brought under control by a combination of biological control and the judicious application of oils. However, as yet there has been no case of insecticides resistance in the warm lowveld of Swaziland, where biological control of red scale will be more difficult to achieve than at Letaba.

In view of the possibility that insecticides resistance could at some time be evolved in the lowveld, it was relevant to examine again the data collected in Swaziland between 1972 and 1975. Analysis of the data might reveal those factors which could be better exploited to lower the mean level of infestation. The questions to which answers were sought were:

(i) What factors caused the seasonal fluctuations in red scale numbers?

(ii) Was the scale population naturally regulated about a mean level?

(iii) If so, which factors, or which natural enemies, seemed to be most effective in regulating the population?

(iv) What factors appeared to limit the numbers of natural enemies?

(v) Why was the mean level of the population so high?

For this analysis the data from Swaziland Irrigation Scheme were used because these data were the most extensive, and because that orchard had been unsprayed with toxic chemicals for the longest period. At the other two estates the populations in the experimental orchards fluctuated widely and were treated with corrective sprays. Eventually the orchard at Tambankulu had to be returned to a full corrective spraying regime because the scale infestation began to damage the trees.

CHAPTER 1

THE BIOLOGY OF RED SCALE

1.1 Red scale affinities, life cycle and natural enemies

The Coccoidea are divided into some twelve families of which the family Diaspididae, which includes red scale, is the largest and most specialised group (Beardsley and Gonzalez, 1975). Relatively few diaspids are serious pests of agricultural or horticultural crops.

Polyphagy is common among diaspids. According to Smit (1964) some 200 hosts have been recorded in southern Africa for red scale where the insect has been known since 1857. It attacks all aerial parts of the plant. When it, and the very closely related yellow scale (*Aonidiella citrina* Coquillet), infest the same tree, the latter species is restricted to leaves and fruit (Flanders 1956).

In the diaspids the gut behind the stomach is discontinuous with the hind intestine (Berlese, 1896). Honeydew is unknown, but excretion from the anus does occur and the material is incorporated into the scale cover (Baranyovits, 1953). The mouthparts consist, as in all Coccoidea, of a relatively short rostrum but four very long thin stylets comprising the rostralis. The inner pair of stylets are the maxillae and form two tubes, one for saliva and the other for food, while the outer or supporting pair of stylets are the mandibles. The process of stylet penetration has been described by several workers (e.g. Weber, 1930; Heriot, 1934). At each moult the stylets are broken off at the base and left in the host plant (Williams, 1970).

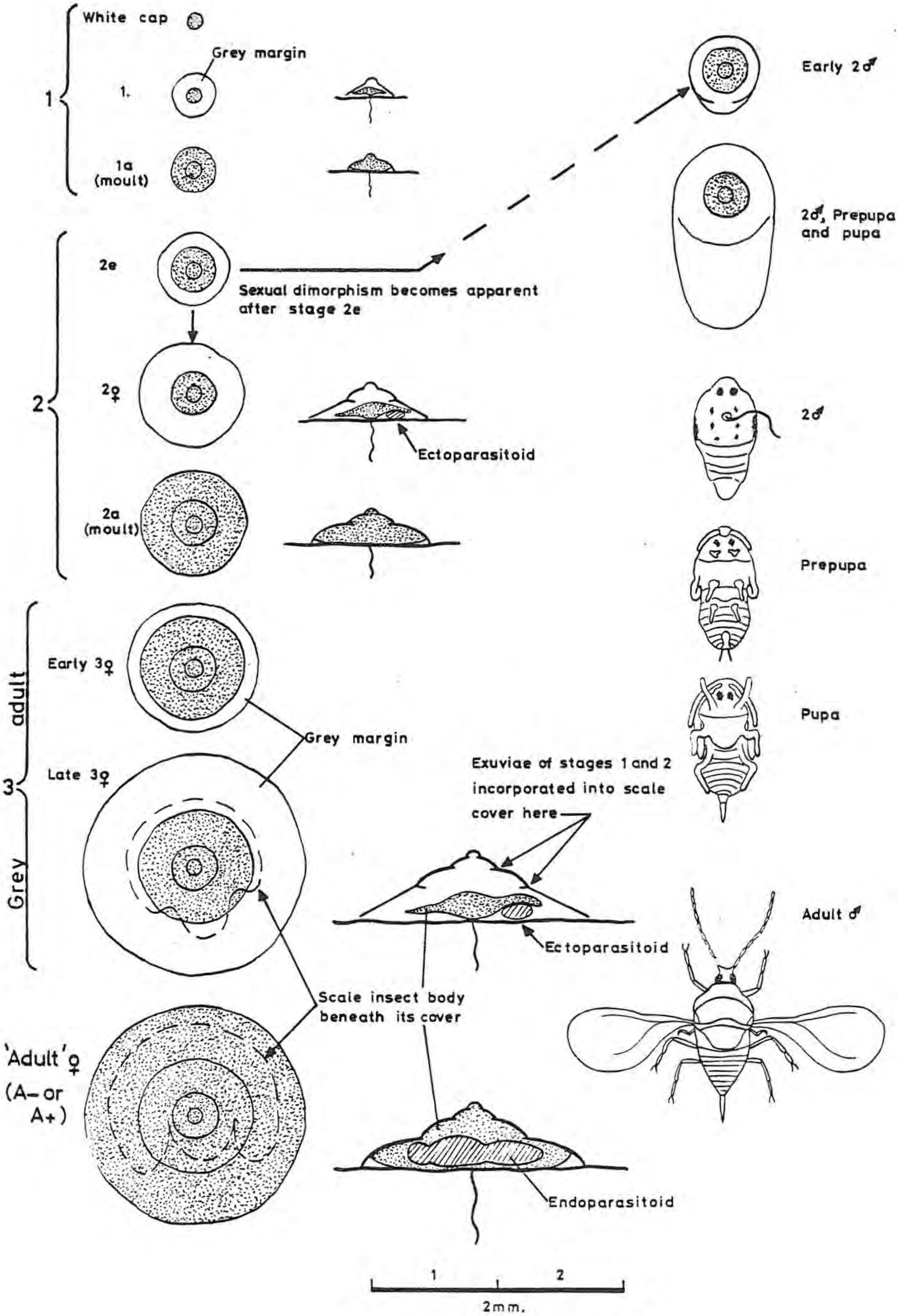
The sexes of diaspids are usually indistinguishable in the first instar, but in the early second instar there are small differences in the distribution of the secretory pores on the pygidium (Boratynski, 1953). However, in the second instar the male soon starts to behave differently; the amplitude of its oscillations decreases while it secretes the scale cover, and an elongated or oval scale results. The female on the other hand continues to turn through wide arcs of up to 270° making a circular scale but does not rotate continuously in the same direction.

The development of diaspids is remarkable. The females are neotenous, maturing in the third instar and are sessile; while the males pass through an essentially holometabolous development (Bodenheimer and Harpez, 1951) of five instars to produce a winged adult. MacGillivray (1921) pointed out however, that the wing buds of the pupa are external and not internal. Both the prepupa and pupa of the male are non-feeding and they lack stylets. In the female the exuviae of the first and second instars are incorporated into the scale cover (hence the name Diaspididae from the Latin, aspis, a shield), but in the male only the first exuviae are so incorporated (Fig. 1).

The scale cover consists of wax filaments secreted from pores on the pygidium (also on the body in the first instar). These filaments are moulded into a matt with fluid from the anus by oscillatory movements of the pygidium (Dickson, 1951) and the exuviae are also incorporated. The composition of the cover, according to Dickson (*loc. cit.*) is 47% proteinaceous material, 45% wax and 8% exuviae, and the only chitin is in the exuviae.

Red scale is bisexual as are most diaspids. The males of this species emerge in the late afternoon, stimulated by falling light intensity and they survive in the laboratory a maximum of 14 hours, with 50% dying within 6 or 7 hours (Tashiro and Beavers, 1968). One male is capable of fertilising up to thirty females according to Tashiro and Moffitt (1968), but the average

Fig 1. Diagrams of red scale stages.



is about twelve, under laboratory conditions. The pygidium of the early adult female stage, the grey adult, is extended before fertilisation takes place, but after fertilisation the pygidium is irreversibly retracted and out of reach of males. This retraction starts 24 hours after mating and is complete in three days (Tashiro and Moffitt, 1968). The grey adult secretes a pheromone (Tashiro and Chambers, 1967), but is no longer attractive to males after fertilisation and retraction of the pygidium. The attractiveness of the grey adult decreases with age, although they may remain attractive for up to 80 days if they are not fertilised (Tashiro and Moffitt, 1968). McLaren (1971) reported that red scale overwinters mainly as the grey adult in the relatively cold conditions of Victoria, Australia; and that this delayed mating results in a greatly increased initial production of young, due to the continued ovulation of the virgin grey adult.

The stages in the life cycle of red scale have been drawn approximately to scale in Fig. 1. The pattern of the development of the female is similar through each stage. First a grey margin is added around the edge of the scale cover by the insect, which is free and not attached to its cover. When the maximum size for the stage is reached, then the insect enters a moult stage during which it becomes attached to its scale cover. The insect reaches sexual maturity in its third instar; but it is convenient to subdivide this instar into a pre-fertilisation or third stage and a fourth post-fertilisation stage, the 'adult' (Fig. 1). The stage 3 female is free of its scale cover and adds a wide grey margin around the edge of this cover; hence the name 'grey adult'. This stage is subject to attack by ectoparasitoids of the genus *Aphytis* (Aphelinidae) as is the second stage of both sexes.

But the post-fertilisation adult becomes attached to its cover, seals the cover down onto the plant surface and retracts its abdomen. It is then no longer suitable for parasitisation by *Aphytis*; neither is the second moult stage, nor are the male prepupa and pupa.

The sealed down 'adult' stage consists of an egg-maturing stage (referred to hereafter as the A- stage) and a reproductive stage (the A+) which produces crawlers daily over a relatively long reproductive life. Red scale is ovoviviparous but most diaspids lay eggs. Crawlers form the only dispersal stage of diaspids, and wander over the plant before settling, inserting their stylets, and secreting a cover. In red scale this initial cover is a loose white structure, the white cap (Fig. 1). Willard (1972 b; 1973 a, b) has extensively studied the factors which stimulate red scale crawler emergence, crawler dispersal, and their wandering and survival times.

Several species of endoparasitoids emerge from the adult female, usually from the A- stage, but occasionally from the late stage 3 or the A+ stage. In Swaziland these parasitoids were the encyrtids *Habrolepis rouxi* Compere (indigenous) and *Comperiella bifasciata* Howard (imported) and a hyperparasitoid, *Marietta javensis* (Howard) (formerly *M. exitiosa* Compere). These parasitoids lay their eggs in any stage from stage 1 onwards, but nearly always emerge from the adult.

In Swaziland the common ectoparasitoid, which parasitised stage 2 of both sexes and the stage 3 female, was *Aphytis africanus* Quednau. *A. melinus* was released, but did not apparently become established during the period of study. A third species, possible *A. lingnanensis* Compere, was rarely recorded. The identification of *Aphytis* species has been discussed by Quednau (1964 a) and is based upon the pigmentation of the ventral surface of the almost-mature pupa.

Ants have long been known to associate with infestations of coccids. Red scale infestations are often exacerbated by ants, which apparently interfere with natural enemy activity (De Bach *et al.*, 1951 a, b). In southern Africa, two genera of ant are commonly implicated, *Plagiolepus* (=*Anoplolepis*) spp. and *Pheidole megacephala* F. (Steyn, 1954 a, b). To exclude ants from the canopy, fruit trees are banded either with a persistant insecticide or with a sticky compound.

1.2 The citrus tree as it affects the scale

In this section are discussed some aspects of the host plant as they affect red scale. So far as is known, seasonal changes in the nutritive value of those tissues of the host which are tapped by scales, have not been studied anywhere.

Citrus trees are evergreen. Leaf fall and replacement are continuous but the greatest leaf-drop occurs during the spring flowering and leaf flush cycles (August/September in southern Africa), and also at other leaf flush cycles (Scott *et al.*,1948). The average age of dropped leaves is 17 months but in the main leaf-falls all ages are included.

Leaf areas of Valencia orange trees were measured by Turrell(1961) and varied from $34m^2$ at three years old to $202m^2$ at thirty years. Since the area of the crown is much less than this, it follows that most leaves must be shaded by others (Erickson, 1968) as must most twigs, so scales on these sites would also tend to be shaded, at least in mature trees.

Flowering can occur out-of-season, but the main flowering and fruit set is in spring. A period of drought followed by rain or heavy irrigation stimulates flowering. Flowering is intense but only 52% of flowers set fruit, and only 5-7% reach maturity as ripe fruit (Reed, 1919). The initial drop (as flowers) does not affect scales, which migrate onto fruit as crawlers around November, but there is another fruit drop at this time, when temperatures rise in summer. This would affect the scale population on fruit but the extent of this mortality is unknown.

Bain (1958) divided fruit growth into three stages: (i) cell division, (ii) cell enlargement, (iii) maturation or ripening. Red scale immigrate onto fruit during early stage (ii), and the population on fruit reaches its seasonal peak in June when ripening takes place. It is not known how these changes in the fruit affect red scale population growth or decline.

In Swaziland on the lowveld, orange trees are picked from June onwards; to as late as September, although gibberellic acid sprays may be needed if the fruit is to hang as late as September. Picking removes a large section of the scale population, not only that on fruit but also by disturbance to the leaves and twigs. Natural enemies are forced to concentrate upon the residual population.

The effect of red scale upon the tree can be severe if the infestation is allowed to reach high levels. Leaf-yellowing and leaf-fall occur, the fruits drop, twigs die-back, and the production of the tree can be retarded for a year or more after the infestation has been controlled. Part of this effect is thought to be due to the injection of saliva by the scales (Ebeling, 1969).

1.3 Climate and red scale status as a pest

Climate dictates the number of generations of red scale

Table 1. Some citrus growing regions of the world rated for warmth and rainfall and red scale status as a pest

Country	Region	Rating	Red Scale Status
U.S.A.	Arizona	Hot/Dry	Minor
	Calif. coast	Warm/Dry	Major
	Calif. inland	Warm/Dry	Major
	Florida	Mild/Wet	Minor
	Texas	Warm/Dry	Major
Med, & North Africa	Morocco	Hot/Dry	Major
	Algeria	Hot/Dry	Major
	Lower Egypt	Hot/Dry	Minor
	Sudan	Hot/Dry	Minor
	Israel coast	Warm/Dry	Major
	Israel inland	Hot/Dry	Major
	Turkey	Hot/Dry	Major
	Greece	Mild/Moist	Minor
	Italy	Mild/Moist	Minor
	Spain	Mild/Moist	Minor
Far East	S. China	Warm/Wet	Minor
	Malaysia	Mild/Wet	Minor
	India (Ganges)	Warm/Wet	Minor
	Ceylon	Mild/Wet	V. Minor
	Japan	Warm/Wet	V. Minor
Australia	Victoria	Mild/Moist	Minor
"	Western	Warm/Moist	Major
New Zealand	-	Cool/Wet	V. Minor
S.America	Argentine	Warm/Moist	Major
	Brazil	Mild/Wet	Minor
Southern Africa	Rhodesia	Warm/Dry	Major
	N. Tvl	Mild/Dry	Major
	W. Tvl	Cool/Dry	Major
	E. Tvl	Mild or Warm/Dry	Major
	Swazi. lowlands	Warm/Dry	Major
	Swazi. midlands	Cool/Moist	Minor
	Cape coast	Mild/Dry	Minor
	Cape inland	Hot/Dry	Major

Hot = Mean summer maxima over 35°C
Warm = 30° - 35°C
Mild = 25° - 30°C
Cool = mean summer maxima below 25°C
Dry = mean annual rainfall under 600mm
Moist = 600 - 1000mm
Wet = mean annual rainfall over 1000mm

which develop per year. These can vary from two in cool climates (coastal California; Ebeling, 1959) to as many as seven in warm climates (Rhodesia; Jones, 1936) but it is debatable whether or not generations can really be distinguished under warm climatic conditions. In Swaziland, breeding continued throughout the winter, whereas in Victoria, Australia, McLaren (1971) states that a significant proportion of adult females remain unmated in winter.

On the Swaziland lowveld, mean daily maximum temperatures vary from 32°C in summer to 26°C in winter; while mean daily minima vary from 22°C in summer to 7°C in winter (20 year means; Murdoch, 1970). Frosts are rare on the lowveld. Annual rainfall averages 530mm (45 year mean; Murdoch, 1970).

This climate is extremely favourable for both red scale and citriculture. In order to view it in the context of other citrus climates of the world, which are often described in the red scale literature in terms such as 'warm', 'dry' or 'hot', Table 1 has been compiled. The sources for the table were Burke (1967), Bodenheimer (1951) and Catling (1971 b). The first two authorities compared regions worldwide, while Catling compared regions within southern Africa.

From this crude comparison it appears that warm dry regions are the most favourable for red scale. Some regions are too hot for the insect to be permanently present, for example Jericho (Bodenheimer, 1951) and in many of the areas listed as hot in Table 1, red scale is a minor pest. Other regions are too wet, for example Ceylon, where it is virtually absent (Bodenheimer, 1951).

In southern Africa, biological control of red scale has been possible only in areas where the total day-degrees above 30°C are less than about 200 D° per annum (Catling, 1971 b). These areas can all be described as mild, with two exceptions; Citrusdal and Clan William. These two areas are both in the Western Cape interior, and although summer temperature extremes are high, the winters are cold. The Swaziland lowveld falls into the warm/dry category with more than 200 D° per annum (Catling, 1971 b).

Table 2.1. Materials applied to the experimental orchard from 1968 onwards. Up to 1967 the orchard received full cover sprays of parathion and oil. All trees were banded with "Formex" sticky compound round the trunk for ant control from 1971 onwards.

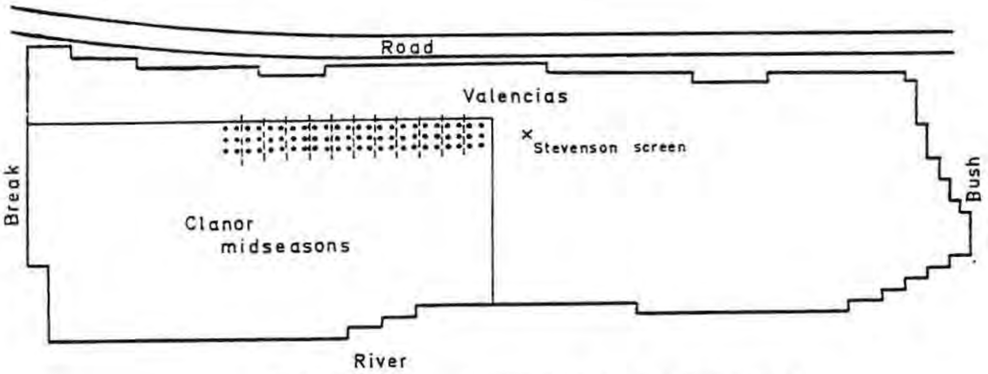
Season	Date	Materials	Remarks
68/69	20/ 9/68	Thiodan 5% dust	Aerial, for boll worm.
	4/12/68	Dithane	Fungicide.
	31/12/68	"	"
	11/ 4/69	Parathion and dimethoate	Corrective for scale
69/70	15/12/69	Dithane	Fungicide.
	16/ 1/70	"	"
	4/ 3/70	Parathion and dimethoate	Corrective for scale.
70/71	29/ 9/70	Parathion and oil	Light application for bollworm.
	12/11/70	2% oil	Corrective for scale.
	10/12/70	Dithane	Fungicide
	5/ 1/71	2% oil	Corrective for scale.
	9/ 2/71	Dithane	Fungicide
71/72	28/ 9/71	Tartox and sugar	Bait spray for thrips. Low toxicity to natural enemies.
	2/11/71	" "	
	3/ 1/72	Dithane	Fungicide.
	15/ 2/72	-Population sampling started in the experimental block	
72/73	5/10/72	Tartox and sugar	For thrips.
	23/10/72	" "	"
	11/12/72	Dithane	Fungicide
	21/12/72	Kelthane	Acaricide
73/74		Nothing	
74/75	15/10/74	Tartox and sugar	For thrips
	27/10/74	" "	"
	14/11/74	" "	"
	27/11/74	Dithane + $\frac{1}{2}$% oil	Fungicide & to discourage scale
	9/ 1/74	" "	Not on experimental block
	14/ 3/74	Dimethoate and oil	Not on experimental block

CHAPTER 2

COLLECTION AND PRELIMINARY ANALYSIS OF THE POPULATION DATA

2.1 The orchard and its history

The experimental orchard was at Swaziland Irrigation Scheme, Tshaneni, 280m above sea level, in the warm lowveld region of the country. The orchard was about 2ha in area with 1800 trees divided about equally between Clanor midseasons and Valencia cultivars of orange. The trees were 15 years old and 4 - 5m high, although some were wasted and dying from root-rot. The scale population was studied in a block of 72 Clanors in the orchard.



Plan of the orchard showing the experimental block.

The outline of the experimental block was altered slightly to exclude trees which developed root-rot symptoms during the period of study.

The history of insecticides useage in the orchard is given in Table 2.1. The last application of very toxic material before sampling began (on 15/February/1972) was in September 1970. Even before that, the frequency of application of toxic materials had been reduced to one corrective spray each season in 1968/69 and 1969/70.

2.2 Sampling methods

The experimental block of 72 trees was divided into 12 groups of 6 trees, each group being assigned a number at random on each sampling date. These numbers denoted the following regions and aspects of the tree canopy:

	N	E	S	W
High (c4m)	1	4	7	10
Middle (c2m)	2	5	8	11
Low (c1m)	3	6	9	12

One twig about 40cm long, complete with leaves and at least one fruit (when bearing), was removed from each tree according to its assigned region number. In this way at each sampling date a sample of 72 twigs was taken from all heights and aspects, without unduly altering the habitat or the population of scales. The twigs were placed in numbered boxes and taken to the laboratory.

The size of the scale population was assessed by counting the numbers of live adult female scales (excluding the virgin adult females, which were regarded as a separate stage) on the main twig axis, on four leaves at random, and on one fruit, on each of 48 - 60 twigs. The lower number was chosen at higher population intensities. At the same time, twig lengths and diameters, leaf lengths, and fruit diameters were recorded so that their areas could be calculated. (Leaf area is proportional to leaf length and could be read from a table prepared by measuring an initial sample of leaves).

Parasitism, predation and mortality from undefined causes were assessed on the remaining 12 twigs in the sample. About 500 scales of all stages were examined and dissected under a binocular microscope, on pieces of twig, whole leaves, and on whole fruits or segments thereof. A total of about 1500 scales was thus examined each sampling date, and the numbers of live, dead, parasitised and predation-damaged scales were recorded according to stage (instar) and site (leaf, twig or fruit).

The numbers of predators and of adult parasitoids were assessed at each sampling date with a D-Vac petrol engined suction machine. This had a 25cm diameter suction cone containing a fine net. Two or three groups of five trees in a row were sampled by walking down one side of the row and back the other. The net was changed for each group of five trees and the closed nets placed in a sweet jar containing cotton wool soaked with ethyl acetate to kill the insects. The trees were large, with the canopies meeting along the rows and sometimes between the rows, so that inter-tree variation in insect numbers was not great. The suction cone was pushed over the ends of the twigs and the number of twigs so sampled recorded with a tally counter.

In the laboratory each net, and all its plant debris, was brushed with a soft brush into petri dishes containing 70% ethyl alcohol. The dishes were examined with a X6 binocular microscope and all predators and parasitoids removed and counted. When parasitoids were extremely abundant, the average number for 4-5 microscope fields was multiplied by the number of fields per dish.

Temperature and humidity in the orchard were recorded with a thermohygrograph, in a Stevenson screen which replaced a missing tree. The temperature was checked periodically with a thermometer and the hairs moistened each week with a spray. Rainfall was recorded 1km away from the orchard.

The sampling interval was 2 - 3 weeks during the first three seasons, but rather shorter in the final season (1974/75). Sampling started in February 1972 and ended in June 1975. The entire sampling procedure measured three parameters of the population complex:

(i) The size of the scale population from counts of adult females on 48 - 60 fruits and twigs, and 192 - 240 leaves, at each sampling date.

(ii) Predation, parasitism and undefined-mortality levels in samples of about 500 scales on each type of site.

(iii) Predator and adult parasitoid numbers in suction-samples from 2 - 3 groups of 5 trees each.

2.3 Intensity or density measurements of insect populations

Southwood (1978,p.2) distinguishes three ways of expressing insect numbers in terms of units of their habitat.

(i) 'Density', or absolute numbers, where the estimates are expressed per unit area (m^2,ha) of ground over which the habitat extends.

(ii) 'Intensity', where the estimates are expressed per unit of habitat (per leaf, per twig, per plant).

(iii) 'Basic population estimates' where the estimates are expressed per unit area of plant surface (per m^2 of branch or leaf area).

In the present case, live adult females were counted on samples of leaves, twigs and fruit, and the areas of the leaves, twigs and fruit were also measured. So numbers could be expressed either per unit of plant (i.e. Southwood's 'intensity') or per unit area of plant surface (i.e. Southwood's 'basic population estimate').

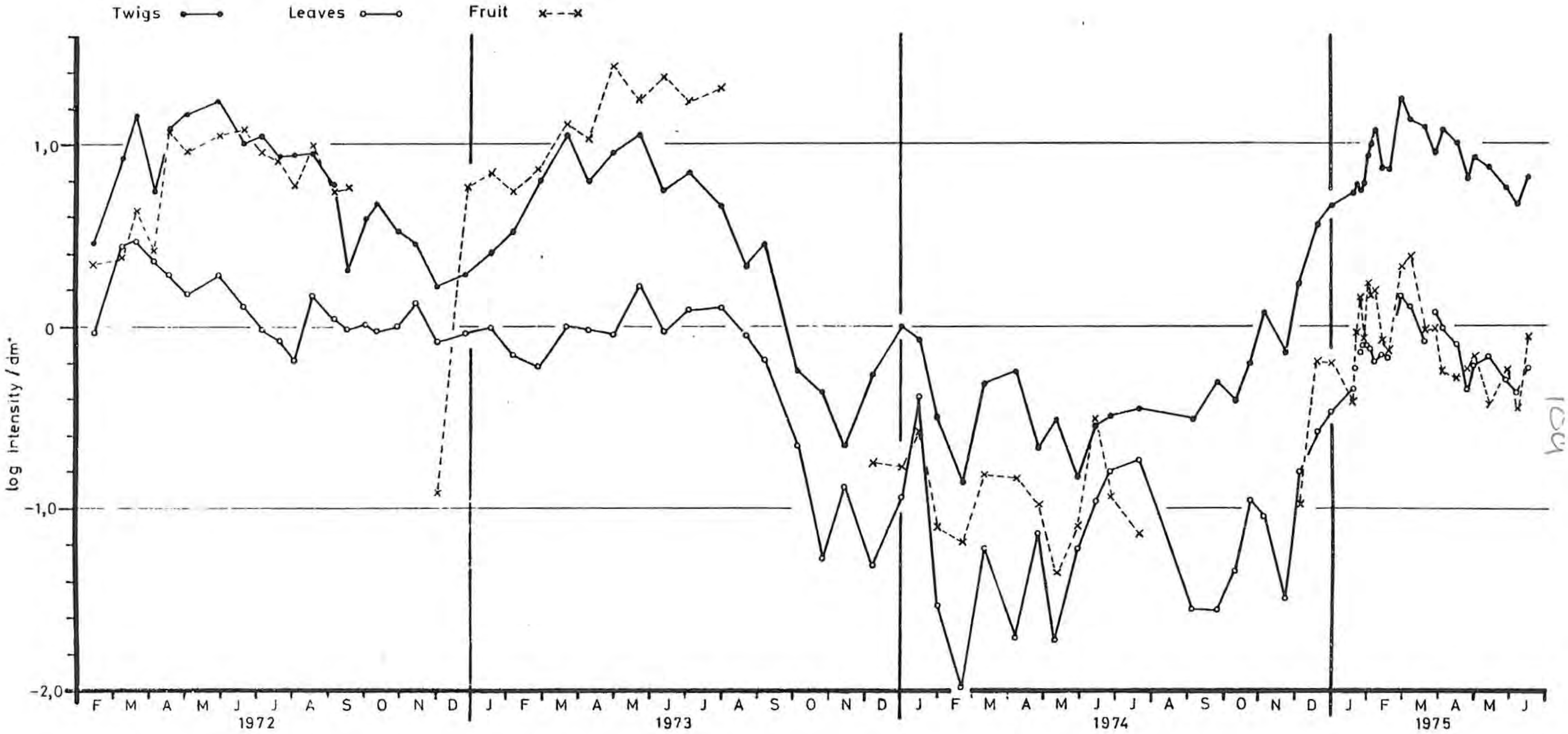
The basic population estimate is, according to Southwood, a unit intermediate between intensity and density. It is a useful unit for expressing insect numbers in forest or orchard habitats, where it is impractical to measure the area of the entire plants. In this account live adult female numbers have been expressed per dm^2 ($100cm^2$) of leaf, twig or fruit surface. There were advantages in treating the three sections of the population separately because reproduction, growth and mortality rates differed on leaves, twigs and fruit. However these basic population units could also be expressed as an average number per dm^2 of tree surface if required, whereas intensities per leaf, twig or fruit could not be similarly averaged over the whole tree. Because 'basic population estimate' is an unwieldy label, intensity/dm^2 has been used here.

Predator and adult parasitoid numbers in suction-samples have been expressed per 'twig', where the 'twig' was complete with leaves and fruit (when bearing), and was intact on the tree. In this account natural enemy intensities mean intensities per 'twig', and are intensities in the strict sense of Southwood (1978).

Southwood (1978) mentions a danger in using intensity or basic population units. Although intensities/dm^2 on, for example, leaves may be low, the absolute density of the population may be high because of the large leaf area on a plant. Therefore in February 1975 the total leaf, twig and fruit areas of a Clanor orange tree were estimated and the total number of adult female scales in the tree was calculated.

One large branch (base diameter 52mm) was removed and the lengths of all its leaves measured, as were the lengths and diameters of all its twigs and small branches, and the diameters of all its fruit. The total areas from these measurements were multiplied by the number of similar branches (51) in the tree.

Fig 2.1. Plots of adult female scale intensities per dm², on leaves, twigs and fruit.



The grand total areas for the whole tree were:

Leaves	100,8m^2	(one side of lamina only)
Twigs	27,8m^2	
Fruit	11,4m^2	(in February, when mean fruit diameter was 55mm).

Leaf area was for one side of the lamina because most scales settled on the upper surface. Assuming live adult female intensities/dm^2 of 0,5 on leaves, 2,5 on twigs and 1,8 on fruit then the numbers on each site in the tree were:

Leaves	5040
Twigs	6950
Fruit	2052
Total	14042

Thus in February, the absolute number of scales on leaves would have been comparable to the number on twigs, despite the low intensity per unit area of leaf surface. On the other hand, as fruit area increased during the season, so the absolute numbers of scale on fruit would have increased.

The conclusion is that fluctuations in intensity/dm^2 cannot have reflected the true changes in the number of scales in the tree. Nevertheless it was the only practical method to make routine censuses of the population.

2.4 Red scale population intensity plots

Intensities/dm^2 of live adult female scales are plotted in Fig. 2.1. Logarithmic plots have been used because there are many advantages in using this transform (Williamson, 1972):

(i) Insect populations are often so variable that they can be conveniently plotted only as logarithms (or on log paper).

(ii) Logarithms of population size tend to modify the frequency distribution of numbers per sample to more closely fit the normal distribution. This is useful when applying statistical tests to the data.

(iii) Relative changes in the size of the population are more easily seen. For example the same change occurs in a logarithmic plot when the numbers double from 10 - 20 as from 100 - 200.

(iv) The standard deviation of the population size gives a convenient measure of the variation in the population. This statistic is independent of the population size and so can be used to compare the variation in populations of different species, or of the same species in different habitats. Since 90% of the measurements of population size fall within 1,5 standard deviations either side of the mean, then antilog three times the standard deviation will approximate the number of times the maximum size of the population exceeded the minimum.

(v) Logarithms of population size fit in with the basic theory of population growth and survival rates. For this reason the logarithm of the survival rate has been used in fisheries, and insect population ecology, to express the effect of mortality on populations of the animals (Williamson,1972).

Some conclusions from Fig. 2.1 are:

(i) Adult female scales first appeared on fruit at the beginning of December. They must have started to colonise the fruitlets as crawlers from twigs during October, because growth from crawler to adult took about six weeks in summer.

(ii) There was a marked seasonal cycle in the population on twigs. In 1974 this cycle was missing. Mean log intensity/dm^2

on twigs was 0,47, equivalent to 2,9 live adult females/dm^2.

(iii) A seasonal cycle was not so evident in the population on leaves and the mean log intensity/dm^2 was much lower, -0,38, equivalent to 0,4 live adult females/dm^2.

(iv) On fruit the maximum intensity reached each season was rather variable. The mean log intensity/dm^2 was 0,11, equivalent to 1,3 live adult females/dm^2.

2.5 Variation in the scale intensity

Standard deviations of the log population intensities/dm^2 were:

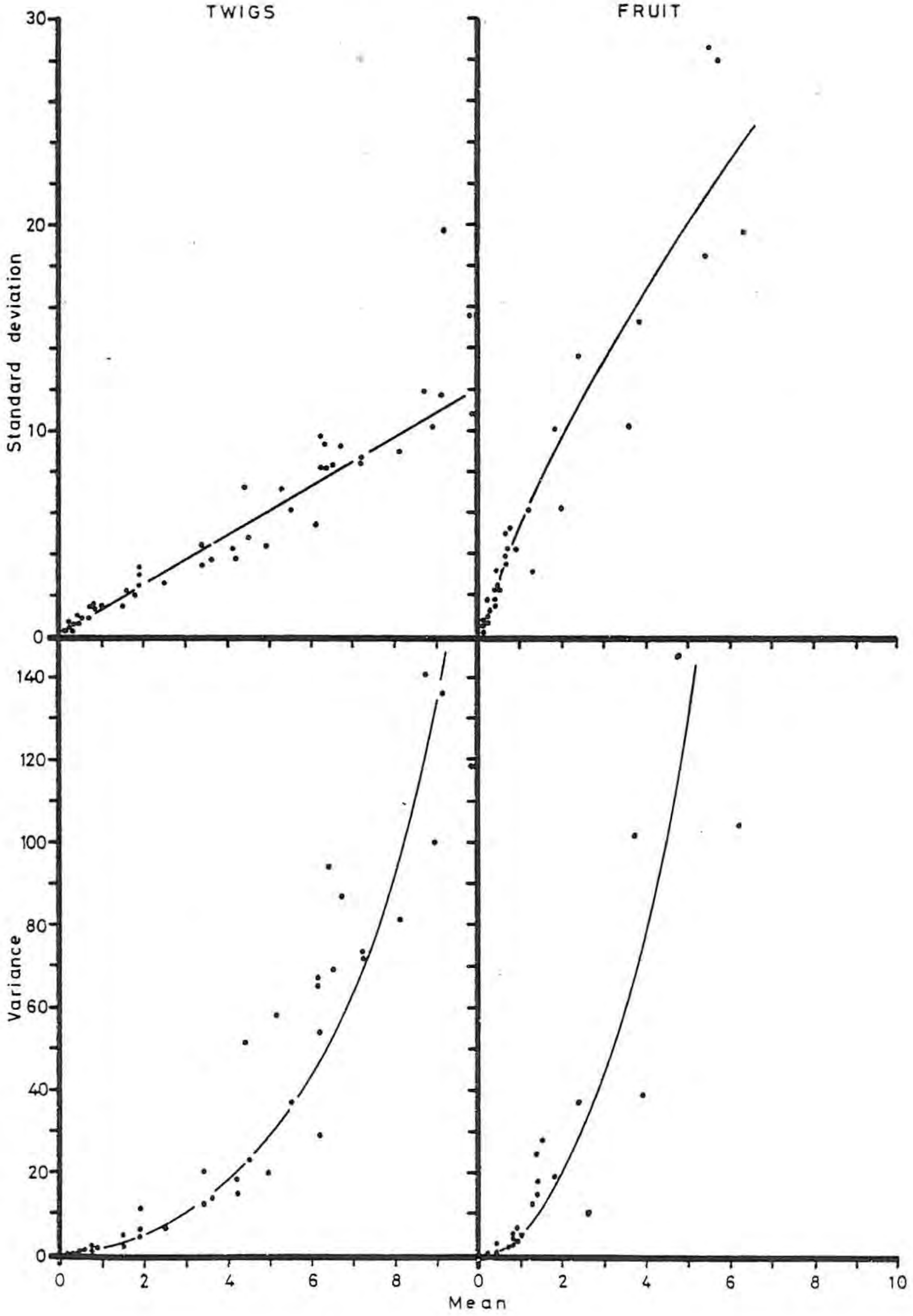
on leaves	0,591
on twigs	0,595
on fruit	0,777.

Variation in the population on fruit was rather greater than it was on leaves or twigs. Based on this information, under lowveld conditions the scale intensity/dm^2 on fruit could be expected to vary up to 200 times its minimum intensity, but on twigs by 60 times. These figures were obtained from antilog three times the standard deviations.

In 1974, when the population intensity/dm^2 on fruit was at a minimum, the cull of fruit for red scale blemish was 10%, which represented a maximum which could be tolerated in commercial operations. If one could reasonably expect up to 200 times that level of infestation, then the future of biological control of red scale under low veld conditions is not promising. In bad years it would be difficult to control such infestations with corrective applications of insecticides.

In Fig. 2.1 there are three kinds of variation:

Fig 2.2. Relationships between standard deviation and mean for untransformed numbers of adult female scales per twig (left) and fruit (right).

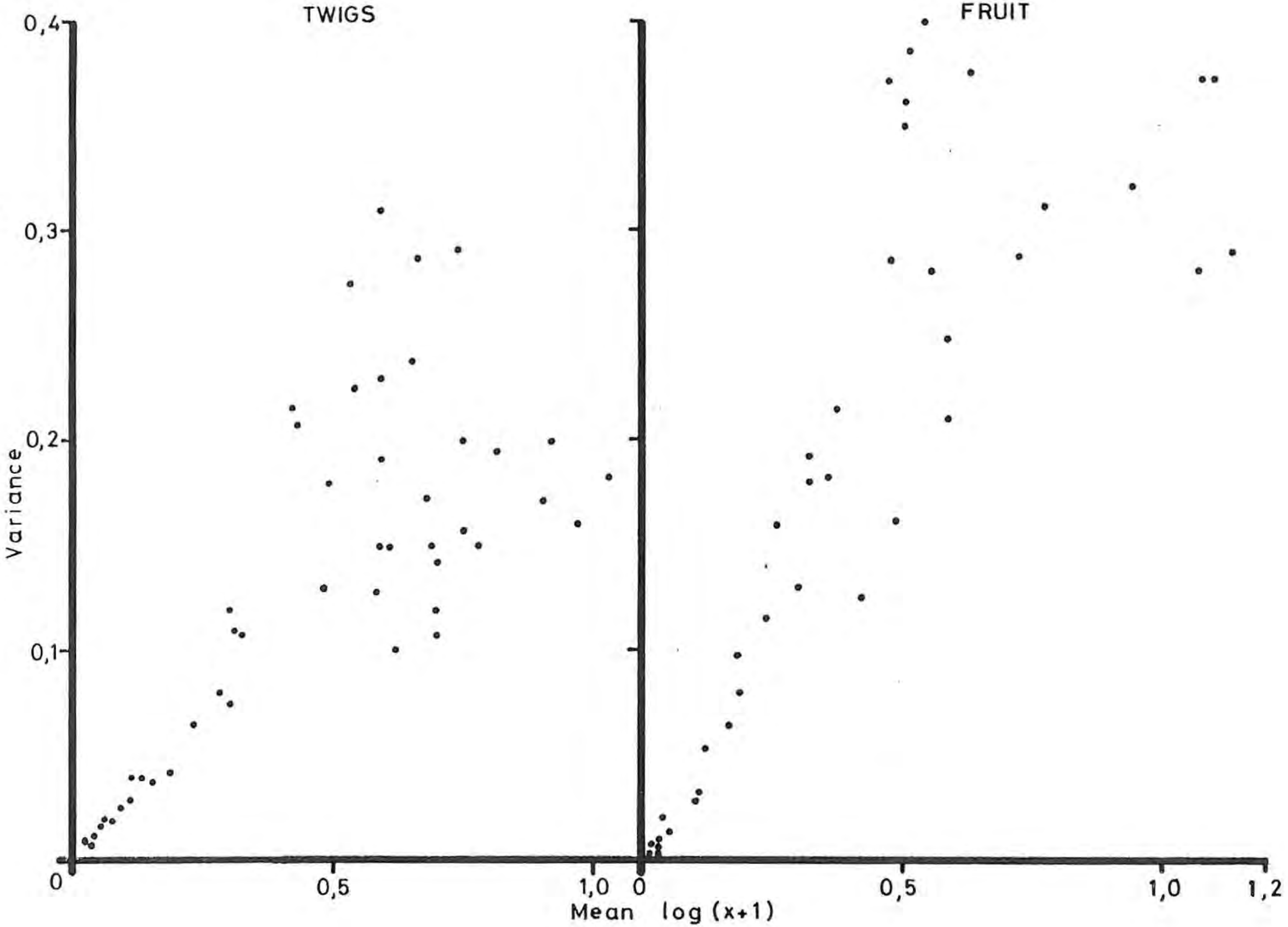


(i) Seasonal, which is discussed in section 2.6; (ii) between-years, about which it is difficult to draw conclusions because of the few years of data available; (iii) short-term variation, which is examined here, to see if it was real or if it represented sampling error.

Readings in Fig. 2.1 are the means of counts on 48 - 60 twigs or fruits, or 192 - 240 leaves at each sampling date. Many of these counts were zeros, while high numbers of scales were rare. This indicated that the frequency distribution of scale numbers in the samples was skewed, which is commonly the case in insect populations where individuals tend to be aggregated (Southwood, 1978). In order to determine confidence limits the data needed to be transformed to approximate a normal frequency distribution. Although taking logarithms helps to do this, highly skewed data may require other transformations (Southwood, 1978; Rayner, 1969). Consequently, frequency distributions were examined in the present data to determine the correct transformations. For this purpose, adult ♀ numbers were expressed as intensities per twig or per fruit, rather than per dm^2 of twig or fruit surface, because this was easier. The population on leaves was ignored. Mean intensities and their standard deviations were calculated for each sample counted on leaves and fruit.

With skewed frequency distributions, the standard deviation and variance increase with the mean. Rayner (1969) has illustrated how the various types of skewed frequency distributions can be recognised by the shape of the relationship between the standard deviation, or the variance, and the mean. Such relationships are shown in Fig. 2.2 for samples of scales counted on twigs and fruit; the distribution in twig samples seems to be lognormal, while on fruit it is either lognormal o negative binomial. The correct transformation for the lognormal distribution is to take logarithms (Rayner, 1969) but because of the many zeros in the present data, it was taken as log(x+1), where

Fig 2.3. Relationships between variance and mean after transforming intensities per twig and fruit to mean log (x + 1). At low intensities the variance still increases with the mean, but at high intensities it is relatively independent.



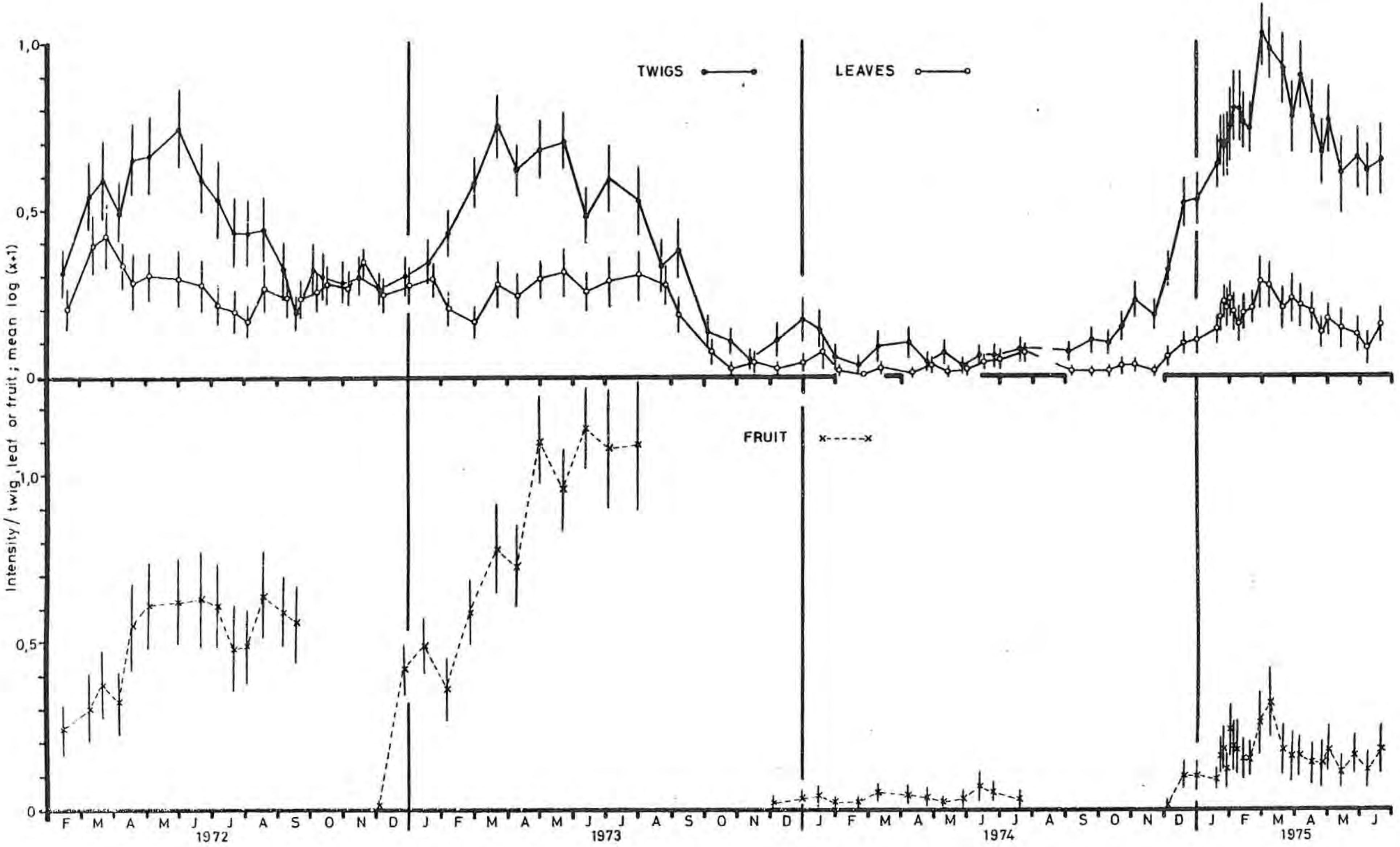
x was the individual count per twig or fruit. The transformation for a negative binomial distribution is $\log(x+\frac{1}{2}k)$ (Rayner,1969), where k is the 'dispersion parameter', an index of clumping (Southwood,1978). To calculate k is laborious, for example different methods must be used for low or high intensities (Southwood,1978). Moreover, values of k are often around 2 for insect populations (Southwood,1978), which would make the transformation similar to $\log(x+1)$. Consequently this latter transformation was used for twig and for fruit sample data.

Fig. 2.3 shows that after transforming to $\log(x+1)$, there was still some dependence of the variance upon the mean at low intensities, but that at higher intensities the variance was independent of the mean. The transformation was more successful for counts on twigs than on fruit.

Transformed intensities per twig, 4 leaves, or fruit are plotted in Fig. 2.4, with 90% confidence limits. Assuming that the counts are now normally distributed about the means, and therefore that many of the adjacent means are significantly different despite having overlapped confidence limits, then much of the short-term variation appears to be real. Bumps and troughs often coincide in the three sections of the population on leaves, twigs and fruit, which strengthens this conclusion. It is possible that heavily infested branches were selected one month and lightly infested ones the next, which would tend to make the bumps coincide on leaves, twigs and fruit; but this does not seem likely when one branch was taken from each of 48 - 60 trees.

Assuming that the bumps are real, the question arises as to what they represent. They could be generations, which start in

Fig 2.4. Adult female scale intensity per twig, 4 leaves,and fruit, transformed to mean log (x + 1). Ninety percent confidence limits suggest that some of the short-term fluctuations are real and not due to sampling error.



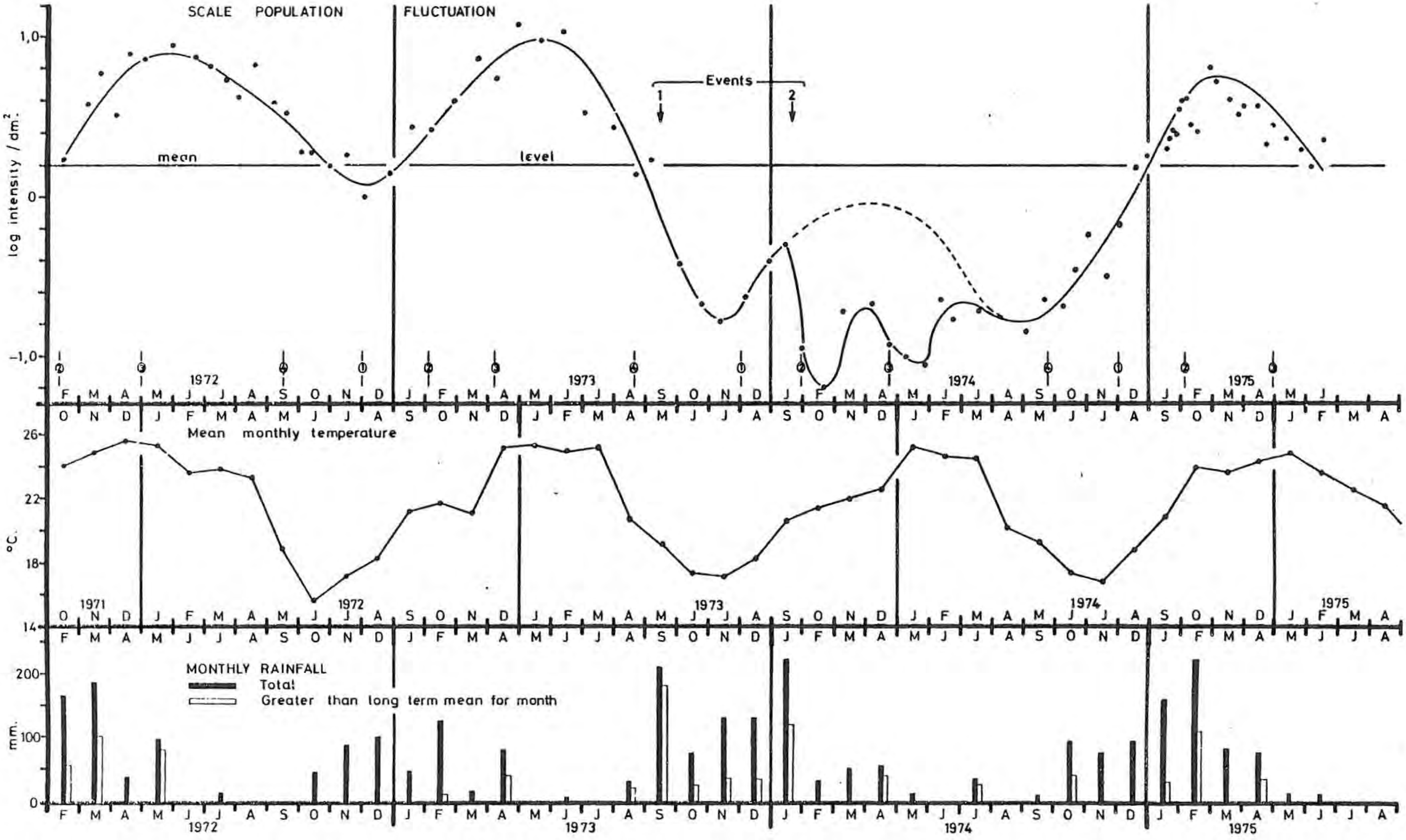
the spring when reproduction rates increase, and these generations would become more overlapped as the season progressed. In cooler climates (for example Queensland, Australia; McLaren, pers. comm.), female scales pass the winter mainly as virgin adults (stage 3), and are fertilised in spring. Adult males are inactive at temperatures below 15°C. In the Swaziland lowveld, reproduction continued through winter but much more slowly than in summer.

There may be other explanations of the short-term variation. For example Varley, Gradwell and Hassell (1974) have discussed how host/parasitoid interactions can induce oscillations in the numbers of both host and parasitoid. May and others (1976) have developed population models framed in difference equations, which suggest that regular or irregular oscillation could be inherent characteristics of the dynamics of some populations. Whatever the cause, such oscillation would be superimposed on the seasonal cycling of the population.

2.6 Seasonal and between-years variation

To investigate the seasonal cycling of the population, adult ♀ numbers on leaves, twigs and fruit were expressed as an average intensity/dm² of tree surface. The total number of live adult females in the samples of leaves, twigs and fruit, was divided by the total area of plant material examined in each sample. A smooth curve (Fig. 2.5) was drawn by eye through the points. The mean log intensity/dm² was 0,175 and a suggested mean level has been drawn at 0,20. The fairly constant upper limit of the cycles in three out of four years suggests that the population may have been regulated, but this is difficult to prove.

Fig 2.5. Average intensity of adult females per dm² of tree surface, compared with monthly rainfall at the same time, and mean monthly temperature four months beforehand. (Numbers in circles at the foot of the intensity plot indicate the number of generation-times which can be fitted into each year, and refer to the discussion in section 5.2.2.)



The seasonal cycle was associated with the temperature about four months beforehand (Fig. 2.5). There is a danger in this kind of correlation, to which Bursell (1974) has drawn attention. Estimates of insect population size and indices of weather are both examples of serially correlated data, in which adjacent readings tend to be related. If one set of data is then slid relative to the other, even though for the best biological reasons, then the chances are greatly increased of getting a correlation between the two sets. Nevertheless, the conclusion here is that temperature c four months beforehand in some way caused the seasonal cycling in scale intensity/dm².

In Fig. 2.5, two events appear to have prevented the 1974 cycle from occurring. Firstly, in September 1973, something caused the population to descend to a very low level. Secondly, in January 1974, the seasonal increase was cut short and the population did not increase again until the following spring. In each of these months the rainfall was well above the long-term mean for that month (52 year means for Homestead, 15km away; Murdoch,1970), particularly in September 1973 (Fig.2.5). However the rainfall was also above average in February and March 1972, and February 1975, but in neither instance was the scale population affected. In the lowveld, citrus is irrigated but the water applied by irrigation in the experimental orchard was not measured. Possibly in 1973/74 the above-average rainfall coincided with irrigation whereas it did not in 1972 or 1975. Certainly the high rainfall during 1973/74 produced changes in the quality of the fruit at S.I.S. and other estates, such that Clanors and other midseasons had to be rejected for export because of low ratios of solids to juice. If the rainfall was sufficient to alter the fruit quality it may also have had some effect upon the soluble materials ingested by the scale insects, not only on fruit but on twigs and leaves.

An alternative explanation for the failure of the seasonal scale increase in 1973/74 is suggested by examining Table 2.1. No fungicides or insecticides at all were applied to the orchard during the 1973/74 season. Although none of these materials was applied to the experimental block in other years, the increased reservoir of natural enemies resulting from the lack of disturbance to their populations in the whole orchard, may have given better scale regulation within the experimental block. If this is the explanation, then the future for biological control under lowveld conditions does not look promising. Low-toxicity insecticides must be used against thrips and sporadic pests, while fungicides are always necessary to control various fruit blemishes.

There were insufficient data to properly examine the between-years in the population. However regressions were calculated between the scale rate of increase each year and indices of rainfall and temperature during the period of increase. The variables were derived as follows:

(i) Rate of increase on twigs: Peak intensity/dm^2 (between February and May; Fig. 2.1) minus minimum intensity/dm^2 (between previous September and November), divided by the number of days from minimum to peak. The minimum in 1971, before sampling started, was taken as the average of the minima in the other three years, and assumed to have occurred in October.

Table 2.2. Effect of rainfall and temperature on the observed rate of red scale increase in each season, 1971/72 - 1974/75, for the populations on twigs and fruit.

Site and Year	Rate of Increase (y)	Rainfall index (x_1)	Temperature index (x_2)	Regressions		
				y on x_1	y on x_2	y on x_1, x_2
Twigs		Sept-Dec	Min-Peak			
1971/72	0,0442	0,6465	0,2659	b_1 -0,0406	b_2 -2,3290	b'_1 -0,0172
1972/73	0,0361	0,4097	0,2851	r^2 0,5006	r^2 0,7554	b'_2 -1,8565
1973/74	0,0017	1,8394	0,2903			R^2 0,8138
1974/75	0,0933	0,5590	0,2616			F 2,1849
Fruit		Oct-Jan	Min-Peak			
1971/72	0,0766	1,4992	0,2505	b_1 -0,1388	b_2 3,6102	b'_1 -0,2527
1972/73	0,2034	0,6566	0,2760	r^2 0,8281	r^2 0,4258	b'_2 -4,6064
1973/74	0,0023	2,0682	0,2429			R^2 0,9641
1974/75	0,0318	1,3302	0,2715			F 13,4090

Rate of increase on fruit: Peak intensity (between March and June), divided by the number of days from 1st December, which was the approximate date when the first adult females matured on fruit.

(ii) The rainfall index, x_1, was the total rainfall over the period of increase, times the number of days of rain. This gave in one index a measure of rainfall and of the strength of showers (which might have washed-off the younger stages; Jones, 1936; Bodenheimer,1951). The index was coded $x10^{-5}$.

(iii) The temperature index, x_2, was the mean daily hour-degrees (h°) above 12°C during the period of increase. (Thermal summation of h° and the threshold temperature of 12°C are discussed in Chapter 3). The index was coded $X10^{-3}$.

The results of simple and multiple regressions are given in Table 2.2. They are not significant because only four sets of readings were available. Nevertheless the high values of the coefficients of dispersion (r^2 or R^2) suggest that if more data were available, then a high proportion of the variation in the seasonal rate of increase might be explained by indices of rainfall and temperature. In Table 2.2, the partial regression coefficients for the temperature indices (b_2') are negative, which indicates that hot summers had an inhibitory effect upon seasonal increase. This, coupled with the inhibitory effect of rainfall (b_1'), suggests that it was dry summers rather than hot ones, which caused high rates of increase. This conclusion agrees with the general conclusion from Table 1 (section 1.3) on the status of red scale as a pest in warm, dry, climates.

Table 2.3 Crawler migration: net loss or gain to each type of site (T,L,F = twigs, leaves, fruit).

Dates 1975/76	Total crawlers deposited on		Total crawlers settled on:			% loss from	Remarks
			Twigs	Leaves	Fruit		
18/3-11/4	Twigs	214	165	47	-	T 22,2	No fruit
18/3-11/4	Leaves	218	39	159	-	L 19,7	"
18/4-12/5	Twigs	178	115	44	-	T 27,7	"
18/4-12/5	Leaves	178	28	100	-	L 21,9	"
18/4-12/5	Fruit	213	0	0	159	F 0	Fruit 80mm dia.
2/9-20/9	Twigs	263	188	-	12	T 6,0	Fruit 25mm dia. Leaves blanked-off
19/1- 8/2	Leaves	421	54	280	-	L 16,2	No fruit
19/1- 8/2	Twigs	603	429	56	12	T 13,7	Deposit site 20cm from fruit
19/1- 8/2	Fruit	653	38	18	565	F 9,0	% gain to fruit (45mm dia.): 2,4 % gain to leaves : 11,3 % gain to twigs : 6,1 % gain to leaves : 2,9 Fruit 50mm dia.

2.7 The relationship between the populations on twigs and fruit

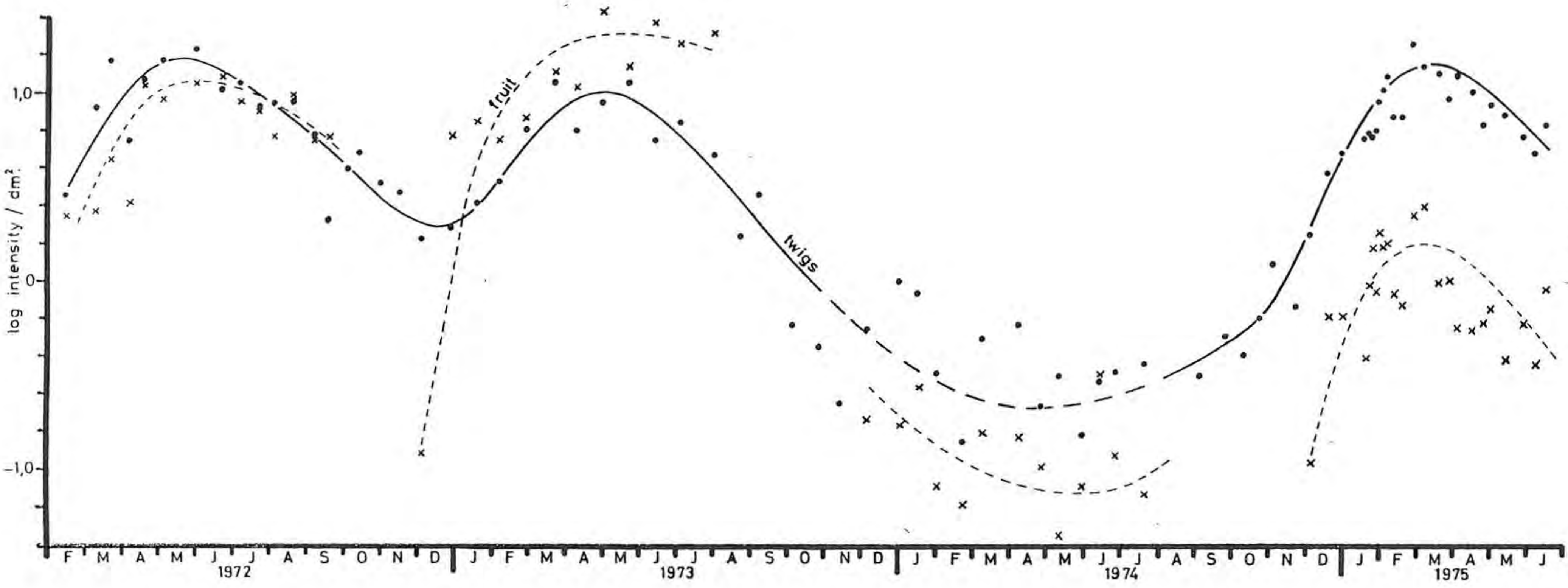
Scales on twigs constituted the residual population after the fruit had been picked. To some extent scales on leaves would also have contributed because leaves stay on the tree about 17 months (Scott *et al.*, 1948), although the rate and duration of reproduction were reduced on leaves compared to twigs (Chapter 4). Adult females first matured on fruit early in December and must therefore have started to migrate onto the fruitlets as crawlers in October.

Measurements of crawler migration between sites (Table 2.3) suggested that the exchange of crawlers between twigs and leaves was about equal at 20%, but that movement from twigs to fruit was small (2,4 - 6,0%) and from fruit back to twigs also small (0 - 9%). However these experiments, performed on seedlings in the insectary, gave no indication of the migration rate onto fruit during early summer (October - December). This rate of immigration probably varied each year.

Fig. 2.6 shows that each season the intensity/dm² on fruit followed that on twigs, except in the final year, 1975, when it failed to catch up. Since the maximum intensity/dm² on twigs in 1975 was similar to the intensities reached on twigs in 1972 and 1973, whereas the intensity/dm² on twigs in spring 1974 was rather low compared to 1973, it follows that the maximum intensity/dm² reached on fruit depended upon the spring intensity/dm² on twigs rather than upon subsequent immigration of crawlers from twigs later in the season.

Fig. 2.7 shows a close relationship between the maximum intensity/dm² reached on fruit each season and the intensity/dm² on twigs the previous November. November would be about the middle of the period of immigration from twigs to fruit; immigration

Fig 2.6. Smooth curves (fitted by eye) to show the relationship between the seasonal trends on fruit with those on twigs.



having started in October and the adult females having become established by the end of December. After the end of December there was not a marked increase in scale intensity on fruit (Fig. 2.6).

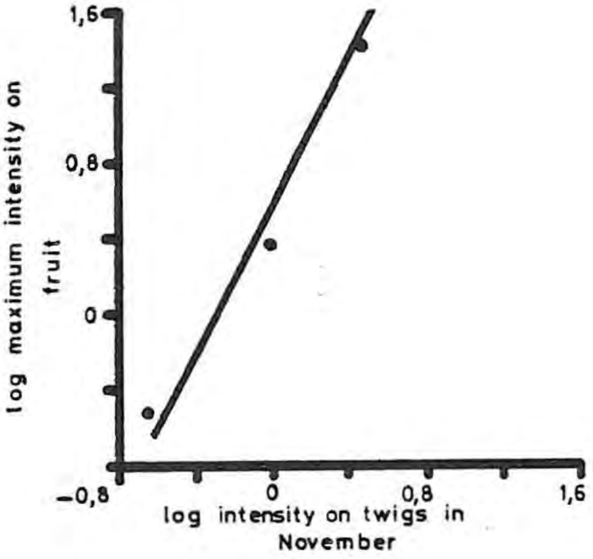
The conclusion is that the scale intensity on fruit largely depended on the rate of crawler immigration from twigs between October and December. Subsequent immigration does not appear to have been important.

2.8 Predation, parasitism and undefined mortality

Predators are defined as insects which consume more than one individual prey insect per predator,to complete their life cycle. Parasitoids are predatory insects which require only one individual prey insect per parasitoid. Whereas predators often attack more than one species of prey, parasitoids are usually adapted to only one species, described as their host. Parasitoid larvae kill their host by feeding in or on the host, which is said to be parasitised.

Predator-damaged scales were distinguished by the ragged holes chewed in the edges of scale covers, or by the cover having been lifted and the scale body removed. Undoubtedly many individuals in this category of mortality were not recorded because the scale covers fell off the tree. In addition, some predators (Chrysopidae) sucked their prey dry and these scales would have been recorded as dead from undefined causes. On the other hand, predation-damaged scales probably remained on the tree for some time, and so tended to accumulate in the population. This tendency would have exaggerated the level of predation and have masked fluctuations in it. Predation of female scales occurred in stages 1 - 3. Adult females were rarely attacked and then only in the region of the pygidium, where crawlers collected after birth. Stages 1 and 2 of males were attacked.

Fig 2.7. Trend of the maximum scale intensity/dm² reached on fruit each season, with the scale intensity/dm² on twigs the previous November.



Aphytis species parasitoids laid their eggs on the outside of the body of stages 2♂, 2♀ and 3♀, and the larvae also fed in this position. They are referred to as ectoparasitoids. A few *Aphytis* eggs, but no larvae, were also noticed on the male prepupa.

Aphytis parasitoids not only oviposit on scales, but probe scales with their ovipositors and feed on the exudates. Such mutilated scales are indistinguishable, except when fresh, from those which have died from undefined causes. According to DeBach (pers. comm.), host mutilation may account for three to five times as much mortality as from parasitism. However Quednau (1964b) published much lower ratios of about 1:1 for laboratory populations of *A. lingnanensis* Comp.; as did Abdelrahman (1974b,c) for *A. chrysomphali* (Mercet) and *A. melinus* DeBach. DeBach's (unpublished) data were based on the open/closed paired-cell technique described in DeBach and Huffaker (1971), which was designed primarily to show the effect of natural-enemy exclusion over a period of time. The accumulation of dead and of mutilated scales, relative to the proportion of parasitised scales, may have exaggerated the calculated proportion of mutilated scales. For this reason a 1:1 ratio of mutilation to parasitism seems more likely than the higher ratios suggested by DeBach.

Eggs and larvae of two encyrtids, *Habrolepis rouxi* Compere and *Comperiella bifasciata* Howard, developed inside the scale body. It is not known which stages were attacked but these endoparasitoids nearly always emerged from the adult female stage. Therefore this is the stage on which they are assumed to have acted although a few emerged from stage 3♀. According to Flanders (1944) and Cilliers (1971), *C. bifasciata* may attack scales as young as stage 1 or 2, but development is delayed until the scales grow. However, in Swaziland endoparasitoids rarely emerged from male scales, which suggests either that the stages usually attacked were late 2♀ and 3♀, or that if earlier stages were attacked then the parasitoids could distinguish their sexes before morphological differentiation had taken place. Both species of endoparasitoids were themselves attacked by a hyperparasitoid, *Marietta javensis* (How.).

Undefined mortality took place in all stages, and there was always a large proportion of dead scales in the population, for which the cause of death was not apparent. These dead scales remained on the tree for an unknown time and there is evidence (section 5.2.7, Chapter 5) that they tended to accumulate. Some of these dead scales must have been killed by *Aphytis* host-mutilation, others by chrysopid feeding, but many probably died because of the death of the host plant cells which they were tapping.

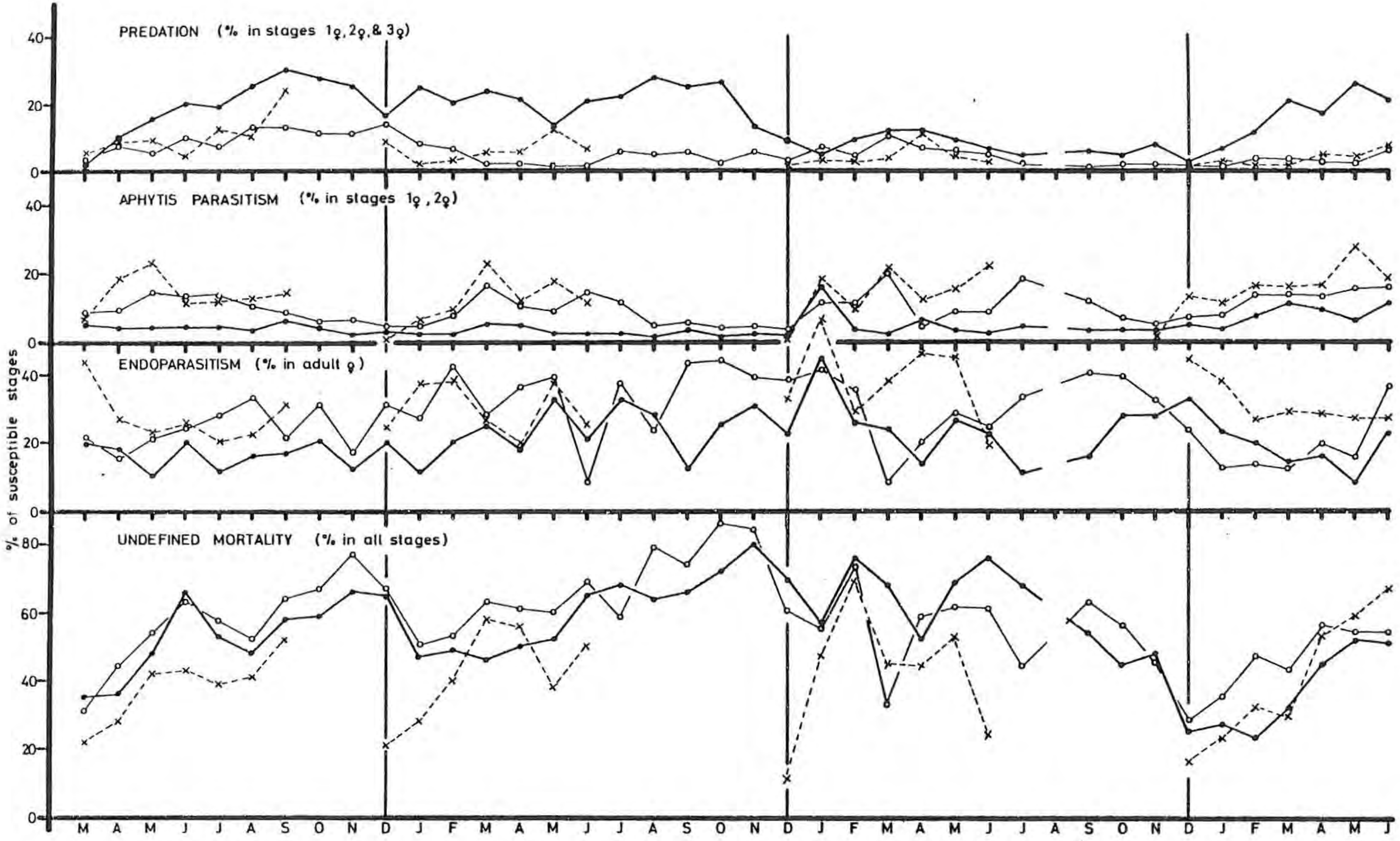
Percentage mortality at each sampling date was calculated in the following categories:

(i) Predation
(ii) Ectoparasitism
(iii) Endoparasitism
(iv) Undefined mortality.

Only limited conclusions could be drawn from these data for the following reasons:

(1) Evidence of predation and undefined mortality had accumulated over unknown periods. This had two consequences. Firstly, it introduced a time-lag between fluctuations in the causal agents (e.g. predator numbers) and the evidence

Fig 2.8. Mortality in female scales, from four causes, expressed as a percentage of the susceptible stage(s). The three sites are compared, leaves (o——o), twigs (●——●) and fruit (x- - -x), to show how percentage mortality from each cause differs on each site.



(2) Several categories of mortality acted on each stage at the same time and it was not possible to say in which order they acted.

(3) The population was continuously breeding so that the generations overlapped, and its numbers cycled seasonally.

For reasons (1) and (2) survival analysis could not be undertaken with these data, for example by the method of Varley and Gradwell (1960) because neither the number of survivors (S) from a given factor, nor the true number (N) before mortality, could be calculated. Reason (1) also made it impossible to infer density dependence, from the shape of the relationship between percentage mortality and the numbers of the stage on which the mortality acted (Varley, Gradwell and Hassell, 1973). Furthermore, delayed density dependence (Varley, 1947) could not have been detected because of the seasonal cycle of numbers.

Because of these reservations, percentage mortality data were used only to assess the relative importance of each category of mortality in the three sections of the population. In Fig. 2.8, each category of mortality has been expressed as a percentage of the total number of scales in the stages on which it acted. The conclusions are:

(i) Predation rates were higher on twigs than on leaves and fruit. Most of the predators were larvae and twigs would have been the pathways they followed between the other sites.

(ii) Ectoparasitism by *Aphytis* was highest on fruit, lowest on twigs, despite the generally higher host intensities on twigs. In order to include the effect of host-mutilation, the levels of ectoparasitism in Fig. 2.8 could perhaps be doubled at the expense of unknown mortality.

(iii) Endoparasitism was also usually higher on fruit and leaves than on twigs. Parasitoids may have tended to search toward the periphery of the canopy.

(iv) Undefined mortality tended to be highest on leaves, lowest on fruit.

2.9 Notes on the predators and parasitoids

The most common predator in the orchard was the small coccinellid, *Lindorus lophantae* Blaisdell, followed by Chrysopidae (probably *Chrysopa carnea* Stephans) the larvae of which were covered with the remains of dead scales. Species of *Scymnus* (Coccinellidae) and of *Cybocephalus* (Nititulidae) were recorded between March/April and October each year. Individuals of the genera *Lotis*, *Pharoscymnus*, *Chilocorus* and *Exochomus* were very rare, although species of the last two genera are usually considered to be among the most important red scale predators. *Chilocorus cacti* L. was introduced at Tambankulu Estate in Swaziland by Catling (1971a) and to this particular orchard during the present study. On both occasions it failed to become established and it was never recorded in suction samples.

The most common species of *Aphytis* recorded was the indigenous species *A. africanus* Quednau. The species of *Aphytis* can be distinguished by the degree of pigmentation of the ventral surface of the pupae (Quednau, 1964a). It is difficult to recognise the species of adults, and all the species determinations were made

Table 2.4 The incidence of *Aphytis melinus* pupae in samples of red scales examined during 1974 and 1975.

Month and year	Nos. of pupae recorded		%
	A. africanus	*A. melinus*	*A. melinus*
12/73	1	1	50
1/74	6	0	0
4/74	7	1	13
5/74	8	19	70
6/74	33	15	31
7/74	16	6	27
9/74	10	2	17
10/74	6	0	0
11/74	4	0	0
12/74	11	0	0
1/75	33	0	0
2/75	84	4	5
3/75	32	0	0
3/75	67	3	4
5/75	8	0	0
6/75	18	1	5

from pupae found in the dissection samples (Table 2.4).

During 1972 and 1973, *A. melinus* DeBach was imported from Israel, cultured and released in Swaziland. According to Catling (1971a,b), the reason why biological control of red scale failed on the lowveld was because *Aphytis* parasitoids were 'limited' by the high summer temperatures. *A. melinus* is well adapted to hot dry conditions. For example DeBach *et al.* (1971) published maps showing how this species had displaced others, notably *A. lingnanensis* from orchards in the hot interior of California. Although there was no evidence that *A. melinus* was better adapted than *A. africanus* to hot dry conditions, it was imported in the hope that it would do better. During 1974 and 1975 the incidence of *A. melinus* was monitored (Table 2.4). It was fairly common in 1974 but rare in 1975. This species preferred to parasitise stage 3♀ rather than stage 2 of either sex, and often super-parasitised the scales with 2 - 3 parasitoids per scale. *A. africanus* rarely super-parasitised the host and preferred stage 2 of either sex. Both species are biparental (Quednau, 1964a).

Habrolepis rouxi Comp. is uniparental (males are rare) and it is indigenous to southern Africa. There is very little information on its biology. *Comperiella bifasciata* How. was imported to Swaziland from the Transvaal by Catling (1971a). It originates from the Far East. Its distribution in Swaziland was assisted by releases during the present study, and it became well established throughout the lowveld. It is biparental and the sexes are easily distinguished. The female, being larger than the male, and larger than *H. rouxi* was a preferred host of the hyperparasitoid *Marietta javensis* (How.), formerly *M. exitiosa* Comp. There are two strains of *C. bifasciata*; the Japanese strain which parasitises yellow scale (*Aonidiella citrina* Coq.) and which is encapsulated by red scale, and the Chinese or red scale strain (Brewer,1971). According to Brewer there is a high proportion of encapsulation in red scale, even of the Chinese strain, which made the parasitoid ineffective for biological control of red scale in Australia, although it was effective on yellow scale. Encapsulated parasitoids become a brittle, brownish material, and this was sometimes noticed inside adult females in the present study, but its incidence was not recorded. At Tambankulu Estate, where the experimental orchard became infested with red scale following treatments with insecticides, *C. bifasciata* was virtually the only natural enemy recorded in the orchard but by itself it made no impression on the scale population.

2.10 Sex ratios in the scale population

Sex ratios were of interest because they entered calculations (Chapter 4) to predict the reproduction rate in the orchard from measurements of reproduction made in an insectary.

In red scale the sexes are distinguishable part-way through stage 2 when the male scale cover becomes elongated (Fig. 1). The early second stage, before differentiation, was called 2e to distinguish it from 2♂ or 2♀ or the second moulting stage of the female, 2a. The stages which were used to determine the fraction of the population which was female, were:

Males: live (2♂ + prepupa) + parasitised 2♂
Females: live (2♀ + 2a) + parasitised 2♀ ,

The stage durations of the sexes were approximately equal between 2♂ and prepupa, and between 2♀ and 2a, but thereafter they differed. Later stages of each sex were therefore ignored to exclude bias due to the different times for which each sex was

Table 2.5 Proportion of the population which is female in each month, calculated from the dissection data (see text for procedure); $\overline{x}$ is the mean, s the standard deviation and n the number of dissection samples which were used.

	Leaves				Twigs				Fruit		
Month	$\overline{x}$	s	n		$\overline{x}$	s	n		$\overline{x}$	s	n
J	0,579	0,103	13		0,665	0,137	13		0,696	0,174	13
F	0,419	0,093	13		0,626	0,120	13		0,619	0,145	13
M	0,409	0,133	11		0,681	0,146	10		0,713	0,145	11
A	0,356	0,138	15		0,677	0,129	14		0,570	0,115	15
M	0,425	0,116	13		0,687	0,152	12		0,567	0,174	13
J	0,445	0,092	10		0,623	0,163	10		0,561	0,140	11
J	0,465	0,092	6		0,725	0,073	6		0,619	0,125	8
A	0,410	0,305	4		0,703	0,278	4		0,710	0,095	3
S	0,480	0,151	5		0,838	0,061	5		0,720	0,071	2
O	0,446	0,187	7		0,779	0,212	7		–	–	–
N	0,569	0,125	7		0,759	0,136	7		1,000	0	1
D	0,508	0,156	11		0,726	0,133	11		0,844	0,160	10

available in the population for sampling. Dead and predation-damaged scales were excluded because they accumulated and would have obscured changes in the ratios. *Aphytis* parasitised scales were included because of a tendency for these ectoparasitoids to attack males in preference to females, especially on leaves.

The fraction of the population which was female each month was calculated from the ratio

No. of females/No. of males + females

and the results are given in Table 2.5. The fraction of the population which was female altered seasonally and differed on leaves, twigs and fruit. Such seasonal and between-site differences could have been due to different mortality rates in each sex. However,*Aphytis* parasitised scales were included to avoid such bias. Several authors have reported seasonal changes in sex ratios (Nel 1933; Jones, 1936; Bodenheimer,1951) while Nel has also noted the preponderance of males on leaves.

Hughes-Schraeder (1948) suggested that environmental factors easily over-ride the genetic mechanism for sex-determination in scale insects, particularly in diaspids which lack sex chromosomes. In diaspids,males are haploid, although in bisexual forms unmated females produce no progeny of either sex, which rules out the usual mechanism of haploid parthenogenesis. Bennett and Brown (1958) and Brown (1965) showed that in *Pseudaulacaspis pentagona* (Targ.) and many other diaspids, the paternal chromosomes are eliminated at late cleavage in the male embryo. Hence it is possible that nutritional factors, or seasonal temperature changes could influence whether or not the paternal chromosomes were eliminated; and so alter sex ratios on different sites in the tree and at different seasons.

2.11 Summary and conclusions

(1) Intensities/dm² of adult female scales were measured in samples of leaves, twigs and fruit at 2 - 3 week intervals over three and a half years. Mortality rates were recorded in four categories: predation-damaged, ectoparasitised, endoparasitised, and dead from undefined causes. Intensities per 'twig' of predators and adult parasitoids were measured at the same time.

(2) Mean scale intensities/dm² were highest on twigs, lowest on leaves, but there was evidence that absolute densities on leaves were comparable with those on twigs. Variation was greatest on fruit, maximum intensities/dm² being up to 200 times minimum intensities/dm². The minimum intensities/dm² represented the maximum permissible level of fruit-cull from red scale blemish.

(3) There was a seasonal cycle in scale intensity/dm² on twigs; a less clear one on leaves. This cycle was associated with the mean temperature about four months beforehand. In 1973/74 the cycle was missing, which appeared to be due, in part, to above-average spring rainfall.

(4) Seasonal rates of increase on twigs and fruit were closely related to indices of temperature and rainfall; dry years rather than hot years appeared to cause high rates of increase. However the results were not statistacally significant because only four sets of data were available.

(5) Adult female scales first matured on fruit in December and must have immigrated to fruit during October. The maximum scale intensity/dm² reached each year on fruit was closely related to the scale intensity/dm² on twigs the previous November.

There was evidence that subsequent immigration from twigs, after December, made little difference to the maximum level of infestation reached on fruit.

(6) Short-term variation in scale intensity appeared to be real and could have represented the generations of scale resulting from the spring increase in reproduction.

(7) For three reasons the mortality data did not lend themselves to either survival analysis or to the detection of density dependence in the population:

  (i) Certain categories of dead scales accumulated in the population.

  (ii) Several categories of mortality acted simultaneously on each stage.

  (iii) The population numbers cycled seasonally.

(8) Sex ratios, which enter predictions of reproduction rates, altered seasonally and differed on leaves, twigs and fruit.

In the next two chapters of this account, 3 and 4, the development and reproduction of red scale are discussed in terms of thermal constants. In Chapter 5 the mortality of scale is examined in order to expand some of the conclusions reached here. In Chapter 6 relationships are sought between natural enemy numbers and various factors.

CHAPTER 3

MEASUREMENTS OF STAGE DURATIONS AND THE CALCULATION OF THERMAL CONSTANTS

A prerequisite for the analysis of insect population numbers is a knowledge of the durations of the various stages, or of the whole life cycle. This chapter describes measurements which were made of the stage durations of red scale, under conditions which were as natural as possible.

3.1 Methods

Measurements of stage durations were made in a gauzed insectary having a translucent roof. The insectary was situated about 5km away from the experimental orchard. Temperature and humidity were measured with a thermohygrograph standing inside the insectary. The plants on which the scales were reared were either Sweet Orange seedlings or Valencia saplings bearing a few fruit. The red scale material came originally from the experimental orchard.

A reservoir of scale was maintained on pumpkins (*Cucurbita pepo*) and crawlers were transferred to leaves, twigs and fruits with a fine brush, and confined there with barriers or collars of 'Prestik' putty or similar slightly sticky material. Provided the material was reasonably fresh and did not become coated with dust, crawlers did not escape over it. Groups of crawlers were transferred to each type of site on the same day, and the development of the whole group on all three sites was inspected daily or every other day, at about 0800h using a X10 hand lens. As a group approached moulting time a few individuals were turned over each day until all had moulted. This method gave a mean and range for the duration in days of each stage in a group of scales on a given site, and a temperature trace was available for the same period. The transition from the grey (unfertilised) adult or stage 3 female, into the egg-maturing adult, was similarly monitored, as was the emergence of adult males from under their scale covers. The surviving adult females were surrounded with a ring of putty about 2cm in diameter and monitored until crawler production began (Chapter 4).

This procedure was repeated with ten successive groups on leaves and twigs, and eight on fruit, between November 1974 and November 1975. This period covered a range of conditions corresponding to one complete fruit-season, and the conditions in the insectary were fairly similar to those in the orchard except that rain was excluded. Attempts to make similar measurements in the orchard were frustrated by wind, dust, rain and the difficulty of preventing immigration to the groups from reproduction elsewhere on the tree.

Stage durations so measured were shortest on fruit and longest on leaves. The range in duration was only a day in early stages during summer, but as much as four days for later stages (e.g. 3♀ and A-) in winter. The method used was destructive of individuals so that it was impossible to tell whether slow developers in stage 1 were also slow in later stages. If this was in fact the case, then the total difference in the life cycle time, from fastest to slowest developers, would be rather greater than has been assumed by simply taking means. However among those adult females which survived the stage duration measurements, the greatest range was only nine days, between the first and the last of a given group on the same site to begin crawler production.

3.2 Thermal constants or 'physiological time'

In insects the development rate varies with temperature and so development times alter seasonally. A convenient way of expressing development times in relation to temperature which several people have used (e.g. Hughes, 1962, 1963; Hardman, 1976; Sands and Hughes, 1977), is as the product of time and temperature, because this product is approximately constant irrespective of the temperature experienced by the insect.

One of the mathematical descriptions discussed by Wigglesworth (1965, p615) for the effect of temperature on development, is that which states that the velocity of development is proportional to temperature:

$$V = k(t-a),$$

where k and a are constants, and t the temperature. The assumption is that the relationship is linear, which is only true over the central (and greater) part of the temperature range. Towards the upper and lower extremes of the temperature range the relationship departs from linearity so that the whole curve is actually sigmoid. However, under natural conditions the fact that a given insect exists in a region suggests that the upper and lower extremes to which it is sensitive do not occur often, or that the insect in some way avoids them. This is perhaps especially true towards the centre of the insect's distribution range, so it can often be assumed that the above relationship applies.

The constant 'a' represents the temperature at which the straight line, when extrapolated, meets the temperature axis. This temperature is the 'developmental zero' (Wigglesworth, 1965) and approximates to the 'threshold temperature for development' (i.e. to the temperature below which development ceases).

The product of development time, measured in days or hours, and temperature in excess of the threshold temperature for development, is approximately constant. Expressed either in day-degrees (D°) or hour-degrees (h°) it was called by Wigglesworth (1965) the 'thermal constant'. Each development process will have a characteristic thermal constant and will require a fixed number of D° or h° to be completed.

The product of time and temperature above the threshold has also been referred to, perhaps rather loosely, as 'physiological time' by some authors (e.g. Hughes, 1962; Hardman 1976; Atkinson, 1977). A criticism which can be levelled is that the product of time and temperature is not time, just as kilogram-meters is not a weight. It is incorrect, strictly speaking, to say that a given stage 'took' so many D°, but permissible to say it 'required' that many D° to complete its development. In this account the following distinctions have therefore been made:

(i) The product of time and temperature for a given stage has been called the 'thermal constant' for that stage.

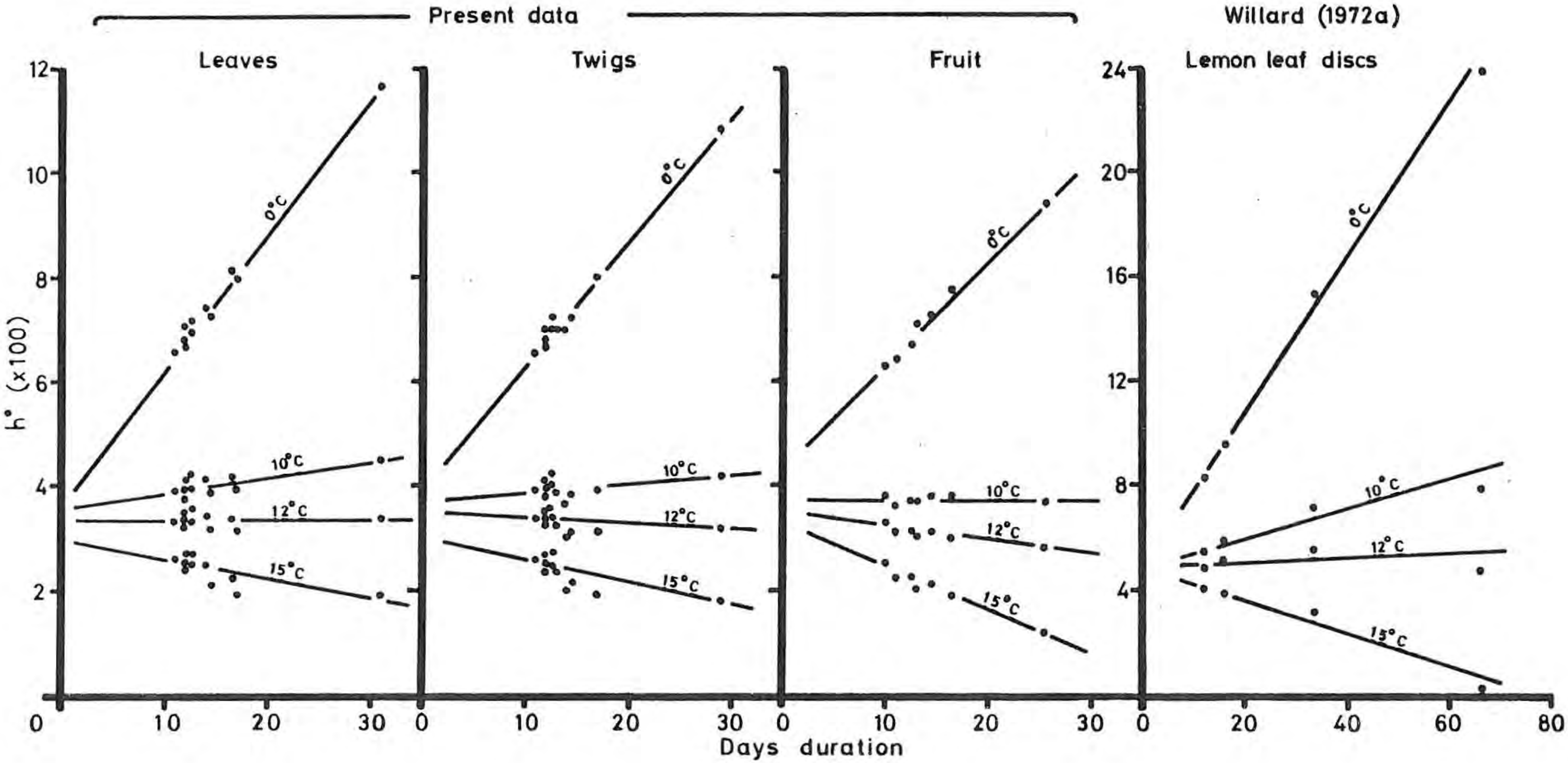
(ii) Although the product of time and temperature is not a period of time, it can be regarded as such; for example in defining an appropriate interval at which to measure the size of the population of a continuously breeding insect. When so used, the product of time and temperature has been referred to as 'physiological time', or if used to express age, as 'physiological age'.

(iii) The process of adding up units of time and temperature has been called 'thermal summation', after Wigglesworth (1965).

3.3 Determining the threshold temperature for development

In the insectary, stage durations were measured to the nearest day. The temperature during development was the ambient

Fig 3.1. Thermal constants in h° calculated above four trial threshold temperatures and plotted against the stage 1 durations in days. Data are from stage duration measurements described in Chapter 3 and from Willard (1972a). The regression lines with slopes closest to zero indicate the probable true threshold for development, which has here been taken as 12°C.



daily temperature, recorded with a thermograph. On some days the temperature cycled, on others (cloudy, rainy days) it remained fairly constant. In summer the entire temperature trace was elevated well above the threshold temperature for development, while in winter only the midday peaks rose above the threshold. In order to capture the effect of this variation, the product of time and temperature was expressed in h° rather than D°, even though the stage durations were only measured to the nearest day. When summing the h° for a stage the number of squares on the thermograph sheets were counted for each 24h and multiplied by two, since each square represented one degree and two hours.

The h° above the appropriate threshold temperature for development should be approximately constant for a given stage. Hence to find the threshold from stage durations at fluctuating temperatures, the number of h° above several trial thresholds were plotted against the observed durations for the stage. Then the regression line with a slope closest to zero, indicated the probable threshold. Fig. 3.1 shows the method applied to the durations measured for stage 1. Four trial thresholds were used. The method was also applied to data from Willard (1972a), who measured stage durations of red scale at constant temperatures.

Plots such as those in Fig. 3.1 indicated that the development threshold was about 12°C for most stages on each type of site. The exceptions were stage 1 and the egg-maturing adult (A-) on fruit, and 2♂ on all sites, for which stages the indicated threshold was 10°C. Moreover Willard's data also suggested that the threshold was 10°C for the 2♂ and A-stages. The durations of the 2♂ and the A-stages are terminated respectively by the

Table 3.1. Thermal constants in h° above 12°C for the stages and life cycle of red scale. L, T, F denote leaves, twigs and fruit; n the number of measurements; S.D. the standard deviations and P the probability levels for the observed differences.

Stage	Host material	Mean h° above 12°C	n	S.D.	Differences between materials		
					Materials	h°	P
1, to moult	L	3363,3	18	224,5	L/T	46,0	n.s.
	T	3317,3	17	251,3	T/F	261,9	0,01
	F	3055,4	13	189,3	L/F	307,9	0,001
2♀, to moult	L	3763,8	16	271,5	L/T	155,0	n.s.
	T	3608,8	19	298,8	T/F	208,2	n.s.
	F	3400,6	14	303,5	L/F	363,2	0,01
♂, first moult to emergence	L	5036,8	19	382,7	L/T	112,4	n.s.
	T	4924,4	18	424,0	T/F	353,7	0,05
	F	4570,7	13	378,7	L/F	466,1	0,01
Prefertilisation adult female (3♀)	L	2780,0	22	386,8	L/T	38,5	n.s.
	T	2741,5	21	413,1	T/F	110,9	n.s.
	F	2630,6	13	374,9	L/F	149,4	n.s.
Egg maturation female (A-♀)	L	4639,9	24	326,1	L/T	165,4	n.s.
	T	4674,5	27	278,3	T/F	263,6	0,05
	F	4410,9	16	425,8	L/F	429,0	0,01
Reproducing female (A+♀)	L	14019,4	49	4250,8	L/T	1547,6	0,01
	T	15567,0	42	6411,0	T/F	973,0	0,05
	F	16540,0	38	7740,0	L/F	2520,6	0,001
Life cycle (crawler to first reproduction) of female	L	14476,9	61	438,8	L/T	263,5	0,01
	T	14213,4	52	455,1	T/F	1071,5	0,001
	F	13141,9	46	613,3	L/F	1335,0	0,001

emergence of the adult male or the first crawlers and according to whether or not the emerging insects received appropriate stimuli to emerge, there may have been some variation in the termination of these stages. Such variation may have influenced the setting of the slopes in the plots to determine the developmental thresholds. If, for example, the emerging insects tended to wait a day or more before emerging, then h° would have been added to the apparent durations of the stages that were terminated. When this happened, the apparent threshold would be lower to get a slope of zero.

It seems unlikely that the threshold would be different in different stages of the insect, or in the same stage reared on different materials. Moreover, Willard (1972b) stated that the threshold for crawler emergence was 12°C, Jones (1936) calculated thresholds of 12,3°C and 12,8°C respectively for scales grown on fruit and leaves, while McLaren (1971) showed that the intrinsic rate of natural increase (r_m) was zero at 13°C. Hence the threshold has been assumed to be 12°C for all stages on all sites.

3.4 Thermal constants of red scale stages

Thermal constants in h° above 12°C are given in Table 3.1. The smallest constants for each stage (except the reproducing adult, A+) were those for scales reared on fruit and the largest for those on leaves. Since the duration of reproductive life was longest on fruit and shortest on leaves, the reverse is true of the thermal constants of the A+ female. Jones (1936) described how development was faster and fecundity greater on fruit compared to leaves. Such differences between the sites presumably reflect differences in the quality or quantity of available nutrients.

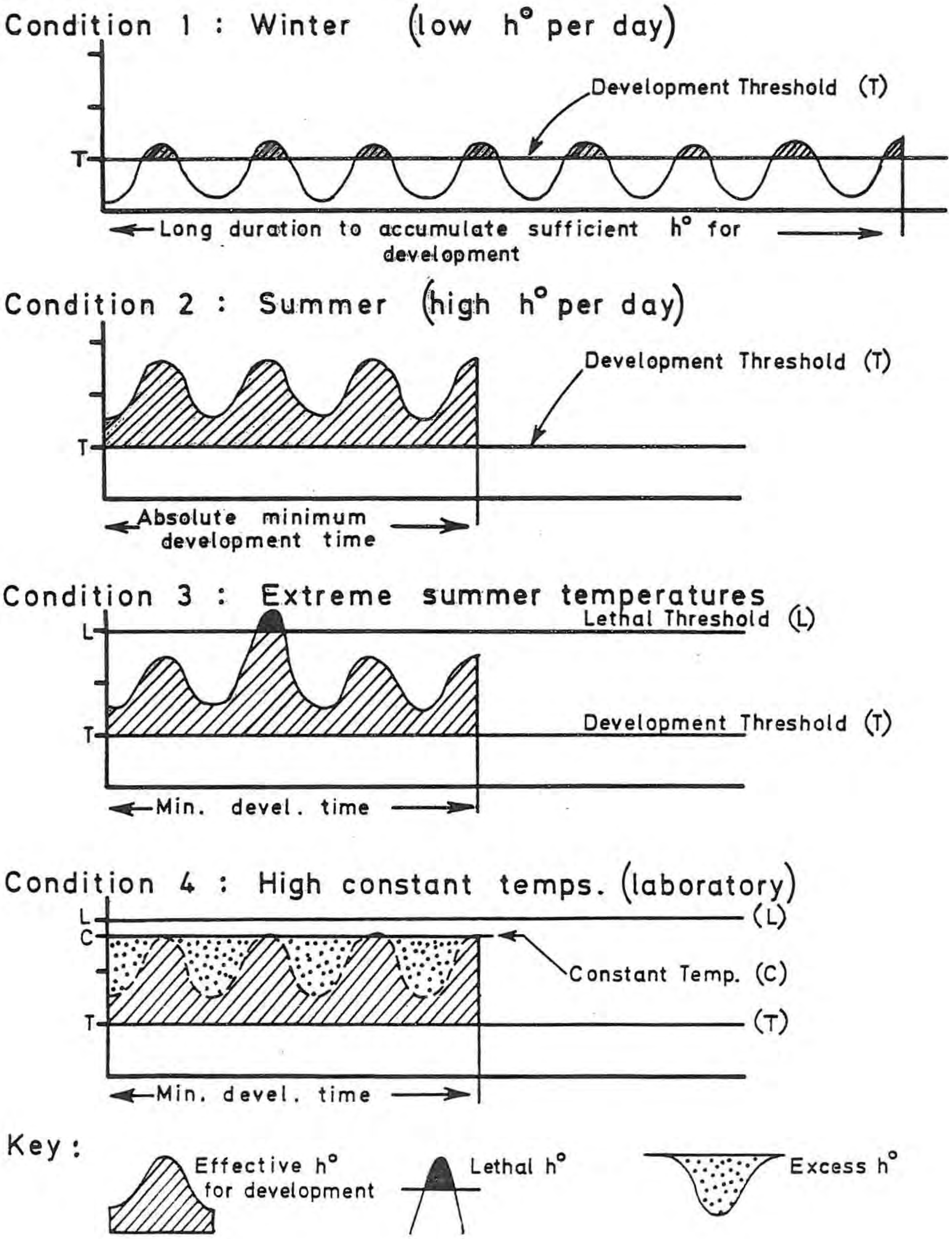
Among the younger stages, the greatest variation in thermal constants (denoted in Table 3.1 by the standard deviation relative to the mean) was in stage 3 females. This stage was terminated by fertilisation, after which the pygidium retracted and the scale cover became sealed-down. Hence the duration of stage 3 was determined by whether or not a male was attracted to and fertilised a female, which might explain the variable duration of this stage. It is possible that in the orchard there was less variability in stage 3 durations because adult males would have been available at all times. In the present experiments,stage 3 females had to await the emergence of adult males in the same group, growing either on the same or another site.

Another stage with variable duration was the reproducing adult female, the duration of which was terminated when reproduction ceased. The duration of reproductive life is as long again as the pre-reproductive life, so that by the time reproduction ceased a female would have been tapping the same area of plant tissue for 3 - 5 months. It is not known by how much a scale can vary the position of its stylets, but the stylets are renewed at each moult. The same stylets have to last a female from the second moult onwards; some 23000 h° or 2 - 4 months. It is therefore probable that a female stopped reproducing because her food supply failed, which might account for the variable duration of the reproductive life.

3.5 The advantages of fluctuating versus constant temperature regimes

Development times are often determined at constant temperatures, because it is easier to calculate relationships between the duration (or the rate) of development and temperature. However, there are advantages in using fluctuating regimes.

Fig 3.2. Diagramatic thermograph traces to suggest how, under constant temperature regimes, thermal summation could give misleadingly large thermal constants.



Wigglesworth (1965) noted that in some cases an alternation of temperatures seemed to stimulate development, compared to development at constant temperatures. For example *Melanoplus* eggs at a constant 32°C hatched in five days, whereas at alternating temperatures of 32°C for 8h, and 12°C for 16h, they hatched in three days. Bursell (1974), quoting several authors, mentions something similar. Sometimes development seemed slower under fluctuating temperatures and sometimes faster, while sometimes there was no difference compared to constant temperatures. Bursell went on to say, "A doubt must remain whether data obtained under laboratory conditions of constant temperature are capable of rigid application to populations of insects living in their normal environment".

The example of *Melanoplus* appears to be a genuine case of development being stimulated by fluctuating temperatures, compared to a constant one. However, when thermal summation is done, to determine thermal constants from stage durations measured at constant temperatures, it is possible that error can arise of a different nature. In Fig. 3.2 an attempt has been made to illustrate this point:

- In condition 1, the fluctuating temperature is low and the duration of development is extended until sufficient h° have been accumulated.
- In condition 2, the fluctuating temperature is high enough for the duration of development to approach its minimum time.
- In condition 4, it can be seen that at a high constant temperture, thermal summation could give an absurdly high thermal constant expressed in h°. (This would not be true if the thermal constant were expressed in D°).

Table 3.2 Thermal constants for red scale stages, calculated from several sources.

	FLUCTUATING TEMPS		CONSTANT TEMPERATURE REGIMES												
	PRESENT DATA LEAVES/TWIGS/ FRUIT		WILLARD 1972a LEMON LEAF DISCS				TASHIRO & BEAVERS 1968 LEMON FRUIT			McLAREN 1971 LIME LEAVES			WENTZEL 1970 LEMON FRUIT		
STAGE	SITE	MEAN h°	TEMP°C	DAYS	h°	MEAN h°	TEMP.	DAYS	MEAN h°	TEMP	DAYS	MEAN h°	TEMP	DAYS	MEAN h°
1	L T F	3363 3317 3055	29 25 19 15	12,2 16,1 33,5 66,4	4978 5023 5628 4781	5102,5	25	8	2496						
2♀	L T F	3764 3609 3401	29 25 19 15	11,5 15,1 31,6 65,1	4692 4711 5309 4687	4849,8	25	13	4056						
PRE-FERTILIZATION ADULT 3♀	L T F	2780 2742 2631					25	7	2184						
EGG-MATURING ADULT (A-)	L T F	4640 4675 4411					25	15	4680	24	16	4608			
TOTAL PRE-REPRODUCTIVE ADULT	L T F	7635 7397 7049	29 25 19 15	20,7 28,2 46,2 77,7	8446 8798 7762 5594[xx]	7650,0	25	22	6864						
TOTAL, CRAWLER TO CRAWLER	L T F	14477 14213 13142	29 25 19 15	44,3 59,5 111,3 209,2	18074 18564 18698 15062[xx]	17599,5	25	43	13416						
REPRODUCING ADULT A+	L T F	14019 15567 16540	30 25 20 15	106,4 123,3 153,2 148,3	45965 38470 29434 10678	31136,8	25	99	30888	24	100	28800	30 25 20	90 88 121	38880 27456 23232
2♂ TO EMERGENCE	L T F	5037 4924 4571	29 25 19 15	12,5 15,8 33,5 76,0	5100 4930 5628 5472	5282,5	25	15	4680						

[xx] Durations shortened by moving scales to 25°C for fertilisation

- Condition 3 illustrates that under fluctuating regimes, lethal temperatures may act for relatively short periods. Under constant temperature regimes, the lethal thresholds which were indicated might be much lower because of the long period over which the temperature acted. This point has been made by Abdelrahman (1974a), who determined the lethal temperatures for each stage of red scale under fluctuating regimes.

Thermal constants in h° for red scale stages were calculated from several sources of data and compared with constants from the present data (Table 3.2). The constants calculated from stage durations measured at constant temperatures are often larger than those from the measurements described here. This is so despite the better host-plant materials used by the authors in the constant temperature experiments. For example in Table 3.2, lemon leaves (Willard, 1972a) are better than orange leaves (present data) for culturing red scale, as are lemon fruit (Tashiro and Beavers, 1968) compared to oranges (present data). These better host-plant materials resulted in much longer reproductive lives, exemplified by the very large thermal constants for the reproducing adults on lemon leaves and fruit or on lime leaves (Table 3.2). However it is difficult to accept that reproductive life lasted more than twice as long on lemon leaves (Willard, 1972a) compared to orange leaves (present data); the very large thermal constants being due in part to the constant temperature regimes. The fact that thermal constants increase with constant temperature is shown in Table 3.2 by the thermal constants for the A+ calculated from Willard (1972a) and Wentzel (1970).

3.6 The applications of thermal summation in population analysis

Many insect populations are continuously breeding and have overlapped generations. The red scale population discussed here was such a one. Methods for estimating mortality in these populations are based (Southwood, 1978) on predicting the increase in numbers over a period of time, under conditions of unlimited population growth. Since population growth depends on generation time, which alters seasonally, there is an advantage in expressing the generation time as a thermal constant.

Several authors have employed thermal constants in this way. Hughes (1963) seems to have been among the first. Other examples are Gilbert *et al* (1976), Hardman (1976), Sands and Hughes (1977), Chubachi (1979). In the present case, thermal constants for the generation times of scales on twigs and fruit have been used (Chapter 5) to select sampling dates spaced one generation apart, from data covering nearly four years.

Gossard and Jones (1977), in developing a model for the reproductive performance of *Pieris rapae*, expressed the reproductive age of the insect in terms of time and temperature (D°). There were advantages in doing this because reproduction was measured under ambient temperature conditions and one day was not equivalent to the next in its ageing effect. A similar procedure was adopted here (Chapter 4) in developing a model to predict the daily rate of crawler production in the orchard from measurements of production in the insectary. In this case the product of time and temperature has been referred to as 'physiological age'.

Thermal summation is sometimes employed in order to assess the effect on a population of extreme temperatures (above or below some lethal threshold) and the time for which they acted. For example Catling (1969c) used thermal summations above several thresholds to determine the effect of weather on the survival of citrus psyllids. He also (1971b) related the difficulty of practising biological control of red scale to the number of D° above 30°C, which prevailed in various citrus growing regions of southern Africa.

CHAPTER 4

MEASUREMENTS OF THE REPRODUCTIVE RATE AND THE PREDICTION OF DAILY NATALITY IN THE ORCHARD

Survival analysis of continuously breeding populations involves the use of predictive models (Southwood, 1978, p. 395), for which estimates are required of the recruitment rate from daily oviposition. Although daily oviposition can be measured in the field, the frequent sampling would be very laborious. In the present case daily crawler production was measured in an insectary. These measurements, and the development of a model to predict daily natality in the orchard, are described here.

4.1 A review of the mating behaviour and post-fertilisation changes in the female

In the succeeding sections of this chapter, references have been made to specific parts of the reproductive process. To make such references more easily understood, this section reviews the mating behaviour of red scale and the changes which take place in the female after fertilisation.

At the time when the male is passing through its pupal stage, the virgin adult female (stage 3) lays down a wide grey margin around the boss formed by the cover of its first and second stages (see Fig. 1). At this stage the female emits a pheromone to attract the male (Tashiro and Chambers, 1967). The pheromone was identified by Roelofs *et al.* 1978). It is continuously present in the stage 3 female, which however can release or withhold it (Tashiro and Chambers, 1967).

Adult males emerge during the afternoon between 1500h - 2000h, reaching a peak at dusk (Tashiro and Beavers, 1968) and they live 2 - 10h, most of them dying in about four hours. According to Tashiro and Moffitt (1968), males are capable of fertilising as many as 30 females, with an average capability of about 12, while females may accept up to seven matings. Fecundity is not increased by multiple matings (Tashiro and Moffitt, 1968). The attractiveness of unmated females decreases slowly up to about six weeks.

During mating the male extends the aedeagus beneath the cover of the female. The female can extend the pygidium to the rim of the cover, but within 24h of fertilisation the pygidium becomes irreversibly retracted and the female becomes kidney-shaped and the cover is sealed down on to the plant surface (Fig. 1). A space remains around the pygidium where, once reproduction begins, a few newly hatched crawlers may collect for a few hours before emerging. Red scale being ovoviviparous, the crawlers are born directly, not as eggs.

The period between fertilisation and the start of reproduction represents the embryonic development time of the first eggs. During this time the adult female has been referred to here as the A- stage. After reproduction commenced it has been called the A+ stage. Thermal constants of these stages are shown in Table 3.1.

According to Willard (1972b) births of crawlers may start before light but the peak of emergence occurs during the first two hours of light. The threshold temperature for emergence is about 12°C and the higher the temperature above this, the earlier in the light-phase is the time or peak emergence (Willard, 1972b). Willard had difficulty determining a threshold light intensity for crawler emergence but gave a figure of c 32 lm/m². Humidity is

Table 4.1. Summary of the details of the groups of A+ females used to measure daily crawler production. Shown are the number of individuals in each group on leaves, twigs and fruit (L, T, F), and the starting and finishing dates of the groups. Measurements ended on 30/11/75; dates with queries were therefore guessed.

Group No.	Site	No. Individuals	Starting dates (first & last individuals)	Finishing date	Remarks
1	L T	10 6	8/ 1 11/ 1 8/ 1 10/ 1	16/ 3 4/ 3	No fruit present
2	L T	2 3	21/ 1 - 19/ 1 20/ 1	3/ 4 1/ 3	No fruit present
3	L T F	5 4 3	5/ 3 8/ 3 5/ 3 - 24/ 2 26/ 2	2/ 7 10/7 23/8	Fruit on different plant. Group on fruit, 8 days older than group on leaves and twigs.
4	L T F	2 7 3	15/ 4 - 13/ 4 15/ 4 2/ 4 3/ 4	9/7 25/9 8/ 9	Fruit on different plant. Group on fruit, 4 days younger than group on leaves and twigs.
5	L T F	3 5 7	7/ 5 9/ 5 5/ 5 8/ 5 2/ 5 3/ 5	30/ 8 23/10 6/11	Same age and plant
6	L T F	11 7 6	14/ 7 20/ 7 11/ 7 20/ 7 28/ 6 8/ 7	21/10 30/11 ? 24/11	" " " "
7	L T F	3 8 10	19/8 20/ 8 11/ 8 18/ 8 30/7 6/ 8	16/1I 30/11? ?	" " " "
8	L T F	14 5 9	15/ 9 17/ 9 13/ 9 15/ 9 6/9 8/9	7/12 ? 7/12 ? ?	" " " "
9	T	4	22/10 25/10	?	Group present only on twigs
10	L T F	9 7 8	9/11 12/11 8/11 10/11 4/11 5/11	? ? ?	Same age and plant

not important according to Willard (*loc. cit.*).

4.2 Methods

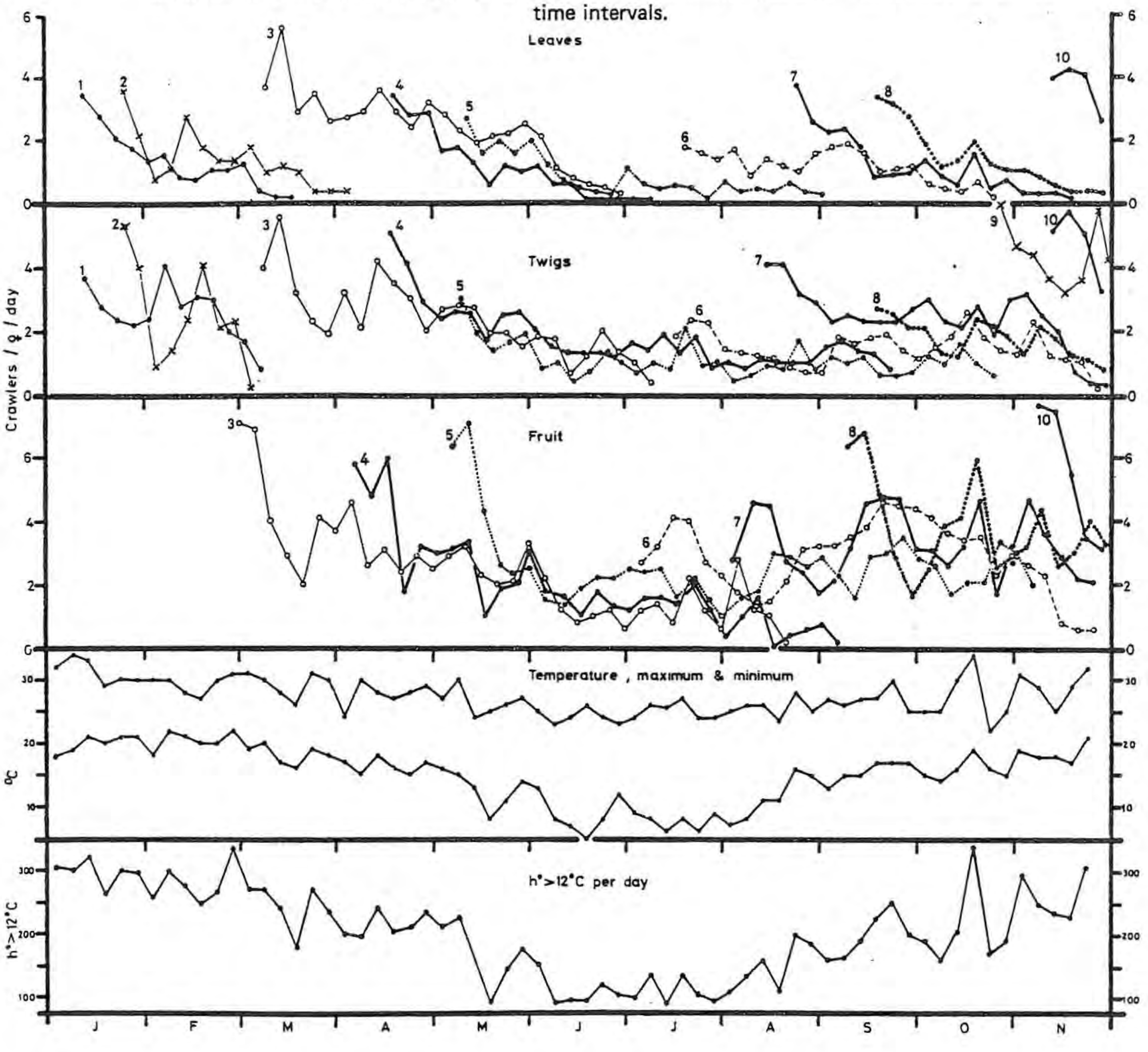
Daily crawler production was measured at ambient temperature and humidity in a gauzed insectary. As described in section 3.1, in order to measure stage durations groups of scales of the same age were reared on the leaves, twigs and fruits of potted orange plants. Adult females which survived these experiments, were surrounded with a ring of sticky putty ('Prestik') and monitored until they started to produce crawlers. Once reproduction started the crawlers or newly settled white caps (Fig. 1), were removed daily at about 0800h, or on alternate days, from inside the rings using a needle and hand lens. Crawlers did not escape from the rings provided the putty did not become too dusty (in which case it was renewed) and provided it was kept well pressed down. The plants were inspected periodically to see whether scales were growing elsewhere, which would mean that crawlers were escaping from one of the rings.

Temperature and humidity were measured with a thermohygrograph standing inside the insectary. This was calibrated weekly with a thermometer and by wetting the hairs with a spray.

4.3 Crawler production

Crawler production was measured in ten groups of adult females on leaves and twigs and in seven groups on fruits. These groups were reared one after the other, so that reproduction was measured in succeeding groups over a period of eleven months, from January to November 1975. The starting and finishing dates of these groups and the numbers of females involved are summarised in Table 4.1. The work ended at the end of November 1975, when some of the later groups had not yet finished reproduction.

Fig 4.1. Daily crawler production per surviving female averaged over 5-day intervals for each group (1 — 10) on leaves, twigs and fruit. Mean maximum and minimum temperatures, averaged over 5-day intervals from the first of each month, are given at the foot of the figure, as are h° calculated for the same time intervals.



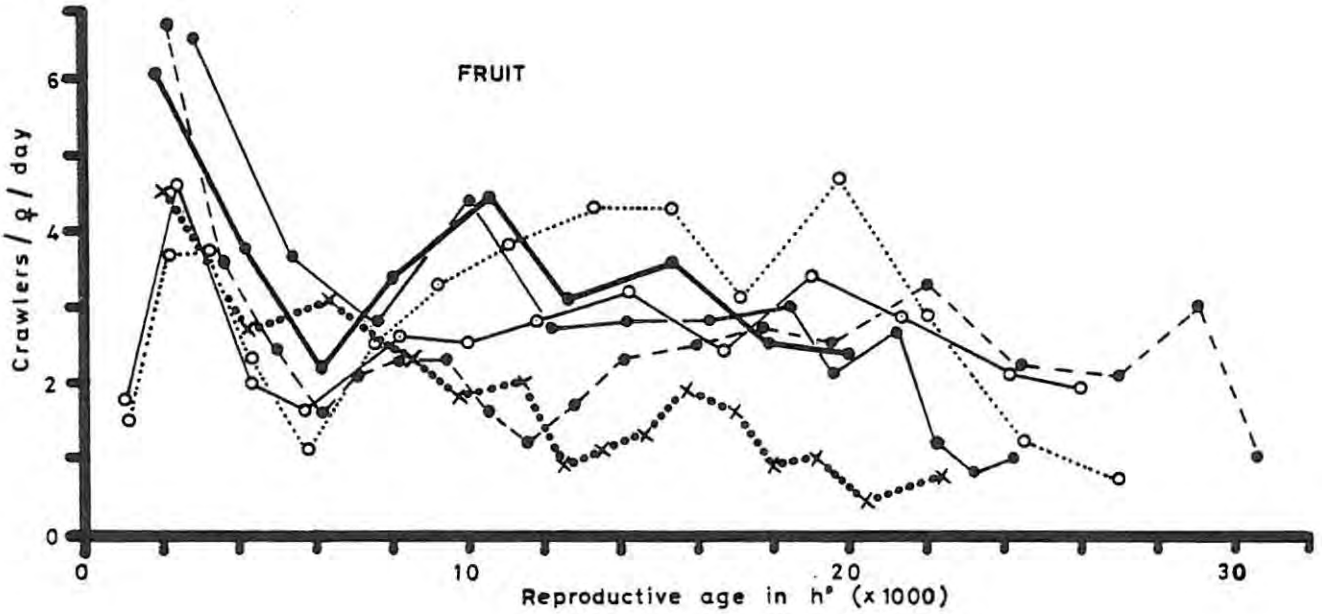
In Fig. 4.1 the daily crawler production per female for each group, has been averaged over five-day intervals and plotted in the middle of each five-day interval. As the females in a group on a given site died, the crawler production of the remainder was expressed per surviving female rather than per original female. The reason for this was that the purpose of the analyses described here,was to develop a model to predict daily natality per female in the orchard; and in the orchard only live (i.e. surviving) adult females were counted. Fig. 4.1 therefore shows age-specific fertility curves which include male as well as female progeny. Such curves have been called hereafter 'egg-curves' (after Laughlin, 1965, although he referred to curves of the product of age specific fertility and age specific mortality).

Out of a group of females of the same age, those on fruit began reproducing earliest and those on leaves latest (Table 4.1). Reproduction continued for longest on fruit (Table 4.1 and Fig. 4.1) and the daily rate of production per female was also highest on fruit (Fig. 4.1), lowest on leaves.

Both the seasonal changes in crawler production, and the short-term fluctuation, were associated with daily temperature averaged over five-day intervals (Fig. 4.1). There was also a good fit between the crawler production per female and the total number of h°>12°C in each five-day interval. The fit was slightly blurred because of differences in the exact dates over which daily crawler production was averaged and those over which h° were accumulated, for each five-day interval.

There were two effects of temperature. There was a seasonal effect, so that in summer the rate of crawler production

Fig 4.2. Daily crawler production per surviving female, averaged over 10-day intervals and plotted against reproductive age expressed in h° > 12 °C. There is a trough in production at about 6 000 h°.



was initially high but declined rapidly with reproductive age, whereas in winter the initial rate of production was low but reproductive life was extended (Fig. 4.1). Secondly, temperature changes caused short-term fluctuations in the daily rate of crawler production. On fruit, some groups which started reproducing during winter, began to reproduce at a high rate if they lived through into spring, but normally fruit would not be left on the trees until spring.

Close inspection of Fig. 4.1 suggested that despite these effects of temperature, after the first burst of crawler production there appeared to be a trough before the daily rate of production increased again. This was most noticeable in the groups on fruit. Egg-curves of scales on fruit were therefore plotted against 'physiological age' expressed in h°>12°C (see section 3.2). The results are shown in Fig. 4.2 and there seems to be a trough in production at about 6000h° in nearly all seven egg-curves.

McLaren (1971) dissected egg-maturing (A-) females reared at 24°C, 15 days after they had been fertilised and were almost ready to start reproduction. He was able to find about 135 eggs in their abdomens, the remainder of the compliment of about 300 eggs being, presumably, still germ cells. In other females, in which crawler production was monitored, an average of 138 crawlers emerged during the first 16 days of reproduction; in other words all of the eggs which were visible in the females which were dissected. Hence, the eggs visible in the abdomen 15 days after fertilisation hatched over the next 16 days. Converting these periods at 24°C to h°>12°C gives, respectively, 4320h° for embryonic development and 4608h° to hatch the first 138 crawlers. These thermal summations agree quite well with the thermal constants for the A- stage given in Table 3.2. Moreover the figure of 4608h° is of the same order as that of 6000h° at which there seems to be a trough in the egg-curves in Fig. 4.2.

These lines of evidence, that in Fig. 4.2 and the argument developed from McLaren's (1971) data, are grounds for thinking that crawlers were matured and hatched in batches. Such batches would be more distinct at the start of reproduction than later in the reproductive life. Temperature changes might modify this tendency, to produce the sort of short-term fluctuations which are seen in the egg-curves in Fig. 4.1.

4.4 Regression analysis of the factors affecting daily crawler production per female

The factors which appeared to influence daily crawler production per female were:

(i) Reproductive age,
(ii) Season,
(iii) Short-term temperature changes.

Relative humidity might also affect daily crawler production per female, although Willard (1972b), concluded that it was unimportant. (It was assumed that the light intensity in the insectary exceeded the possible threshold suggested by Willard (1972b), even on cloudy days).

The effects of these factors (excluding light intensity, which was not measured) were investigated by multiple regression analysis. The independent variables were derived as follows:

(i) Reproductive age: The rate of ageing would have depended on temperature as well as time, so reproductive age was

Table 4.2 Data on the spans of egg curves in h° for experimental groups in the screenhouse and the orchard, and the average number of crawlers per female in each group.

				Mean Reproductive Span (h°)		Average Total No. Crawlers/♀ for group	
Site	Group No.	Approximate Dates	n	Screenhouse	Orchard	Screenhouse	Orchard
Leaves	1+2	Jan - Mar	12	13083		80,6	
	A	Feb - Jun	4	-	19684	-	102,5
	3	5/3 - 2/ 7	5	17919		230,0	
	4	15/4 - 9/ 7	2	12920		99,0	
	5	7/5 - 30/ 8	3	18020		108,7	
	6	14/7 - 21/10	11	12921		103,0	
	7	19/8 - 16/11	3	10826		90,3	
	8*	15/9 - c7/12	14	14209		105,2	
			Grand mean	14019,4	19684,3	116,7	102,5
			S	4250,8	3704,6	50,9	-
			n	50	4	7	-
Twigs	1+2	Jan - Mar	9	12975		126,7	
	A	Feb - June	4	-	14253	-	115,5
	3	5/3 - 10/ 7	4	17701		240,5	
	4	13/4 - 25/ 9	7	19371		241,6	
	5	5/5 - 23/10	5	18576		140,5	
	6*	11/7 -c30/11	7	14559		127,9	
	7*	11/8 -c30/11	8	15079		216,1	
	8*	13/9 -c 7/12	5	12202		102,8	
			Grand mean	15567,0	14252,4	170,9	115,5
			S	6411,0	4341,0	59,5	
			n	45	4	7	-
Fruit	3	24/2 - 23/ 8	3	16018		261,0	
	A	Feb - Jul	7	-	15332	-	214,9
	4	2/4 - 8/ 9	3	15116		200,7	
	B	Apr - Aug	3	-	13410	-	188,0
	5	2/5 - 6/11	7	22338		389,3	
	6	28/6 - 24/11	6	20426		397,2	
	7*	30/7 - ?	10	-		221,2	
	8*	6/9 - ?	9	-		244,2	
			Grand mean	18207,5	14755,4	285,6	201,4
			S	11310,3	6938,0	85,9	19,0
			n	38	10	6	2

* Egg curves incomplete because experiment terminated.

expressed in h°>12°C, starting from the date that a female began to reproduce. Egg-curves plotted on this scale tended to be roughly the same length (Table 4.2, column 5) both in the orchard and in the insectary. Gossard and Jones (1977) expressed the egg-curves of *Pieris rapae L.* on a scale of D° for groups of the insect breeding in outdoor cages.

(ii) Season: This was presumably the effect of the average temperature over a fairly long period, acting either directly on the adult female or via the physiology of the host plant. The period over which temperature acted on the host plant was unknown, so a measure of season was sought which might have affected the adult female itself. A reasonable measure seemed to be the thermal constant for the crawler maturation time, the mean value of which from Table 3.2 was 4643h° (standard deviation 155,1). Accordingly, the number of days required to accumulate 4643h° was taken as the measure of season. (In Table 3.2, thermal constants for crawler maturation are similar irrespective of host plant material. Crawler, or embryo, maturation was therefore independent of the food supply although fecundity was not.)

(iii) Short-term temperature changes: The temperature, in h°> 12°C, on the day of emergence was taken as the measure of the temperature immediately preceding emergence.

Factors (i) - (iii) are all measures of temperature over different periods.

(iv) Maximum saturation deficit was taken as a measure of the drying-power of the air on the day of emergence.

The effects of these variables were investigated with the equation

$$y = c + a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4 + a_5x_1^2 + a_6x_3^2$$

Table 4.3. Results of regression analysis to find which variables to use in a model for daily crawler production per female. The equation fitted was

$$y = c + a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4 + a_5x_1^2 + a_6x_3^2$$

Site	Variable		Significance of partial regression coeffs.		Simple r
			t	p	
Leaves	Age	x_1	7,9	0,001	-0,54
(n = 351)	Season	x_2	3,0	0,01	-0,27
	Temp.	x_3	2,6	0,02	0,24
	Max.Sat.Def.	x_4	0,6	n.s.	0,08
	Age²	x_1^2	4,6	0,001	-0,47
	Temp.²	x_3^2	2,6	0,02	0,19
	$R^2 = 0,397$				
Twigs	Age	x_1	4,5	0,001	-0,54
(n = 373)	Season	x_2	1,1	n.s.	-0,31
	Temp.	x_3	2,6	0,02	0,31
	Max.Sat.Def.	x_4	1,5	n.s.	0,09
	Age²	x_1^2	1,1	n.s.	-0,50
	Temp.²	x_3^2	1,1	n.s.	0,27
	$R^2 = 0,406$				
Fruit	Age	x_1	5,5	0,001	-0,56
(n = 311)	Season	x_2	1,2	n.s.	-0,19
	Temp.	x_3	3,7	0,001	0,27
	Max.Sat.Def.	x_4	0,8	n.s.	0,16
	Age²	x_1^2	2,3	0,05	-0,50
	Temp.²	x_3^2	3,0	0,01	0,21
	$R^2 = 0,410$				

where y was the daily crawler production per surviving female and the independent variables were as shown in Table 4.3. The squared terms were introduced in case the relationships concerned were curvilinear. The contribution made by each variable was assessed by the statistical significance of its partial regression coefficient (Table 4.3).

Maximum saturation deficit was not significant on any site and was dropped. The other variables were significant on one or more sites and were retained in order to keep the model the same for all three sites. Thus, the variable for season (x_2) was highly significant on leaves but not on twigs or fruit, and was retained in the final model.

Although there were over 300 readings of crawler production on each site, there were only 46 - 59 A+ females involved (Table 4.1) and many of these readings came from the same individual females. From a statistical viewpoint it would have been better if there had been more females involved. Regression analysis assumes that each set of readings is independent of the others but here, readings from the same individuals would have been to some extent related.

4.5 A model for daily crawler production per female

All the variables listed in Table 4.3, with the exception of saturation deficit, were used in a model for the daily crawler production per female. The purpose of the model was to be able to estimate crawler production in the orchard. An exponential equation was employed because it implied proportional change in the dependent variable rather than incremental change, for each unit of change in an independent variable. A term for the interaction of age and season was also introduced. The

Table 4.4 Regression coefficients for the model:

$$\log y = a + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_1^2 + b_5x_3^2 + b_6x_1x_2$$

Where y is the daily crawler production per surviving female.

Site	Variable	Partial regression coefficient	t	p	Simple r
Leaves (n=351)	Age b_1	-0,561900 x10^{-4}	7,9	0,001	-0,59
	Season b_2	-0,934550 x10^{-2}	4,0	0,001	-0,30
	Temp. b_3	0,231138 x10^{-2}	3,7	0,001	0,25
	Age² b_4	0,105221 x10^{-8}	3,1	0,01	-0,53
	Temp.² b_5	-0,493327 x10^{-5}	3,6	0,002	0,21
	Age x Season b_6	0,486274 x10^{-6}	2,1	0,05	-0,59
	Constant term a	0,5977151			
	$R^2 = 0{,}468$				
Twigs (n=373)	Age b_1	-0,357251 x10^{-4}	5,0	0,001	-0,63
	Season b_2	-0,860286 x10^{-2}	3,7	0,001	-0,31
	Temp. b_3	0,217764 x10^{-2}	4,0	0,001	0,32
	Age² b_4	-0,703635 x10^{-10}	0,3	n.s.	-0,61
	Temp.² b_5	-0,348842 x10^{-5}	2,9	0,01	0,27
	Age x Season b_6	0,590520 x10^{-6}	2,9	0,01	-0,64
	Constant term a	0,5596254			
	$R^2 = 0{,}520$				
Fruit (n=311)	Age b_1	-0,164023 x10^{-4}	2,7	0,02	-0,60
	Season b_2	-0,246723 x10^{-2}	0,9	n.s.	-0,21
	Temp. b_3	0,329278 x10^{-2}	5,7	0,001	0,31
	Age² b_4	-0,138080 x10^{-9}	0,8	n.s.	-0,58
	Temp.² b_5	-0,570241 x10^{-5}	4,5	0,001	0,24
	Age x Season b_6	0,937614 x10^{-7}	0,5	n.s.	-0,60
	Constant term a	0,3450357			
	$R^2 = 0{,}489$				

model was

$$\log y = a + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_1^2 + b_5x_3^2 + b_6x_1x_2$$

where y was the daily crawler production per surviving female and the independent variables were as listed in Table 4.4. The variable for season was significant in the case of leaves and twigs, as was the interaction between age and season, although neither season nor the interaction were significant on fruit (Table 4.4). This may have been because groups of females reproducing in summer were not represented on fruit (see Fig. 4.1). The squared term for age was not significant on twigs and fruit but was highly significant on leaves. For simplicity in applying the model to orchard data, the non-significant terms in the relationships for twigs and fruit were retained, in order to keep the model the same for all three sites.

The model explained about 50% of the variation in daily crawler production per female ($R^2 = 0{,}468$ on leaves; 0,520 on twigs; 0,489 on fruit). There are several possible reasons why no more of the variation was explained.

(i) There was evidence to suggest that crawlers may have been matured and hatched in batches (section 4.3). If this was so there would have been unexplained variation due to whether or not a batch of crawlers was ready to emerge at a given reproductive age.

(ii) Crawler hatching and emergence from under the parent scale may involve behaviour on the part of the adult female as well as the crawlers. In this study crawlers tended not to emerge on cool, overcast days but many emerged on the first of a series of warm days leaving few to emerge on succeeding equally warm days. It was not clear whether they did not hatch on cool overcast days, or whether they hatched but did not emerge. According to Willard (1972b) the ratio of the hours of light to darkness influences the rhythm of crawler emergence, which suggests that the adult female may respond to light.

According to Willard (1972b) the time of peak emergence was affected by temperature as well as light, being earlier in the light phase the higher the temperature. In the present work, daily crawler counts made at 0800h may not always have reflected the full emergence pattern for each day. However, in choosing readings for the regression analyses, days were excluded when crawler counts were done on alternate days.

(iii) Seasonal changes in the physiology of the host plant may have influenced the fecundity of the scales. Thus equivalent temperatures in spring and summer may not have produced similar rates of crawler production. There is no doubt that the quality of the host plant material affected fecundity because the rate of crawler production and the total number of crawlers produced (Fig. 4.1 and Table 4.2 respectively) differed on leaves, twigs and fruit. Evidence was reviewed by McNeill and Southwood (1978) showing that the sizes of the populations of sap-sucking insects altered with the seasonal availability of nutrients in their host plants.

(iv) The several rates of oogenesis, embryogenesis, hatching and crawler emergence could not be adequately explained by such crude indices of season and daily temperature as were used in the regression analyses. Gossard and Jones (1977) accounted for 68% of the variation in the daily rate of egg laying of *Pieris rapae* but their data were based on only 17 females in four groups, all reproducing in the same season, summer. With an insect such as *P. rapae* which has a relatively short reproductive life, variation in host plant physiology may be unimportant. Furthermore, the variation inherent in embryogenesis and hatching would have been absent from the data.

There are two considerations relating to the further refinement of this model designed for orchard application. Firstly, even if more of the variation could be explained, could the additional variables possibly be measured in the orchard? Secondly, is it really necessary? For example, although it might be possible to modify the model to account for the periodicity in crawler production, it would be impossible to get such detail from the orchard, and it would be unnecessary in an orchard population of mixed reproductive ages. Again, the variation in crawler emergence as a result of the erratic response of adults (or crawlers) to daily temperatures, would be smoothed out over a few days; just as many crawlers would have emerged over a period of a few warm days irrespective of whether most of them emerged on the first warm day or whether they emerged in equal numbers on each day.

4.6 Estimating daily natality in the orchard

The model was used to predict the daily crawler production per A+ female in the orchard:

(i) Variables x_2 (season) and x_3 (daily effective temperature)

Table 4.5 Midpoints of egg-curves calculated in 5-day intervals and then converted into the equivalent number of days and h°>12°C. Average midpoints are given for each site, in h° ($\bar{x}$ is the mean; s.d. the standard deviation).

Site	Group No.	Midpoints in:			Average midpoint (h°)
		Age units	Days	h°	
Leaves	1	5,07	25,3	6835	
	2	6,04	30,2	7868	$\bar{x}$ 6520
	3	9,11	45,5	9857	s.d.1631
	4	5,11	25,5	4907	n 8
	5	9,05	45,2	5699	
	6	8,76	43,8	5437	
	7	6,63	33,2	5692	
	8	6,23	31,2	5862	
Twigs	1	5,86	29,3	7700	
	2	4,10	20,5	5202	$\bar{x}$ 8851
	3	10,13	50,6	10938	s.d.1965
	4	12,82	64,1	10291	n 7
	5	15,51	77,5	9658	
	6	13,88	69,4	9899	
	7	9,61	48,1	8268	
Fruit	1	12,87	64,3	14545	
	2	10,61	53,0	9865	$\bar{x}$ 11184
	3	17,73	88,7	11016	s.d.1958
	4	14,20	71,0	10750	n 5
	5	11,72	58,6	9743	

were derived from orchard thermograph records converted to h° > 12°C per day. (Tables were constructed of h°/day covering the period of field sampling).

(ii) Variable x_1 (reproductive age) was not measured in the orchard population, although it is possible that it could have been measured from changes in the ovaries of the adult females. In the absence of such measurements, midpoints were calculated for the egg-curves shown in Fig. 4.1 and converted to h°. The midpoints were calculated from the expression:

$$\text{Midpoint} = \Sigma x m_x / \Sigma m_x$$

(which is similar to the expression given by Birch (1948) but without age specific survival) where x was the age interval in five-day units since the start of reproduction, and m_x the age specific fertility. Midpoints calculated in this way are given in Table 4.5. The average midpoint in h° was assumed to be representative of the average reproductive age of A+ females in the orchard.

At times of rapid recruitment to the A+ stage, the average reproductive age would have been younger than the values given in the last column of Table 4.5. At such times the rates of crawler production per female would have been higher than that predicted by the model using the average ages in the table. In December, there must have been rapid recruitment of A+ females on fruit and the mean reproductive age was taken as 5000h° instead of 11184h°. On the other hand, if A+ females had lived for longer in the orchard than in the insectary, their reproductive ages would have been rather greater than the values in Table 4.5. However, the few data available from the orchard (Table 4.2) suggested that mean reproductive spans were comparable to those measured in the insectary, and that similar total numbers of crawlers were produced by A+ females in both environments. The rather flat shapes of the egg-curves (Fig. 4.1) meant that quite large errors either way in the assumed average age of A+ females, would make little difference to the predicted daily rate of crawler production per female.

Only the female portion of the population was considered, so the daily crawler production per female, predicted by the model, was corrected to the proportion which was female. The appropriate fractions in Table 2.5 were used for this purpose.

This procedure gave the daily production of female crawlers per A+ female in the orchard. The daily natality in the orchard was calculated by multiplying by the intensity/dm^2 of A+ females per dm^2 of leaf, twig or fruit surface, as follows:

(i) Orchard intensity/dm^2 counts of adult females, which consisted of A- as well as A+ females, were converted to intensities/dm^2 of A+ females alone by multiplying by the proportion of A+ in the samples of scales which were dissected at the same time.

(ii) Daily A+ intensities/dm^2 were obtained by interpolating between the estimated A+ intensities/dm^2 on adjacent sampling dates.

Tables were constructed of the predicted daily natality of female crawlers in the orchard. These tables covered the period of orchard sampling between 1972 and 1975, and they have been used (Chapter 5) to estimate the recruitment of crawlers to cohorts of adult female scales in order to check the mortality rates in the orchard, which were calculated by another method.

4.7 Conclusions

The rates of crawler production and the durations of reproductive life differed greatly on leaves, twigs and fruit. Coupled with the different rates of development, different sex ratios, and even different rates of mortality from the several categories of mortality which were recorded, there were strong arguments for treating the three sections of the population separately in analysis.

The rate of reproduction per female was strongly dependent on temperature. In Chapter 2 it was concluded that the temperature four months beforehand caused the seasonal cycle in adult female intensity. In Chapter 3 it was shown that the life cycle requires about 14000h°, which in summer was about six weeks and in winter about four to five months. These points suggest that temperature, in causing the seasonal cycle, acted mainly upon the rate of recruitment.

The predictive model for crawler production has been used in section 5.2.4 to check estimates of mortality made by another method.

CHAPTER 5

INVESTIGATIONS OF THE MORTALITY IN THE POPULATION

The seasonal cycle in the population was associated with the temperature about four months beforehand (Chapter 2). Furthermore, excessive rainfall in the spring of 1973/74 appeared to have suppressed the seasonal cycle for that year. The rate of daily crawler production was a function of temperature (Chapter 4) and since the life-cycle time varied from 6 - 18 weeks, this would account for the displacement of the effective temperature relative to the population cycle. Apparently the greatest effect of temperature was on the rate of recruitment.

In order to substantiate these conclusions the mortality in the population was investigated. The account falls into three parts. In part 5.1 the relative importance of the various categories of mortality is assessed; in part 5.2 the generation mortality is estimated and checked; lastly, in Part 5.3 the generation mortality is related to climatic and biotic indices.

5.1 The relative importance of the various categories of mortality

The data for this assessment came from dissections of scales of all stages, on all three sites, made at each sampling date (section 2.2).

5.1.1 Summary of the categories of mortality and the stages on which they acted

Four kinds of mortality were recognised acting on female scales (section 2.8). They were:

(i) Predation, mainly by *Lindorus lophantae* and lacewings, which preyed on stages 1 - 3, rarely on the adult.

Predation-damaged scales accumulated in the population. It is likely that many of the younger stages were removed entirely by predators, while larger scales may have fallen off the trees. Finally, scales sucked dry by chrysopidae would have been confused with scales which had died from undefined causes.

(ii) *Aphytis* parasitism acted on stages 2 and 3, but parasitoids also stung scales which they did not parasitise. Such stung scales were indistinguishable from undefined mortality, but a reasonable ratio of parasitised to stung scales seemed to be 1:1. Hence, to assess the importance of *Aphytis* on the scale population the numbers of parasitised scales might be doubled, and the difference deducted from undefined mortality. Scales from which parasitoids had emerged were included.

(iii) Endoparasitism by *H. rouxi* and *C. bifasciata* emerged from adult female scales, rarely from stage 3, but the stages attacked were not known. Endoparasitism was assumed to have acted on the adult. Both endoparasitoids were attacked by the hyperparasitoid, *M. javensis*. Hyperparasitised scales, and those from which parasitoids had emerged were included, because other categories of mortality also consisted of retrospective evidence.

(iv) Mortality from undefined causes acted on all stages and scales which had died for no apparent reason were common in the population. They accumulated for an unknown time although they reached a minimum between January and March each year (Fig. 2.8) at the end of the rains.

Fig 5.1. Scales on twigs in each category of mortality, expressed as a fraction of the total number of dead (or dying) scales in the samples. *Aphytis* parasitised scales do not include a measure of host-stinging.

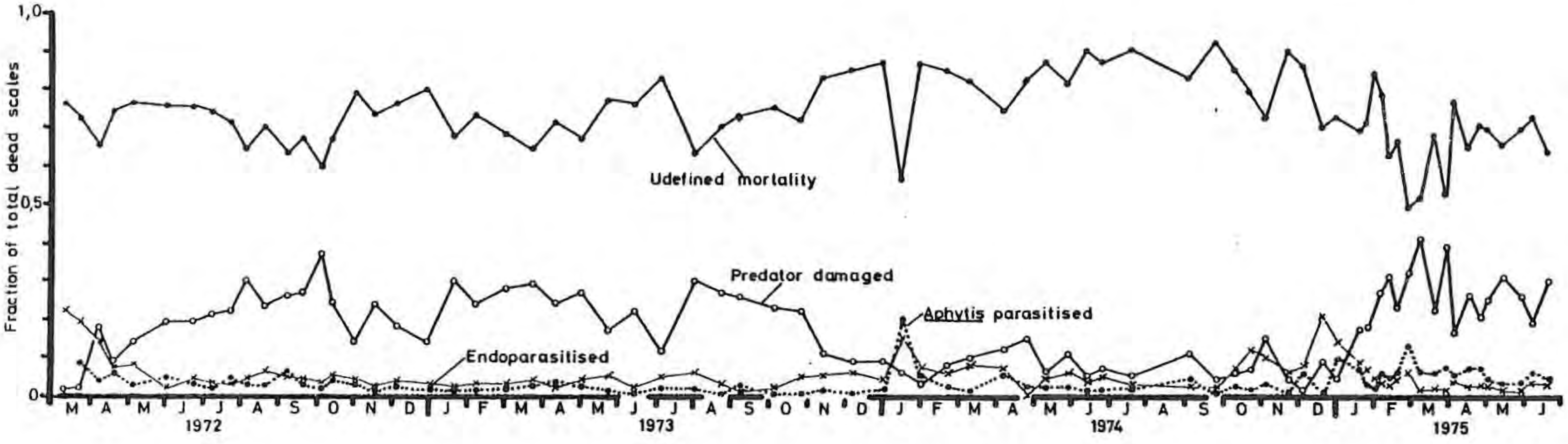
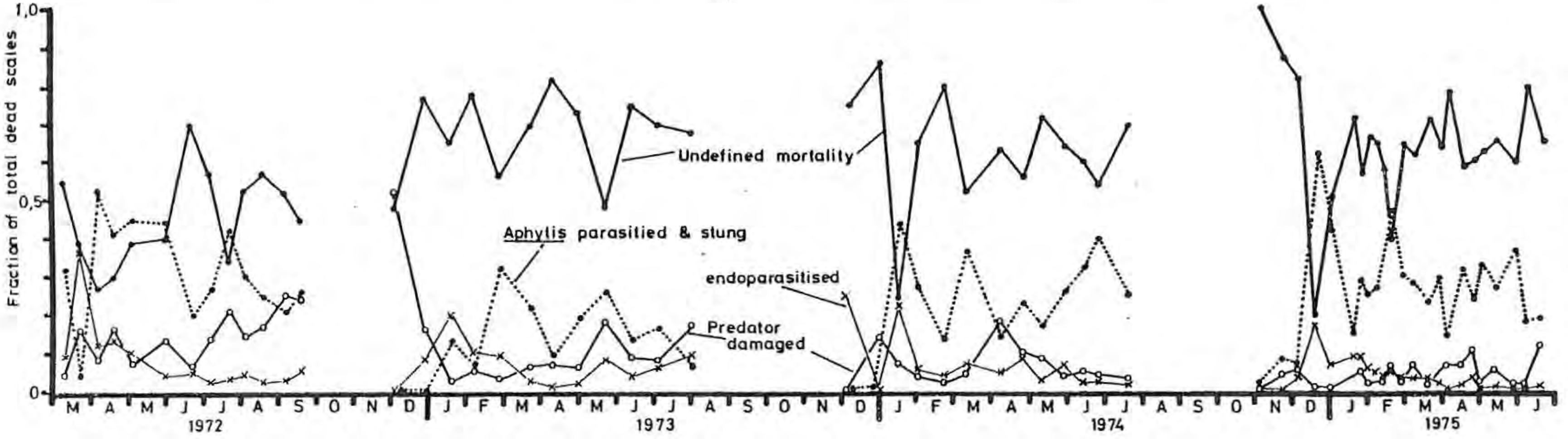


Fig 5.2. Scales on fruit in each category of mortality, expressed as a fraction of the total number of dead (or dying) scales in the samples. *Aphytis* parasitism has been doubled to include a measure of host-stinging, and the difference deducted from undefined mortality.



5.1.2 Assessment of the importance of each category of mortality

In the scale population several categories of mortality acted contemporaneously on each stage. For example predation, *Aphytis* parasitism, undefined mortality and possibly endoparasitism all acted together on stages 2 and 3 and it was not possible to say in which order they acted. Furthermore, the evidence of undefined mortality and predation accumulated in the population. Consequently neither the numbers surviving (S) from a given category of mortality, nor the initial numbers in the stage before mortality (N) could be known, and it was not possible to use the data from scale dissections for survival analysis. Instead, the data were used simply to identify the most important categories of mortality although there was no way to quantify their effect on the scale population.

At each sampling date the number of scales in each category of mortality was expressed as a fraction of the total number of dead scales in the sample. The results were plotted against the sampling dates. On twigs (Fig. 5.1), the most important category was undefined mortality. Even allowing for an accumulation of dead scales it was much larger than the others. The second most important category was predation. On fruit (Fig. 5.2), the number of *Aphytis* parasitised scales was doubled to account for host-mutilation, and the difference deducted from the number dead from undefined causes. On this assumption there were two important categories, undefined mortality and *Aphytis* induced mortality. Endoparasitism did not appear to be important on either site.

5.1.3 Conclusions

Undefined mortality probably included mortality from several sources; for example, unrecognised predation damage, the effects of overcrowding and being forced off the surface by younger individuals beneath, the weather acting either directly on scales or via the host-plant's physiology. It is unlikely that extremes of high temperature would have caused much direct mortality, because the LD_{50} peak temperature for the most susceptible stage of the female is about 47°C according to Abdelrahman (1974a). Stevenson screen temperatures in the orchard rarely exceeded 40°C, and although scales in direct sunlight may have been exposed to higher extremes than this, most of the scales would have been shaded. The LD_{50} trough temperature for female scales is about 6°C (Abdelrahman, 1974a) and in the orchard Stevenson screen temperatures fell as low as 2°C. Willard (1972a) recorded high mortality at a constant temperature of 15°C but this may have been due in part to the adverse effect on the floating lemon leaf discs he used as host material. Hence, low temperatures may have caused some direct mortality but their effect would have been mainly via the host plant's physiology.

This method of identifying the most important category of mortality constitutes a key-factor analysis but is not quantitative. A key mortality factor accounts for most of the change in the size of a population from one generation to the next. The concept was first proposed by Moris (1959). The method of analysis which he developed has been criticised (e.g. Southwood, 1967; Hassell and Huffaker, 1969; Luck, 1971) and the method most often used is that of Varley and Gradwell (1960), by survival analysis. Where there is difficulty identifying the key factor(s), Podoler and Rogers (1975) proposed a refinement to the Varley and Gradwell method.

If a key-factor can be identified and quantified then it can be used to predict population trends. With the method used here, this was not possible because undefined mortality could not be quantified. In order to reach conclusions about the factors which caused the fluctuations in the size of the population, the total mortality in the life cycle was estimated (section 5.2) and then relationships were sought between it and climatic or biotic indices (section 5.3).

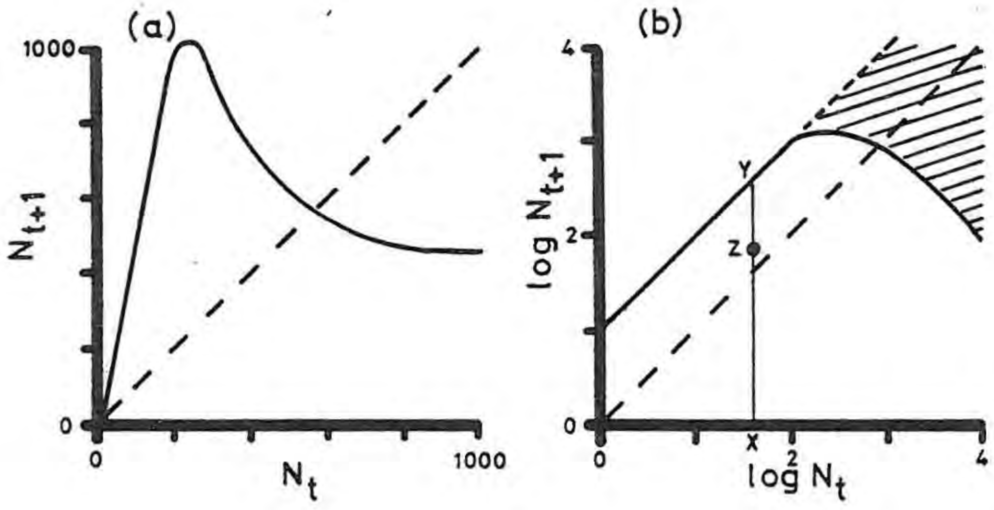
5.2 The estimation of generation mortality

In survival analysis of insect populations, the logarithm of the survival rate from each mortality factor is called a k-value (Varley and Gradwell, 1960; Williamson, 1972). Strictly speaking $k = -\log(S/N)$, where S is the number of survivors and N the number before mortality. The advantage of taking logarithms, apart from the advantages mentioned in section 2.4, is that successive k-values can be added. The sum of all the k-values in the life cycle gives the log generation survival, K. In the present case, although the various k's could not be calculated for the reasons given in the previous section, it was possible to estimate K. The procedure is described here.

Populations of continuously breeding insects do not lend themselves to survival analysis by age-specific life tables (Southwood, 1978) because it is difficult to follow the fates of distinct groups of individuals through their life cycles. Neither can time-specific methods (Southwood, 1978) be used because stable age, or stage, distributions cannot be assumed; firstly because insects are usually grouped by stages which are of unequal duration, secondly because temperature-changes alter the rates of development.

Instead, for such populations, Southwood (1978) defines an alternative approach employing 'predictive population models'. These models predict the size of the population after a period of unlimited growth, for comparison with the actual, measured, population size obtained in field samples. The difference gives the survival rate. According to Southwood, the various approaches to survival analysis are not as different as they

Fig 5.3. From Rogers (1979): (a) Ricker and (b) Moran curves for logistic growth of a population with a tenfold rate of increase. The solid curves represent growth in the absence of density independent mortality. Where they cross the 45° line is the point of equilibrium. The hatched area represents density dependent limitation. The Rogers/Moran method assumes that YZ is a measure of density independent mortality acting during the interval t to t+1 on a population which is at level X at time t.



appear and they grade into each other.

In the present case, two methods of survival analysis were used, both of them based on the predictive model approach. The first is a method described by Rogers (1979) employing Moran (1950) diagrams. The second method, used to check the first, is based on a method suggested by Southwood *et al* (1972).

A central problem with the predictive model approach is the choice of the time interval at which the population size is to be measured. If the interval is too short the predicted population numbers will be too low compared to the numbers in the samples, and vice versa if too long. In the present case, the chosen interval was one generation time, and since this interval varied with temperature, it was expressed as a thermal constant. Sampling dates were selected at intervals of one thermal constant for the generation time, from the samples covering three and a half years.

5.2.1 The Rogers/Moran method : rationale

Ricker (1954) adopted one of Moran's (1950) ways of plotting population data. The population numbers at one time (N_{t+1}) are plotted against the numbers of the same stage at the time before (N_t) to form a scatter diagram. In data with small standard errors (e.g. laboratory populations) the dots form a line rather than a scatter, with a trajectory roughly as in Fig. 5.3(a). Rogers (1979) pointed out that if the data are transformed to logarithms then, (i) the exponentially increasing part of the curve is linearised, (ii) the elevation of this linear part of the curve above a 45° line through the origin, gives a measure of the log finite rate of increase of an individual over the time interval t-t+1. The curve, which Rogers now calls a Moran curve, then appears as in Fig. 5.3(b). According to Rogers, the point where the curve bends over and returns towards the 45° line through the origin, is the point at which environmental resistance (Varley, Gradwell and Hassell, 1973) begins to limit the population growth. In other words, density dependent mortality begins to act at this point. Where the curve cuts the 45° line through the origin, is the point of population equilibrium.

If data from a field population are plotted in this manner, the points form a scatter and each point generally falls some way below the Moran curve. According to Rogers this is because density independent mortality has acted upon the population. Thus the reason that a population at level X in Fig. 5.3(b), only reaches level Z one interval of time later, and not level Y, is because of density independent mortality of magnitude YZ. Since Y and Z represent, respectively, potential and actual population densities expressed in logarithms ,the distance YZ gives the difference between two log densities and hence is a k-value.

Rogers (1979) tested the method of analysis with a simple model designed to simulate a slowly breeding insect, the tsetse fly. He came to the following conclusions about the method:

(i) When the density independent mortality acted on only one stage in the life cycle, the method estimated qualitative changes in that mortality. When the density independent mortality acted equally on all stages, the method also estimated quantitative changes in that mortality.

(ii) Estimates of density independent mortality made within the range of action of density dependent mortality (i.e. within the hatched area in Fig. 5.3b), were under-estimated.

However in a relatively slowly breeding population the seasonal cycle depresses the population below the realm of operation of density dependent mortality for much of the year. Hence much of the density independent (weather induced) mortality would be estimated correctly by the method.

(iii) The method cannot be applied to populations showing a gradual trend over the years, either upwards or downwards, because the highest populations reached fix the point at which density dependent mortality can be detected. Density dependence can only be detected where the Moran curve starts to bend over. If there is a long-term trend then the trend must be corrected for.

5.2.2 Rogers/Moran method : discussion

Since the elevation of the Moran curve above a 45° line through the origin represents the log maximum possible finite rate of increase, then distances by which points fall below this curve must represent measures of the generation mortality, K, including changes in natality (and, presumably, the effect of the changing rate of development upon the population growth rate). The finite rate of increase is sometimes labelled R_o (Southwood, 1978) or λ (May,1976). Here, it has been called R.

If the interval between t and t + 1 is too long then the expected rate of increase will be too great and mortality will be overestimated. On the other hand, if it is too short then individuals surviving from one interval to the next will appear on both axes of the plot, effectively increasing the reproductive rate, and mortality will be underestimated (Rogers,1979). Furthermore, if the interval is incorrect then the periods over which climatic indices are averaged (or summed) will also be incorrect and it may be difficult to get statistically significant relationships with the estimated mortality.

Although Rogers (1979) used the method for continuously breeding populations (of tsetse flies) there may be objections to doing so with such populations, in which generations cannot be distinguished:

(i) The data are arbitrarily divided into units, referred to as cohorts, which are assumed to correspond to generations. (However, the very act of taking samples at more or less extended intervals has a similar effect.)

(ii) If there are delayed mortality effects, acting on subsequent generations rather than the present one and producing cyclical changes in numbers, then the method may not be valid. According to Williamson (1972), Moran plots only work well if the delay is of exactly one generation. In the present case, the most important delayed effect would probably have been the seasonal temperature changes. Referring back to Fig. 2.5, the delay was about four months; while the cohort generation time averaged three months (Appendix 1, column 3: see also the numbers in circles in Fig. 2.5, suggesting the number of generations, expressed as a thermal constant, which fitted end-to-end into each year. In Fig. 2.5, generations take 2 - 5 months. The thermal constant of the generation time is discussed in the next section, 5.2.3).
Hence, for this red scale population the delay was almost equivalent to a generation time and there seems to be no reason why Moran plots should not work well.

Individuals in the cohorts referred to above are assumed to have been born at time t and to have reporduced at time t + 1, or to have died in the meantime.

5.2.3 Estimating the mortality in the scale population

(a) The sampling interval: The relation between the numbers in successive generations of an exponentially growing population is

$$N_{t+1} = N_t \, e^{rT} \text{ --------------------- } (1)$$

where r is the intrinsic rate of increase and T the mean generation time. T is therefore an appropriate interval at which to measure the size of the population. According to Birch (1948), for a group of females of the same age, that is for a cohort, T may be approximated by

$$T = \quad x \, l_x \, m_x / \quad l_x \, m_x \text{ -----------------} (2)$$

where x is the age class, l_x the proportion of the original numbers in the cohort surviving at the start of each age class and m_x the fertility in each age class (the number of living female progeny per female). This expression gives the mean time, T, from the birth of the cohort to the midpoint of the cohort egg-curve, at which point the cohort is considered to reproduce (Birch, 1948). It is advantageous to express T as a thermal constant (section 3.6).

In the insectary, l_x was not measured in the pre-reproductive stages, only in the A+. Therefore thermal constants of T were calculated as follows for scales on twigs and fruit (the population on leaves being ignored in this analysis):

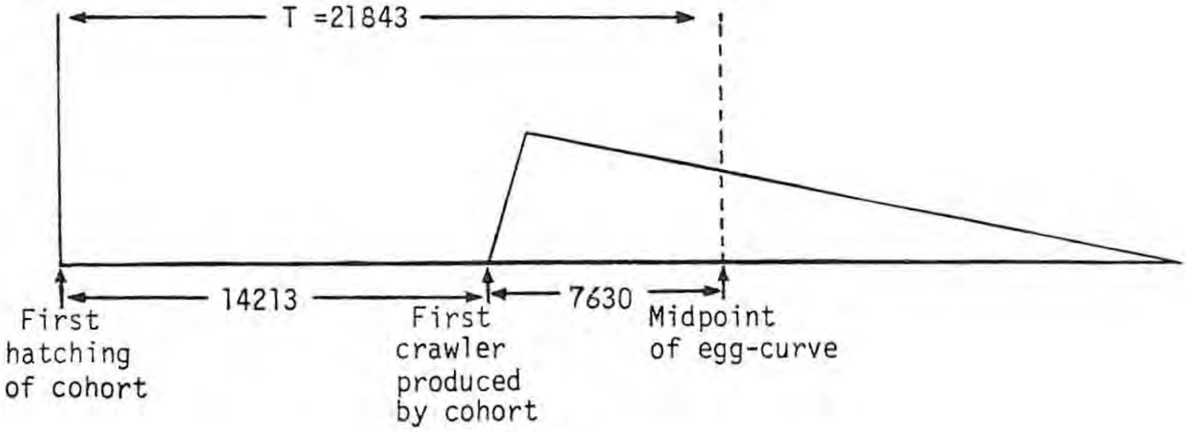
(I) Thermal constants for the life cycle times, from birth to first reproduction, were on twigs 14213h° and on fruit 13142h° (Table 3.1).

(II) Midpoints of the cohort egg-curves were calculated from equation (2) above, in five-day age intervals from the start of reproduction, and converted to hour-degrees.

The average thermal constants for midpoints of egg-curves on twigs and fruit were respectively 7630h° and 10013h°.

(III) Summing termal constants for life cycle times and cohort egg-curve midpoints gave totals of 21843h° on twigs, and 23155h° on fruit.

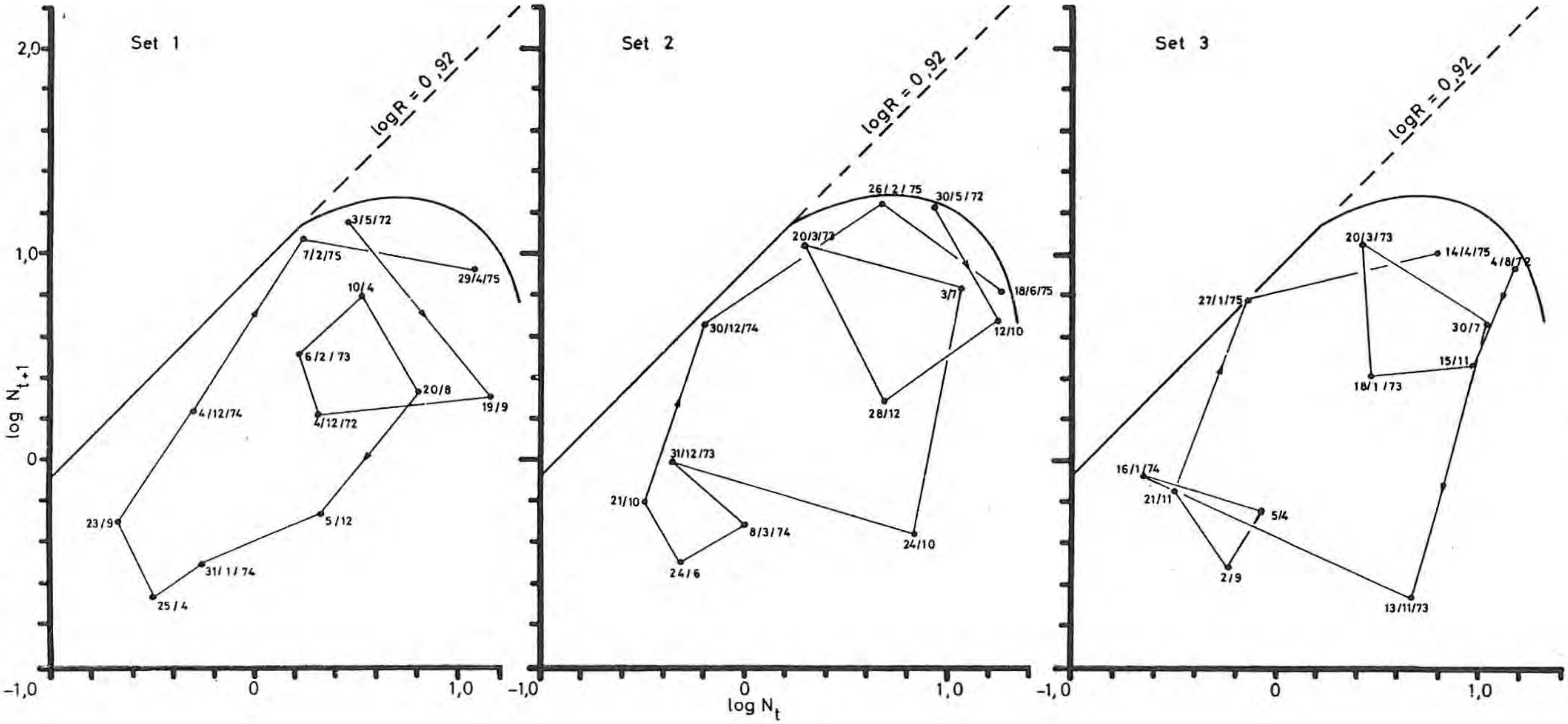
The procedure for finding T is summarised in the following diagram, where the figures refer to thermal constants on twigs:



(IV) The generation times of scales on twigs and fruit were therefore assumed to be approximately 20 000h°.

(b) Moran plots: From the census data, sampling dates were chosen which were separated by intervals of, as nearly as

Fig 5.4. Moran plots of adult female scale intensities/dm² on twigs. Plots 2 and 3 employ intensity readings intermediate between those in plot 1. Figures in the plots denote the dates at times t + 1. The log maximum finite rate of increase, 0,92, is set by point 27/1/75 in plot 3. The point 20/3/73 is common to both plots 2 and 3 (see Appendix 1).



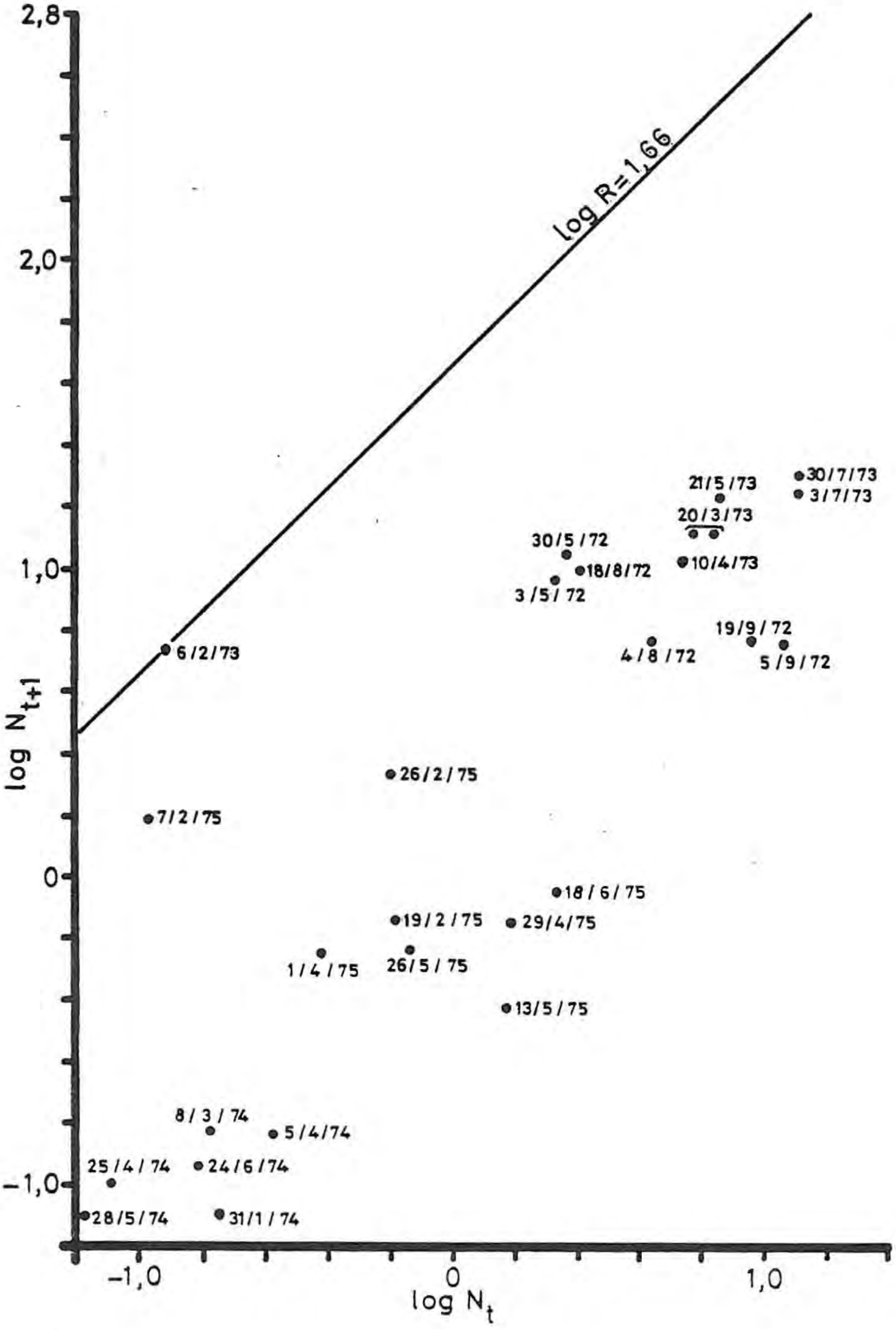
possible, 20000h°. For the population on twigs, three sets of sampling dates were selected in this manner, each set intermediate between the others. The principle is illustrated in Appendix 1 (column 3). The mean generation time between the chosen dates was 19952h° (n = 38 cohorts, standard deviation 1790,3).

The three sets of readings of scale intensity/dm² were plotted as three Moran diagrams (Fig. 5.4). As a first approximation the height of the Moran curves was set by the point showing the greatest increase of log N_{t+1} over log N_t. In Fig. 5.4 this point is at 27/1/75, and corresponds to a log finite rate of increase of 0,92. The Moran curves were therefore set at this height in all three plots. In populations of mobile insects, immigration may occur and some of the points would then correspond to impossibly high rates of increase. Such points would fall above the line of the log maximum possible finite rate of increase. The height at which the Moran curve was set, and the mean level of mortality which was estimated, are discussed in section 5.2.4.

On fruit, the scale population was discontinuous because of picking. In order to get as many points as possible for a Moran plot from the relatively short runs of data for each fruit season, up to five sets of readings were selected. The cohort intervals are shown in Appendix 2 (column 3). The mean generation time was 19924h° (n = 27 cohorts, standard deviation 1883,5).

Values of log N_{t+1} were plotted against log N_t for the fruit population (Fig. 5.5) but the points were not linked up in sequence because of the congestion. In any case the cycles were incomplete because the fruit were picked. The level of

Fig 5.5. Moran plot of adult female scale intensities/dm^2 on fruit. Figures in the plot denote the dates at times t + 1. The log maximum finite are of increase, R = 1,66 is set by point 6/2/73, and is discussed in the text.



the Moran curve was fixed by the point at 6/2/73, corresponding to a log maximum finite rate of increase of 1,66. The level of the Moran curve is further discussed in section 5.2.4.

Values of the generation mortality estimated by this method for scales on twigs were labelled ${}_1K_T$, to distinguish them from values estimated by the check methods (section 5.2.6). Values of ${}_1K_T$ are listed in Appendix 1 and plotted in Figs. 5.7 and 5.8.

Values of the generation mortality of scales on fruit were not checked and were labelled K_F. They are listed in Appendix 2 and plotted in Fig. 5.9.

(c) Density dependent mortality: Referring to Fig. 5.4, the dates of the points in the Moran plots show that the population decreased from March or April each year, so this decrease could be attributed either to falling temperature or to density dependent mortality. Density dependent and density independent mortality may be distinguished by the distances, respectively, above or below the curved portion of the Moran curve. This curved part in Fig. 5.4 was drawn by eye, so the distinction between density dependent and density independent mortality was subjective. Moreover, the method assumes that density dependence was direct and not delayed, which seems unlikely if the parasitoids had any regulatory effect on the scale population. For these reasons, no further attempt was made to detect the presence of density dependent mortality by this method.

5.2.4 Checking the mean level of the estimated mortality

According to Rogers (1979) the Moran curve-fitting method will identify changes in mortality but not necessarily the correct mean level about which these changes take place. This is

Table 5.1 Values of r_m for red scale from three sources in the literature, together with values of R calculated from them assuming a generation time of 62 days. In the experimental orchard during December and January, 20 000 h° required about 62 days (see text and Table 5.2).

Source	Host plant material	Regime		r_m per day	lnR	R	logR
		°C	%RH				
Willard, 1972a Table 6	Floating lemon -leaf discs	30 35 20 15	humid " " "	0,064 0,044 0,026 0,011	3,97 2,73 1,61 0,68	52,88 15,30 5,01 1,98	1,72 1,19 0,70 0,30
McLaren, 1971, Fig. 3	Rangpur lime leaves	35 32 29 24 18 13	75 75 45 45 75 75	0 0,048 0,045 0,038 0,019 0	- 2,98 2,79 2,36 1,18 -	- 19,61 16,28 10,55 3,25 -	- 1,29 1,21 1,02 0,51 -
Wentzel, 1970, Table 2.	Lemon fruit	30 25 20	80 80 80	0,062 0,049 0,017	3,84 3,04 1,05	46,71 20,86 2,87	1,67 1,32 0,46

Table 5.2 Total number of h°>12°C in each month from November 1971 to June 1975. Figures for the first three months (November, December, 1971 and January, 1972) were not recorded in the experimental orchard, but at a station 20 km away. In each season the hottest months were December and January, with an average total of 19384 h° for the four fruit-seasons 1971/2 - 1974/75.

Year	J	F	M	A	M	J	J	A	S	O	N	D
1971	-	-	-	-	-	-	-	-	-	-	7905	9806
1972	10793	8438	8135	7360	4187	2390	3669	4566	6590	7517	6779	9856
1973	9715	8652	9927	6058	5182	3876	3800	4841	6242	6717	7714	8416
1974	10946	8204	8419	5784	4758	3056	2947	4542	6035	7600	7800	9242
1975	8761	7576	7158	5797	4556	2597	-	-	-	-	-	-

because the position of the Moran curve is fixed, as a first approximation, by points which are liable to errors on both axes of the plot. These errors, which may arise from sampling, migration, or in the choice of sampling interval, tend to raise the level of the curve.

The main sources of error with mobile insects would be immigration to the population, which would exaggerate the rate of increase from one generation to the next; or emigration, which would have the reverse effect. With the scale population, emigration would tend to have occurred on twigs, and immigration on fruit. Other sampling errors would have been minimal. The mean level of the estimated mortality was checked as follows:

(i) Values of log R were calculated from published values of the intrinsic rate of natural increase, r_m, of red scale (Table 5.1). The equation used was

$$\ln R = r_m T$$

where T is the generation time when the generations completely overlap and a stable age distribution exists (Laughlin, 1965). A generation time of 62 days was assumed because during the hottest months , December and January (Table 5.2), there was an average total of 19384h° in 62 days.

Maximum values of log R (Table 5.1) were between 1,67 - 1,72.

(ii) Rogers (1979) pointed out that at population equilibrium the finite rate of increase, R, should be equal to the average rate of mortality; that is log R = mean K. For the populations on twigs and fruit, regressions were calculated between the observed rates of increase from one

Table 5.3 Regression equations for the finite rates of increase from one generation to the next (N_{t+1}/N_t), on the K- values estimated by the Rogers/Moran method. Observed values of N_{t+1}/N_t are tabulated in Appendices 1 and 2, as are the K- values estimated by the method.

Site	Regression equation	Predicted K at equilibrium
Twigs	$N_{t+1}/N_t = 5{,}095 - 3{,}397\ K$ ($r^2 = 0{,}72$)	1,21
Fruit	$N_{t+1}/N_t = 24{,}430 - 14{,}345\ K$ ($r^2 = 0{,}60$)	1,63

generation to the next, N_{t+1}/N_t, on the corresponding values ${}_1K_T$ or K_F (see Appendices 1 & 2). From the regression equations (Table 5.3) mean values of ${}_1K_T$ or K_F were predicted when $N_{t+1}/N_t = 1$ (no increase or decrease).

(iii) Predicted equilibrium values of ${}_1K_T$ were 1,21, and of K_F, 1,63. The value of ${}_1K_T$ was less than the maximum values of log R in Table 5.1 by about 0,50 suggesting that the level of mortality on twigs was underestimated by this much. However on fruit the predicted average value of K_F (1,63) compared well with the maximum values of log R (1,67 - 1,72), indicating that the estimated level of mortality was correct on this site.

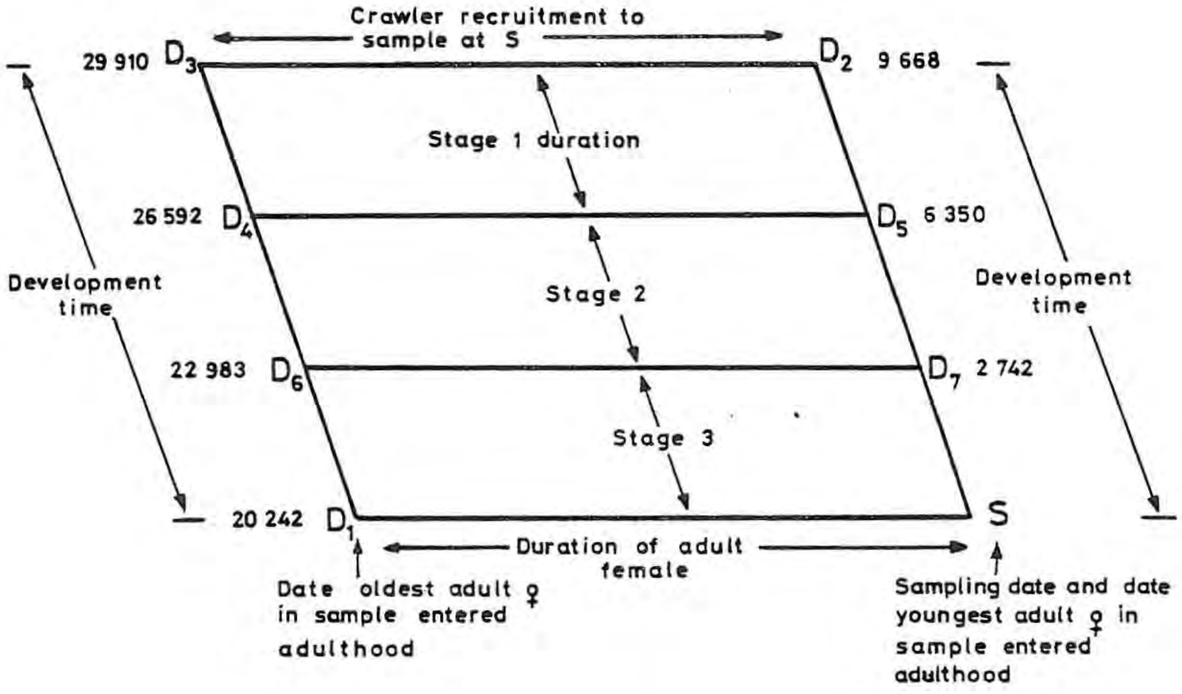
The underestimation on twigs may have been due to emigration of crawlers to fruit, or to the lower natality on twigs compared to fruit.

5.2.5 Checking the fluctuations in the estimated mortality

Fluctuations in the estimated mortality on twigs were checked by another method but the estimated mortality on fruit was not checked. The check method was based on a simple predictive model proposed by Southwood *et al.* (1972) and summarised by Southwood (1978, p. 399). In the model, the number of adults expected on a given date is predicted from the number of eggs laid over some previous interval which is defined by the development time from egg to adult. The difference between the expected number on that date and the observed number in a sample, provides a measure of the mortality which has occurred since laying.

The model, as described by the authors, allows for the effect of variable hatching and development rates to be incorporated into the prediction. In the present case, although the development

Fig 5.6. Diagram defining the recruitment dates, D_3 to D_2, relative to the sampling date, S, when the adult female stage was counted in orchard samples. Intermediate dates D_4–D_7 define immature stages on this framework. Figures are cumulative durations in h° backward from S, for scales living on twigs.



times were measured (section 3.1) variations in the development times were not, because of the destructive sampling necessary to determine when the scales had moulted into the next stage. A simpler model was devised using the average development time from crawler to adult. It is described in the following paragraphs.

The object of the model was to predict the intensity/dm² of adult females which would have been expected on a given sampling date in the absence of any mortality; in other words, to predict the crawler recruitment of the cohort of adult females sampled on that date. The crawlers would have emerged between certain dates sometime beforehand. Fig. 5.6 shows how these dates were defined by thermal constants for the average development time from crawler to adult, and for the duration of the adult female stage.

In Fig. 5.6, the sampling date is denoted by S. The youngest adult female which could possibly be present in the sample at S would have entered adulthood on the same day, S. The oldest individual which would possibly be present at S would have entered adulthood one 'adult duration' previously, at date D_1. The dates between which all the adult females which are observed at S, themselves emerged as crawlers, are defined by the development times from crawler to adult, extended beckwards from dates D_1 and S. Hence the date when the oldest adult female emerged as a crawler is D_3 and the date when the youngest emerged is D_2. The dates $D_1 - D_3$ and S are shown (Fig. 5.6) as the corners of a quadrilateral for clarity because they overlap, but in fact they extend back in time from S as a single line. The other dates in Fig. 5.6 ($D_4 - D_7$), define the intermediate stages on this framework.

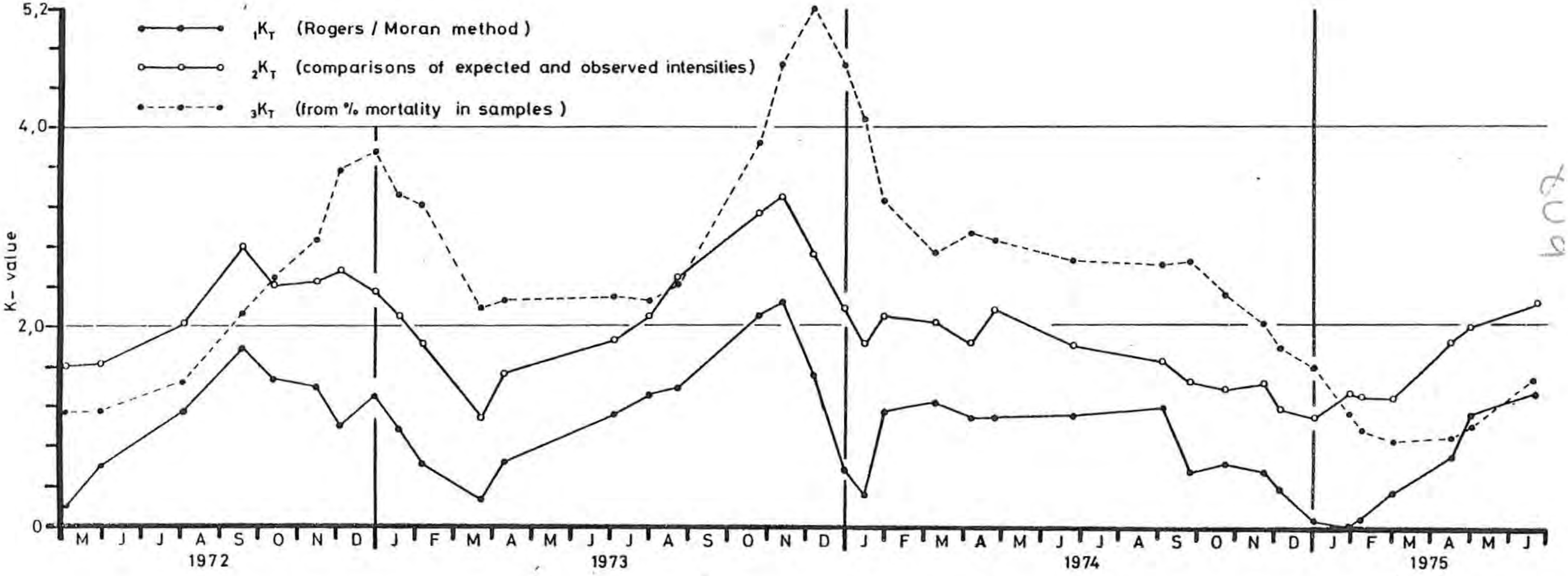
If the durations of the adult female stage and of the crawler - adult female development time, are expressed as thermal constants then opposite sides of Fig. 5.6 become equal. Cumulative durations backward from S are given in h° in Fig. 5.6 for scales on twigs. For example the youngest adult female which could possibly be present at S would have emerged about 10.000h°, or one summer month, before S. The oldest adult female would have emerged 30.000h° or three summer months before S. (It should be emphasised at this point that the date S in this model is equivalent to time t+1 in the Rogers/Moran method; and that time t, 20.000h° before time t+1, would fall between dates D_3 and D_2).

Dates D_1 - D_7 were defined by summing daily h° values backwards from each sampling date. The h° values were estimated from thermograph charts recorded in the orchard. There were 77 sampling dates, between February 1972 and June 1975, and the daily summations were performed by means of a computer programme devised by M.G. Murdoch (South African Sugar Association Experiment Station, Mount Edgecombe).

The daily natality (crawlers per dm^2), estimated by the methods described in sections 4.6 and 4.7, was summed between the dates D_3 and D_2 for each sampling date. The result was the crawler recruitment, or the expected adult female intensity/dm^2 in the absence of mortality, at each sampling date. The log expected intensity/dm^2 minus the log observed intensity/dm^2, gave values of the generation mortality (labelled ${}_2K_T$) with which to check values of ${}_1K_T$ derived from the Rogers/Moran method.

A third check was made by calculating the generation mortality from the average percentage mortality in each stage of the life cycle. Scales of all stages were dissected every sampling

Fig 5.7. Total mortality in female scales on twigs estimated by the Rogers/Moran method ($_1K_T$) and by two checks ($_2K$ and $_3K_T$) which were based on a method described by Southwood *et al.* (1972).



date and the percentages of dead and parasitised scales recorded. These percentages were averaged between the appropriate dates (Fig 5.6) for the stages in a cohort. For example, percent mortality in stage 1 was averaged for samples falling between dates D_3 and D_5; stage 2, between D_4 and D_7; stage 3, between D_6 and S; and the adult female between D_1 and S. If the average percent mortality in stage 1 was, say, 50%, this gave a k-value of 0,30; and the k-values in subsequent stages of the cohort were summed to get an estimate of the generation mortality, which was labelled ${}_3K_T$.

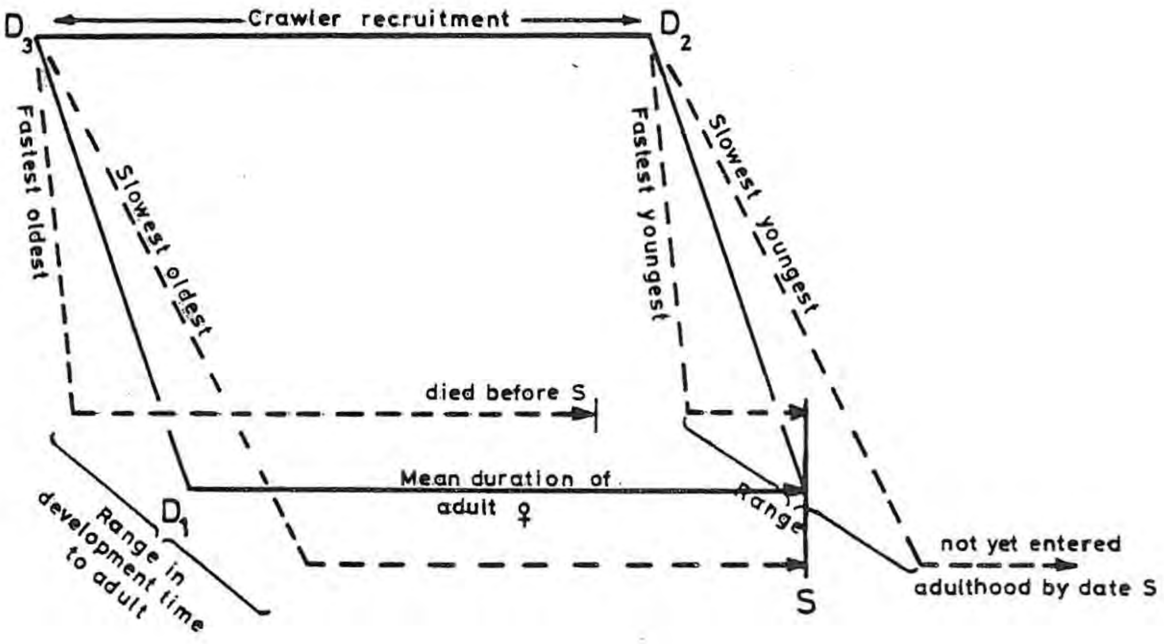
The cohorts referred to in both these check methods based on the model of Southwood *et al.* (1972), are assumed to have been recruited between dates D_3 and D_2 and to have been sampled at date S.

5.2.6 Conclusions about the estimation of the generation mortality

Estimates of mortality, made by each of the three methods, are plotted in Fig. 5.7 and the fluctuations agree quite well. However, it is obvious that values of ${}_3K_T$ were exaggerated by the tendency for dead scales to accumulate (see sections 2.8 and 5.1.1) and so the third method has not been considered any further.

The methods used to derive ${}_1K_T$ and ${}_2K_T$ were not independent of each other because the same scale intensity/dm² was used at time t+1, or at S, respectively. Furthermore, the intensity/dm² at time t which was used in the Rogers/Moran method, would have fallen between dates D_3 and D_2 (Fig. 5.6) and so would have entered calculations to predict the crawler recruitment in the second method. Nevertheless, the two methods represent two different ways of estimating the generation mortality from substantially the same data and the fact that the changes in mortality agreed in each

Diagram showing that neither the fastest developing oldest individuals, nor the slowest youngest, would be present in the sample at S.



case, strengthens the belief that these changes were real. It is the changes in mortality, rather than the mean level, which are important when seeking relationships with climatic and biotic indices.

The mean levels of mortality estimated by the first and second methods differ quite markedly (Fig. 5.7). The level of mortality estimated by the Rogers/Moran method appears to be approximately correct (section 5.2.4), although a factor of 0,50 could be added to the values of ${}_1K_T$ which would bring the levels of mortality slightly closer together in Fig. 5.7. It is possible that the rate of crawler recruitment (sections 4.6 and 4.7) was consistently overestimated. Alternatively, the reason why mortality was overestimated by the second method may lie in the different ways that cohorts were defined. The predictive population model, as used here (Fig. 5.6), took no account of the effect of individual variation in the rates of development. Assuming that individual differences in the thermal constants for development, were normally distributed about the mean constant, then many of the slowest developing oldest individuals, and the fastest developing youngest, could not possibly have been present in the sample at S (see diagram opposite). Hence the expected numbers at S would have been somewhat exaggerated.

There appear to be two objections to these methods for estimating the generation mortality. The first, which was mentioned in section 5.2.2, is that it is not realistic to divide into cohorts the data from a continuously breeding population and to treat such cohorts as discrete generations. (Similarly, it may not be realistic to use intermediate sets of cohorts in order to get more continuous estimates of mortality.) The second objection is that the intensity/dm² of adults taken in a sample at one time (whether time t, t+1 or S) did not represent the total intensity/dm² of individuals in a cohort which survived to pass through the adult stage. The intensities/dm² in samples at t and t+1 (or S) only reflected the total intensities/dm² of individuals which entered adulthood in the respective cohorts. This may be another reason why the second method overestimated mortality. In that method, the total recruitment of female crawlers to a cohort was estimated, but the intensity/dm² of adult females in the sample at S did not represent the true intensity/dm² in the cohort which entered adulthood.

5.3 Mortality related to climatic and biotic indices

Relationships were sought between the estimated mortality (${}_1K_T$ and K_F) and indices of weather, and of predator or parasitoid abundance. The object was to infer which environmental factors caused the seasonal and year to year changes in scale intensity/dm².

There were three reasons for seeking relationships between climatic factors and scale mortality, rather than intensity/dm²:

(i) Scale intensity/dm² would have depended in part on the intensity/dm² of th previous generation, whereas mortality would have been independent of intensity/dm² (except at high intensities/dm² when there would have been some density dependence).

(ii) Weather may have determined changes in intensity/dm² but not the actual intensity/dm². On the other hand, weather would directly have determined mortality.

(iii) Fortuitous correlation can arise when two sets of serially correlated data, such as insect intensity and weather indices, are slid relative to each other to get a good fit (Bursell, 1974). By using pairs of intensity/dm² readings separated by an interval of 20000h° to estimate mortality, and by summing or averaging the weather indices over the same interval, (a) the necessity for sliding one set of data relative to the other was obviated, (b) some of the serial correlation may have been removed, because the data were then framed in particular ways.

5.3.1 Derivation of the indices

Most of the indices were derived by summing or averaging measures of potential mortality factors (temperature, rainfall, predators) over the generation time, t - t+1. Some of the indices were derived by summing or averaging over the first or second half of the generation time. In one case (index 4, Table 5.4) temperature was averaged over a period extending from 5000h° before time t to 5000h° after it, to see whether temperature acted mainly upon the rate of crawler recruitment.

Threshold temperatures for thermal summation of day degrees were set at 12°C, 15°C, 20°C and 30°C (Tables 5.4, 5.6) for the following reasons:

(i) The threshold temperature for development was 12°C (section 3.3) and day-degrees below this level were summed.

(ii) Willard (1972a) recorded greatly increased scale mortality at a constant temperature of 15°C, compared to 19°C, or higher, constant temperatures. Day-degrees below 15°C were summed.

(iii) McLaren (1971) found that the intrinsic rate of natural increase of red scale fell sharply at constant temperatures above 30° - 32°C, and below 20° - 24°C. Day-degrees above 30°C and below 20°C were summed.

A logarithmic transformation was used for all the indices of thermal summation in order to linearise the resulting relationships.

Measures of the drying-power of the air were given by evaporation from a Class A pan situated 15km away from the orchard, and by saturation deficit calculated from relative humidity readings recorded in the experimental orchard. Waterhouse and Amos (1968) concluded that saturation deficit was a better estimate of the drying power of the air than relative humidity. Evaporation also includes the effect of wind velocity and should in theory give an even better measure of the drying power. In the present case it was not expected that the dryness of the air would affect the insect, which tapped a continuous source of water, but it might have influenced the host plant.

Rainfall was recorded 1km from the orchard. Indices which measured excess rain, greater than the long-term mean, were calculated as follows:

(i) Murdoch (1970) published 52 year means of the monthly rainfall at a station 20km from the orchard. Long-term monthly means were converted to daily means which were summed between t and t+1.

(ii) The total rainfall between t and t+1, minus the total for the long-term daily means, gave the excess rainfall (which was recorded as zero whenever it was negative).

Predator and parasitoid numbers were expressed as intensities per 'twig' (section 2.3) and averaged between times t and t+1, or over the first or second half of the generation time. Logarithmic transformations were used for the reasons discussed in section 2.4.

Table 5.4 Mortality on twigs: Simple correlation and regression coefficients for mortality on climatic or biotic indices (n = 38; n.s. = not statistically significant). Crosses (righthand side) mark indices selected for multiple regression analysis (Table 5.5).

Factor	Index	Correlation coefficient		Regression coefficient		
		r	$100r^2$	b	P	
	CLIMATIC					
Temperature	(1) Mean maximum during generation time	-0,589	34,7	-0,176	0,001	
	(2) Mean minimum " " "	-0,629	39,5	-0,115	0,001	X
	(3) Mean mininum in first $\frac{1}{2}$ of generation time	-0,576	33,2	-0,099	0,001	
	(4) Mean min. during 5000h° either side time t	-0,470	22,1	-0,076	0,01	
	(5) D°>30°C during generation time (log)	-0,212	4,5	-0,325	n.s.	
	(6) D°<20°C " " " (log)	0,627	39,3	0,725	0,001	
	(7) D°<15°C " " " (logx+1)	0,610	37,2	0,339	0,001	
	(8) D°<12°C " " " (logx+1)	0,582	33,9	0,329	0,001	
Evaporation	(9) Mean daily during generation time	-0,403	16,3	-0,197	0,01	
Saturation deficit	(10) Mean daily during generation time	-0,357	12,7	-0,155	0,05	
	(11) Mean maximum daily during generation time	-0,411	16,9	-0,096	0,01	X
	(12) Mean max. daily during first $\frac{1}{2}$ of gen. time	-0,336	11,3	-0,062	0,05	
Rainfall	(13) Total in generation time	-0,015	0,1	-0,001	n.s.	
	(14) Total in first $\frac{1}{2}$ generation time	-0,175	3,1	-0,001	n.s.	
	(15) Total in gen. time>long term mean	0,372	13,8	0,003	0,02	X
	(16) Total in first $\frac{1}{2}$ generation time >l.t.m.	0,017	0,1	0,002	n.s.	
	BIOTIC					
Predator intensity	(17) Mean during generation time (log100x)	0,725	52,5	1,204	0,001	X
	(18) Mean during first $\frac{1}{2}$ generation time (log100x)	0,411	16,9	0,980	0,001	
Aphytis intensity	(19) Mean during generation time (log10x)	0,151	2,3	0,087	n.s.	
	(20) Mean during first $\frac{1}{2}$ generation time (log10x)	0,205	4,2	0,152	n.s.	
	(21) Mean during last $\frac{1}{2}$ generation time (log10x)	0,113	1,3	0,076	n.s.	
Endoparasitoid intensity	(22) Mean during generation time (log10x)	0,185	3,4	0,578	n.s.	
	(23) Mean during first $\frac{1}{2}$ generation time (log10x)	0,400	16,0	0,955	0,01	X
	(24) Mean during last $\frac{1}{2}$ generation time (log10x)	0,011	0	0,029	n.s.	

5.3.2 Indices related to mortality on twigs

Simple correlation and regression coefficients are listed for 24 indices in Table 5.4. The usefulness of an index was assessed by its correlation coefficient, r, and by the percentage of the variation in mortality which it described, given by $100r^2$, provided that the relationship was statistically significant. The significance of the regression coefficient was tested, rather than that of the correlation coefficient because, according to Bailey (1959), it is safer to do so. Whereas in correlation analysis it is assumed that the variables being compared are normally distributed, no such assumption need be made in regression analysis.

Mortality was more closely related to low temperature than to high temperature (Table 5.4); for example the index of temperature summed above 30°C (index 5) was not significant. The best index of temperature was (2), mean minimum temperature, which remained significant in multiple regression analysis (Table 5.5).

Indices of evaporation and saturation deficit, while they were significant in simple regression analysis (Table 5.4) fell away in multiple regression (Table 5.5). This suggested that these indices merely reflected the effect of maximum temperature on mortality, because the dryness of the air would be closely related to maximum temperature.

Excess rainfall above the long term mean (15) was statistically significant (Table 5.4) and remained so in multiple regression analysis (Table 5.5).

Mean predator intensity during the generation time expressed as log 100x (index 17) was very closely related to scale mortality on twigs, and explained

Table 5.5 Mortality on twigs: Values of Student's t, and their probability levels, for the partial regression coefficients of mortality on five, four or three of the indices shown. The index with the lowest absolute value of t was dropped from the regression if its coefficient was not statistically significant, until all remaining coefficients were significant. This condition was reached with indices (2), (15) and (17) in the regression. (n = 38; n.s. = not significant).

Indices	Number of indices in regression					
	5		4		3	
	t	P	t	P	t	P
(2) Mean minium temperature during generation time	-3,3	0,01	-3,2	0,01	-2,8	0,01
(15) Rainfall in generation time>long term mean	4,1	0,001	4,8	0,001	4,3	0,001
(17) Mean predator intensity during generation time (log100x)	4,0	0,001	5,0	0,001	4,6	0,001
(11) Mean maximum daily sat. def. during generation time	1,6	n.s.	1,8	n.s.	-	-
(23) Mean endoparasitoid intensity during first $\frac{1}{2}$ gen.time (log10x)	0,8	n.s.	-	-	-	-

52% of the variation. One reason for this strong relationship was the high degree of correlation between predator numbers and temperature; the mutual correlation coefficient between indices (17), predator intensity, and (2), mean minimum temperature, was -0,621. However, in multiple regression analysis (Table 5.5), where the effect of each variable is assessed when the other variables are held at their means, index (17) was still highly significant.

Endoparasitoid intensity, averaged over the first half of the generation time and expressed as log (10x), was significant in simple regression analysis but not in multiple regression. There was no significant relationship between scale mortality on twigs and *Aphytis* intensity.

Multiple regression analysis was used to assess the relative effect of the best index of each factor. In Table 5.4, all five indices marked with a cross were entered into the regression and those indices which were not significant were dropped off. The procedure is demonstrated in Table 5.5. Three significant indices remained in the final regression equation, which was

$$ {}_1K_T = 1{,}064 - 0{,}059t + 0{,}872p + 0{,}0027r $$

where t is the mean minimum temperature (°C) during the generation time,

p is the mean predator intensity during the generation time, expressed as log (100x),

r is the excess rainfall (mm) greater than the long term mean during the generation time.

These three indices described 72,8% of the variation in mortality on twigs. They are plotted with mortality in Fig. 5.8. Substituting index (6), $D^\circ < 20^\circ C$, for index (2), mean minimum temperature,

Table 5.6 Mortality on fruit: Simple correlation and regression coefficients for mortality on climatic or biotic indices (n = 27; n.s. = not statistically significant). Crosses (right hand side) mark indices selected for multiple regression analysis (Table 5.7)

Factor	Index	Correlation coefficient		Regression coefficient		
		r	100r²	b	P	
	CLIMATIC					
Temperature	(a) Mean maximum, during generation time	-0,444	19,8	-0,107	0,02	X
	(b) Mean minimum, " " "	-0,316	10,0	-0,051	n.s.	
	(c) Mean maximum, during first $\frac{1}{2}$ of generation time	-0,481	23,1	-0,116	0,01	
	(d) D°>30°C, during generation time (log)	-0,371	13,8	-0,465	n.s.	
	(e) D°<20°C, " " " (log)	0,333	11,1	0,325	n.s.	
Evaporation	(f) Mean daily, during generation time	-0,536	28,7	-0,206	0,01	
Saturation deficit	(g) Mean daily, during generation time	-0,565	31,9	-0,189	0,01	
	(h) Mean maximum daily, during generation time	-0,566	32,0	-0,103	0,01	X
	(i) Mean max. daily during first $\frac{1}{2}$ of generation time	-0,560	31,4	-0,074	0,01	
Rainfall	(j) Total in generation time	0,101	1,0	0,000	n.s.	
	(k) Total in generation time>long term mean	0,282	7,9	0,002	n.s.	
	(l) Total in first $\frac{1}{2}$ generation time>l.t.m.	0,250	6,3	0,002	n.s.	
	BIOTIC					
Predator intensity	(m) Mean during generation time (log 100x)	0,382	14,6	0,658	0,05	X
	(n) Mean during first $\frac{1}{2}$ generation time (log100x)	0,310	9,6	0,528	n.s.	
Aphytis intensity	(o) Mean during generation time (log10x)	0,214	4,6	0,155	n.s.	
	(p) Mean during first $\frac{1}{2}$ of generation time (log10x)	0,524	27,5	0,374	0,01	X
	(q) Mean during last $\frac{1}{2}$ of generation time (log10x)	0,052	0,3	0,048	n.s.	
Endoparasitoid intensity	(r) Mean during generation time (log10x)	0,071	0,5	0,001	n.s.	
	(s) Mean during first $\frac{1}{2}$ of generation time (log10x)	0,134	1,8	0,334	n.s.	
	(t) Mean during last $\frac{1}{2}$ of generation time (log10x)	-0,260	6,7	-0,634	n.s.	

increased fractionally the proportion of explained variation to 73,0%. It was not possible to better this model by the inclusion of second order terms (see Appendix 3).

5.3.3 Indices related to mortality on fruit

Simple correlation and regression coefficients are listed for 20 indices in Table 5.6.

In contrast to the results for scales on twigs, indices of maximum rather than minimum temperature were more closely related to mortality on fruit (Table 5.6, a - e). This was because scales were present on the fruit mainly during summer, although they also lived through into winter, and in summer the daily minimum temperatures were well above 15°C, often above 20°C. The comparatively high correlation coefficient for mean maximum temperature during the first half of the generation time (index c) suggests that the main effect of temperature was upon the rate of crawler recruitment.

Indices of evaporation and saturation deficit were more closely related to mortality on fruit than those of any other factor (Table 5.6, f - i). The negative coefficients indicate that mortality was high in moist air. Index (h), the mean maximum saturation deficit during the generation time, was the only statistically significant index of any kind to emerge from multiple regression analysis (Table 5.7).

There were no statistically significant indices of rainfall or of endoparasitoid intensity. However, indices of predator intensity and *Aphytis* intensity were significant in simple regression although they fell away in multiple regression. *Aphytis* intensity was closely related to temperature and to saturation deficit; for example the correlation coefficient between (p),

Table 5.7 Mortality on fruit: Values of Student's t, and their probability levels, for the partial (or simple) regression coefficients of mortality on four, three, two or one of the indices shown. The index with the lowest absolute value of t was dropped from the regression if its coefficient was not statistically significant, until only index (8) was left in the regression. (n = 27; n.s. = not significant).

Indices	Number of indices in regression							
	4		3		2		1	
	t	P	t	P	t	P	t	P
(a) Mean maximum temperature during generation time	1,0	n.s.	—	—	—	—	—	—
(h) Mean maximum sat. def. during generation time	-1,4	n.s.	-1,1	n.s.	-2,8	0,01	-3,4	0,002
(m) Mean predator intensity during generation time (log 100x)	1,6	n.s.	1,3	n.s.	1,2	n.s.	—	—
(p) Mean *Aphytis* intensity during first $\frac{1}{2}$ of gen. time (log10x)	1,4	n.s.	1,0	n.s.	—	—	—	—

mean *Aphytis* intensity in the first half of the generation time, and (h), mean maximum saturation deficit during the generation time, was -0,763. This close mutual correlation between the indices can be seen in Fig. 5.9.

The best significant index of each factor in Table 5.6 was selected for multiple regression analysis. It was found that all these indices were so mutually correlated that none of them was statistically significant in the presence of the others (Table 5.7). The best single index was (h), mean maximum saturation deficit during the generation time, which described 32% of the variation in scale mortality on fruit:-

$$K_F = 3,173 - 0,103S$$

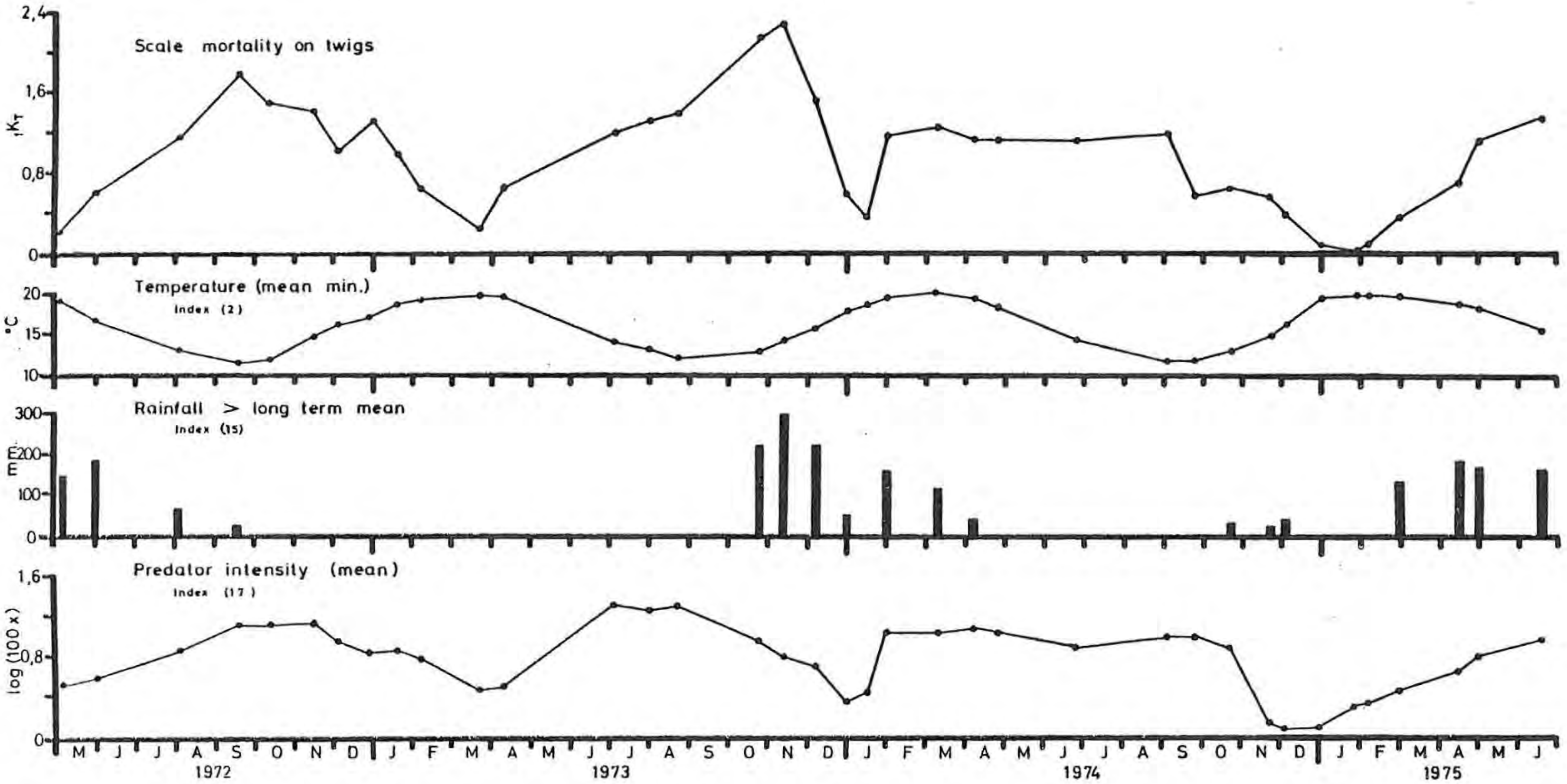
where S was the mean maximum saturation deficit.

5.3.4 Conclusions about the factors causing the fluctuations in the generation mortality

On twigs, indices of three factors explained 73% of the variation in scale mortality. These were mean minimum temperature, excess rainfall, and predator intensity. The role of temperature needs little discussion. It must have acted on the rates of reproduction and development so that in winter the finite rate of population increase fell below its maximum rate. Low-temperature extremes may also have caused some direct mortality, as was mentioned in section 5.1.3. There was no evidence that high temperatures caused scale mortality which confirms the supposition in 5.1.3. Not only was mean maximum temperature negatively related to scale mortality on both twigs and fruit, but temperature summations above 30°C were not significant in either case.

The role of excess rainfall is not easy to define. It seems unlikely that scales were washed off the trees, as was suggested by Bodenheimer (1951) and Gentile and Summers (1958).

Fig 5.8. Mortality of scales on twigs plotted against indices of temperature, rainfall and predator-intensity. All indices were derived between times t and t + 1 (Table 5.4.). All points are plotted at time t + 1.

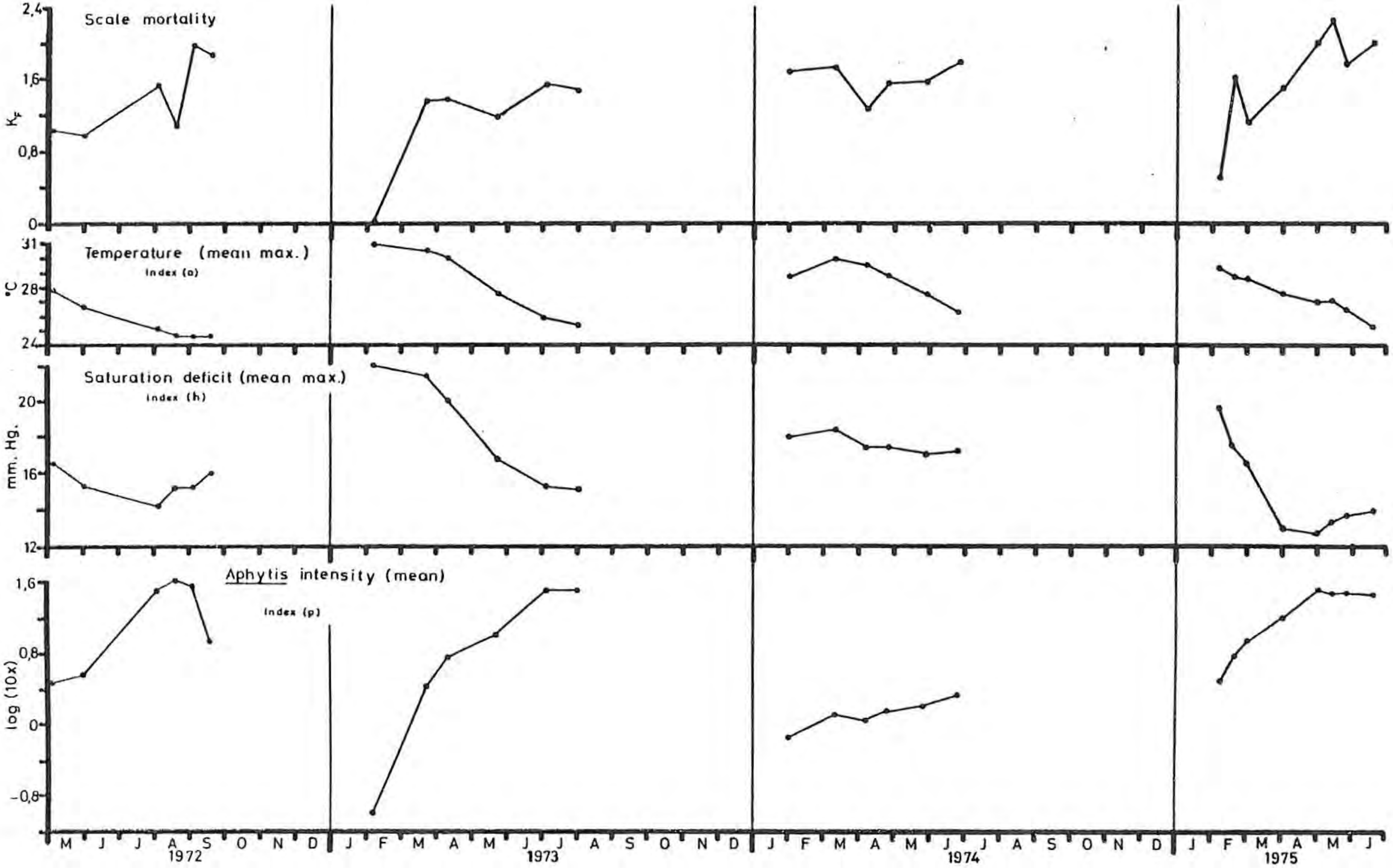


For example, an index of rainfall greater than 10mm per day of rain (this index is not shown in Table 5.4) was not significant; nor were indices of rainfall during the first half of the generation time (Table 5.4) when the small scales would have been more vulnerable to rain.

The excess rainfall in 1973/74 caused low ratios of solids to juice in Clanors and other midseason orange cultivars, which made the fruit unmarketable. This suggests that the excess rainfall at that time may have affected the physiology of the trees. The excess rainfall in 1972 fell during February/March and that during 1975 during January/February, and in neither case was it associated with scale mortality on twigs (Fig. 5.8). However, the excess rainfall during the 1973/74 season fell mainly in spring and early summer (see Fig. 2.5) and it was associated with high rates of scale mortality on twigs (Fig. 5.8). Although there was no significant relationship between excess rainfall and scale mortality on fruit, the earliest cohorts on fruit in which mortality could be estimated matured in February (Fig 5.9), well after the excess rainfall of spring and early summer had fallen.

Catling (1969b) described three main leaf-flush cycles of orange trees in Swaziland. The main one was in August/September at flowering, followed by lesser ones in October/November and January/February. It is common commercial practice to stress citrus trees in spring by withholding irrigation, and then to flood the trees with plenty of water to induce uniform flushing and flowering throughout the orchards. These facts, together with the arguments in the preceding paragraph, suggest that high rainfall in spring could have affected the growth-cycles of the

Fig 5.9. Mortality of scales on fruit plotted with indices of temperature, saturation deficit and *Aphytis*-intensity. All indices were derived over the generation time t – t + 1 (Table 5.6.) and all points are plotted at time t + 1.



trees, and so influenced the availability of nutrients to the scales in such a way that the spring increase in scale numbers did not begin. McNeill and Southwood (1978) showed that the grass *Holcus mollis* L. has two annual flows of soluble nitrogen, one in spring and the other in autumn, and how the numbers of sucking insects feeding on the grass were associated with these flows. The authors also reviewed other data of a similar nature; for example how spring peaks in amino acid levels of sitka spruce foliage were associated with the numbers of aphids feeding on the leaves.

Predators must have responded to the seasonal changes in temperature as did the scales, and would also have responded numerically to fluctuations in the numbers of their host,albeit with a time lag. One might expect a mutual interdependence between predator numbers and temperature to be manifest by an interaction term in multiple regression analysis which included second order terms. However, this was not the case (see Appendix 3) and there was no evidence for any such interaction. On this evidence, temperature effects and predation acted independantly of each other on scale mortality.

In section 5.1.2 the most important category of mortality recorded on twigs was death from undefined causes, but it is probable that a good deal of unrecognised predation was included in this category. Furthermore, many predator-damaged scales probably fell off the trees entirely, so percent predation was probably underestimated in relation to undefined mortality. The evidence advanced here suggests that predation was a very important source of mortality on twigs.

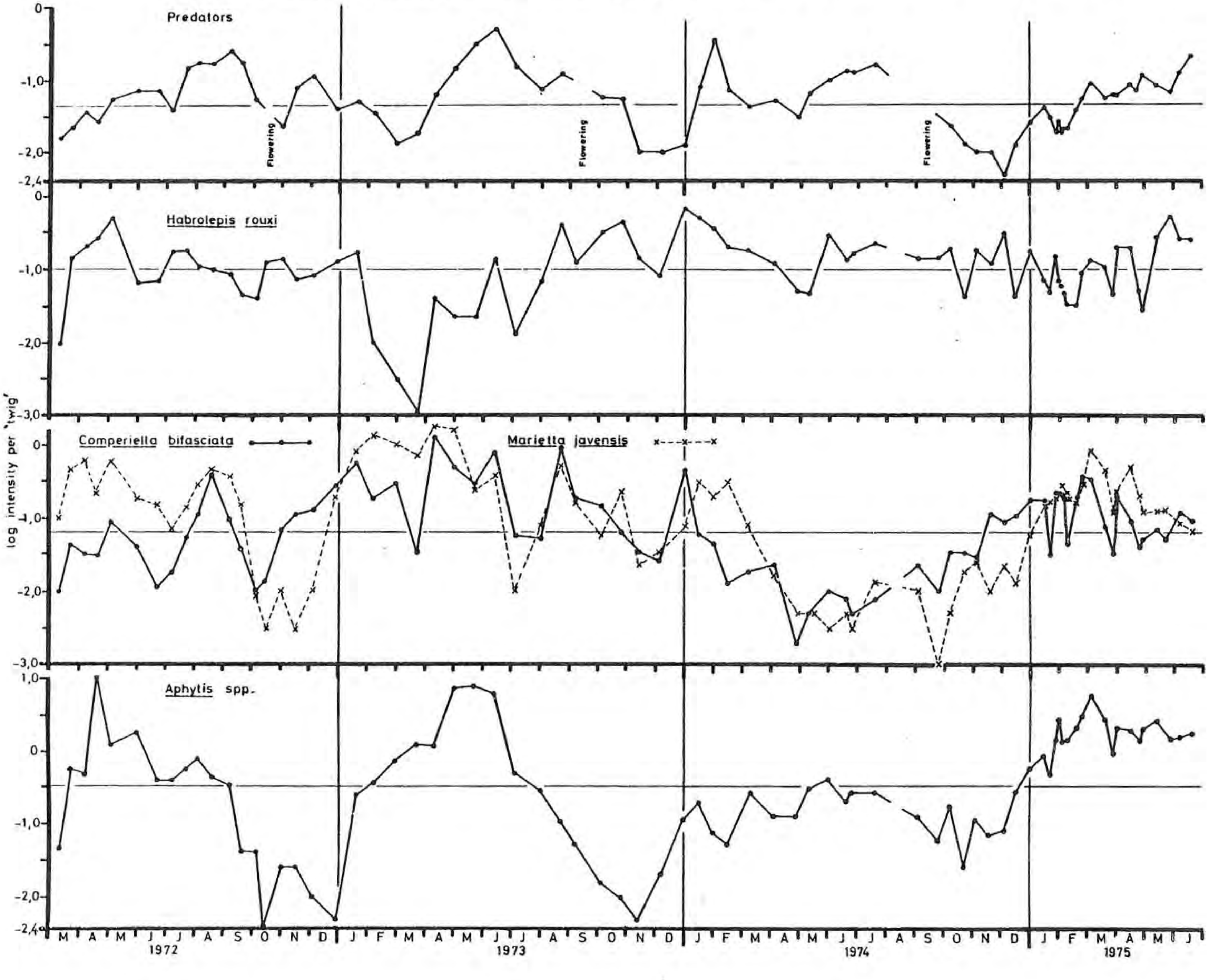
The scale population on fruit existed for only a short period each year, mainly during summer. There was little seasonal variation therefore, but a large amount of year-to-year variation (sections 2.5 and 2.7). For these reasons the same indices would not be expected to explain the variation in mortality on fruit as on twigs.

The only statistically significant factor to emerge from multiple regression analysis was saturation deficit, and the negative coefficients indicated that mortality was lowest in dry conditions. Since the maximum scale intensity each year on fruit was (apparently) largely a function of the rate of immigration from twigs in early summer (section 2.7), the conclusion reached here is that dry weather conditions may have favoured crawler migration on to fruit,as well as scale survival.

The rate of crawler emergence was independent of saturation deficit (section 4.4), which confirms Willard's (1972b) finding that relative humidity did not affect crawler emergence. Although Willard (1973b) found that crawler survival times were inversely related to relative humidity, he did not (1973a) examine the effect of humidity on wandering times, so no further conclusions can be drawn about crawler migration in relation to the dryness of the air.

Greathead (1972) noted that high humidity adversely affected the sugarcane scale, *Aulacaspis tegalensis*. Red scale seems to assume pest status in relatively dry citrus growing areas (Table 1.1). In an examination of the year-to-year variation of the rate of scale increase (section 2.6) it transpired that dry years rather than hot years favoured high rates of increase. White (1969, 1974, 1976) proposed the idea that moisture stress of a host plant may benefit the insects feeding on the plant. It may be that dry air tended to stress the trees slightly and so reduced scale mortality, but this is not a convincing explanation.

Fig 6.1. Logarithmic plots of intensities of predators and adult paarasitoids. Horizontal lines in the plots indicate mean levels. Predator counts in September/October are omitted because a coarse-mesh net, ahead of the collecting bag, was used to remove flower-debris and it affected predator collections.



CHAPTER 6

FACTORS AFFECTING THE ABUNDANCE OF NATURAL ENEMIES IN THE ORCHARD

6.1 Introduction

In Swaziland, according to Catling (1971a,b), parasitoids were 'severely limited' by high summer temperatures and for this reason biological control was unsuccessful in the lowveld. One of his criteria of the severity of the climate on parasitoids, was if the total number of day-degrees between November and March exceeded 200 D° above 30°C. During the present study, the totals for these five months in 1972/73, 1973/74, 1974/75 were respectively 334D°, 282D° and 230D°. All these totals exceeded the critical values suggested by Catling, yet parasitoids were abundant in the orchard each year (Fig. 6.1).

Abdelrahman (1974a) derived LD_{50} peak temperatures for the most susceptible stages of several natural enemies of red scale and they were:

Aphytis chrysomphali (adult)	38°C
A. melinus	39°C
Comperiella bifasciata (adult female)	44°C
Lindorus lophantae (adult)	42°C

Presumably *A. africanus* is also susceptible to temperatures of 38 - 39°C. Although temperatures of over 40°C were rare, those of about 38°C were not uncommon and may have caused some mortality among parasitoids or predators, unless the adults avoided them by seeking more favourable microclimates.

In order to see what effect the weather had on natural enemies, relationships were sought by regression analysis between the intensity per 'twig' (section 2.3) of each natural enemy and climatic indices. In each case, an attempt was made to account for the variation in natural enemy intensity due to the intensity/dm^2 of the host, and of the intensity of the previous generation of the natural enemy itself, by including measures of these variables in the regressions.

A disadvantage of this approach to population analysis is that although changes in the weather may determine changes in the intensity of an insect, the weather cannot determine the intensity itself. For example a given change in temperature could cause a two-fold change in the intensity of an insect at either a high, or a low mean intensity. It is better, if possible, to determine the effect of weather on mortality.

The mortality of natural enemies could not be estimated in the same way as it was for the host because their generation times were not known; except for an approximate estimate in the case of *Aphytis*. In the literature there was no information about the life cycle durations of either *Lindorus lophantae* (the most important predator) or *Habrolepis rouxi*. The life cycle duration of *Comperiella bifasciata* varies according to the stage of the host (1 - 3) which is attacked (Flanders, 1944; Cilliers, 1971), and the same may be true of *H. rouxi*. It is not possible to say in retrospect which stage of the host was attacked.

The intensity of each insect was transformed to logarithms because this implied proportional rather than incremental change in intensity, for each unit of change in an index.

6.2 *Aphytis* spp.

The intensity of *Aphytis* parasitoids showed marked seasonal cycles (Fig. 6 . 1), which were similar to those of the host (Fig. 2.5). In order to find the correct period over which to average

Table 6.1 Durations of the life cycles of *Aphytis* spp. at various constant temperatures

Temperature regime: °C	Days duration	Species	Authority
27	12,0	*A. coheni*	Quednau (1965)
"	12,25	*A. melinus*	
"	12,5	*A. lingnanensis*	
"	13,5	*A. africanus*	
20	25,5	*A. chrysomphali*	Abdelrahman (1974b)
25	15,4	"	
30	13,3	"	
20	28,5	*A. melinus*	
25	16,2	"	
30	13,1	"	

Table 6.2 *Aphytis* spp. life cycle durations at four constant temperatures (columns 1 - 2) taken from Table 6.1; together with the number of h° above several trial thresholds (0° - 15°C) in order to determine the threshold temperature for development. The most constant series of h°, denoted by the standard deviation at the foot of each column, indicates the threshold, which is here 12°C.

Temperature regime °C	Assumed days duration	h° above thresholds of:				
		0°	10°	12°	13°	15°
20	27,0	12960	6480	5184	4536	3240
25	15,8	9480	5688	4930	4550	3792
27	13,5	8748	5508	4860	4536	3888
30	13,2	9504	6336	5702	5386	4752
Mean Std. Dev.		10173 1890,8	6003 477,0	5169 381,9	4752 422,5	3918 625,0

or sum, climatic indices, for comparison with *Aphytis* intensity, an approximate thermal constant was calculated for the generation time.

6.2.1 Estimating the thermal constant for the generation time of *Aphytis*

There was no literature available which gave the durations at several different temperatures, of the life cycle of *A. africanus*, the main species of the genus in the orchard. However, the durations of the life cycles of several other species of *Aphytis* have been measured by Quednau (1965) and Abdelrahman (1974b). These are listed in Table 6.1.

From Table 6.1, four temperatures were selected (20°, 25°, 27°, and 30°C) and tabulated with the corresponding mean duration of the life cycle of a species of *Aphytis* (Table 6.2, columns 1 and 2). In order to derive the threshold temperature for development, thermal constants were calculated above several trial thresholds (Table 6.2, columns 3 - 7). The threshold temperature giving the series of constants with the smallest standard deviation was assumed to approximate to the true threshold temperature for development. In Table 6.2 the threshold temperature is 12°C, which is slightly higher than that published by Abdelrahman (1974b) for *A. melinus* (11°C), but much higher than that which he gave for *A. chrysomphali* (8,5°C). The threshold for development of the host is about 12°C, so it is reasonable to assume that the threshold for the parasitoid would be similar, and 12°C was used here.

Abdelrahman (1974b) published values of the intrinsic rate of natural increase, r_m, for *A. melinus*, together with measures of the number of female progeny per female, R_o, at three temperatures (Table 6.3). Using these data, and the expression

Table 6.3 Data from Abdelrahman (1974b): Intrinsic rate of natural increase (r_m) at three constant temperatures and number of female progeny per female (R_o) at the same temperatures. Generation times (T) were calculated from these data and converted to the equivalent thermal constants in h° >12°C.

Temperature regime °C	r_m/day	R_o	T (days)	T (h°)
20	0,075	42	49,8	9562
25	0,140	55	28,6	8923
30	0,180	65	23,2	10022
			Mean = 9502	

$$\ln R_o = r_m T,$$

values of T were calculated in days and were converted to thermal constants above 12°C (Table 6.3). The mean value of the thermal constants was 9502h°, and so a figure of approximately 10000h° was taken as the constant for the generation time when deriving climatic and biotic indices.

6.2.2 Derivation of the indices

The intensity of adult *Aphytis* was measured every sampling date. Assuming that the sampling date was time $t'+1$, then time t' was found by thermal summation to a total of 10000h°>12°C.

Most of the indices were derived by summing or averaging measures of the various factors between times t' and $t'+1$, or else in the first or second halves of this interval. *Aphytis* intensity in the previous generation was simply the intensity at the sampling date nearest to time t'. Rainfall in excess of the long term mean was derived in the same way as described in section 5.3.1.

6.2.3 Indices related to *Aphytis* intensity

Aphytis intensity per 'twig' was transformed by multiplying by ten and taking logarithms. The relationships between the transformed intensity and 18 indices were investigated firstly by simple regression and correlation analysis (Table 6.4). The statistical significance of each relationship was assessed on the regression coefficient. The best significant index of each factor in Table 6.4 was marked with a cross on the right hand side of the table and these (five) indices were then investigated by multiple regression analysis.

In Table 6.4, index (4), mean minimum temperature during

Table 6.4 Adult-*Aphytis* intensity per 'twig' (log10x): Simple correlation and regression coefficients for relationships with climatic or biotic indices (73 sets of readings; n.s. = not statistically significant). Crosses, right hand side, mark indices selected for multiple regression analysis (Table 6.5).

Factor	Index	Correlation coefficient		Regression coefficient		
		r	$100r^2$	b	P	
	CLIMATIC					
Temperature	(1) Mean maximum during generation time	-0,059	0,4	-0,024	n.s.	
	(2) Mean minimum " " "	0,178	3,2	0,042	n.s.	
	(3) Mean maximum in first $\frac{1}{2}$ generation time	0,058	0,3	0,022	n.s.	
	(4) Mean minimum " " $\frac{1}{2}$ " "	0,350	12,2	0,084	0,01	X
	(5) Mean maximum in second $\frac{1}{2}$ generation time	-0,108	1,2	-0,033	n.s.	
	(6) Mean minimum " " $\frac{1}{2}$ " "	0,070	0,5	0,016	n.s.	
	(7) $D^{\circ} > 30^{\circ}C$ in generation time (log)	-0,389	15,1	-0,631	0,002	
	(8) $D^{\circ} > 30^{\circ}C$ in second $\frac{1}{2}$ generation time (log)	-0,451	20,3	-0,751	0,001	X
	(9) $D^{\circ} > 25^{\circ}C$ in generation time (log)	-0,309	9,6	-1,750	0,01	
Saturation deficit	(10) Mean maximum daily during generation time	-0,428	18,3	-0,114	0,001	
	(11) " " " " 1st.$\frac{1}{2}$ gen. time	-0,285	8,1	-0,059	0,02	
	(12) " " " " 2nd.$\frac{1}{2}$ " "	-0,460	21,2	-0,112	0,001	X
Rainfall	(13) Total in generation time	0,136	1,9	0,013	n.s.	
	(14) Total > long term mean in generation time	0,009	0	0,001	n.s.	
	BIOTIC					
Aphytis intensity	(15) At time t′ (log10x)	0,579	33,5	0,577	0,001	X
Host intensity/dm^2	(16) Mean adult ♀ scale intensity during gen. time (log)	0,538	29,0	0,714	0,001	
	(17) " " " " 1st $\frac{1}{2}$ gen. time (log)	0,462	21,3	0,604	0,001	
	(18) " " " " 2nd $\frac{1}{2}$ gen. time (log)	0,606	36,7	0,772	0,001	X

the first half of the generation time, expresses the effect of the seasonal temperature changes on the immature stages of *Aphytis* rather than on the adult. Mean minimum temperature was better than mean maximum temperature in this respect, as it was also in explaining the seasonal changes in the mortality of the host (section 5.3.2). Catling (1971a,b), who based his ideas on the work of DeBach *et al.* (1955) felt that temperatures above 30°C were critical for red scale parasitoids. This is confirmed by the negative relationship between the transformed *Aphytis* intensity and index (8), total day degrees above 30°C in the second half of the generation time. The fact that there was a closer relation with D°>30°C in the second, compared with the first, half of the generation time, suggests that the adults were more affected by high temperature extremes than were the immature stages. This pattern of susceptibility of the stages to high temperatures confirms the experimental findings of Abdelrahman (1974a).

Similarly, the mean maximum saturation deficit in the second half of the generation time (index 12) explained more variation than did the same index in the first half of the generation time (index 11); presumably the adults would have been more exposed to desiccation than the sheltered immature stages.

The *Aphytis* intensity at time t' was included as a biotic index in order to express the effect of the parental numbers on those of the progeny. This index (no. 15) was of interest only in multiple regression analysis where it explained some of the variation in the transformed intensity.

The best measure of host intensity/dm² was index (18), the mean adult female intensity/dm² in the second half of the generation

Table 6.5 Adult-*Aphytis* intensity (log10x): Values of Student's t, and their probability levels, for the partial regression coefficients of intensity on five or four of the indices shown, taken from Table 6.4. Index (12) was not significant (n.s.) and was dropped from the multiple regression. (73 sets of readings)

Indices	No. indices in regression			
	5		4	
	t	P	t	P
(4) Mean minimum temperature in first half of generation time	5,8	0,001	5,7	0,001
(8) D° > 30°C in second half of generation time (log)	3,2	0,01	3,2	0,01
(12) Mean maximum saturation deficit in second half of gen.time	1,1	n.s.	-	-
(15) *Aphytis* intensity at time t′ (log10x)	3,8	0,001	3,6	0,001
(18) Mean adult ♀ scale intensity/dm^2 in 2nd 1/2 of gen.time (log)	3,7	0,001	3,6	0,001

time. This was a measure of the intensity/dm^2 of the hosts from which the adult *Aphytis* emerged rather than of the hosts which were attacked. There was no measure available of the intensity/dm^2 of the stage attacked because only adult female scale intensity/dm^2 was measured in sampling.

In multiple regression analysis with these five indices, saturation deficit was not significant (Table 6.5), probably because it was closely related to both the indices of temperature. The remaining four indices described 66,2% of the variation in the transformed *Aphytis* intensity. The regression coefficients were:

(15)	*Aphytis* intensity in previous generation (log 10x)	0,3565
(18)	Host adult ♀ intensity/dm^2 in second half of generation time (log)	0,3952
(4)	Mean minimum temperature in first half of generation time	0,1026
(8)	Total D°>30°C in second half of generation time (log)	-0,4330
	Constant term in the regression	-0,1044

6.3 *Lindorus lophantae*

L. lophantae was the most important predator species in the orchard. Although the intensities of larval stages were recorded, only the intensity of the adult stage was used to determine the effect of weather on the insect. This was because it would have been difficult to guess the periods over which indices should be averaged, or summed, in the case of the larvae.

The intensity per 'twig' of *L. lophantae* was transformed by multiplying by 100 and taking logarithms. Because there was no information about the life cycle duration of *L. lophantae*, climatic and biotic indices were derived by averaging or summing measures of each factor over periods required to accumulate

Table 6.6. Adult-*Lindorus lophantae* intensity per 'twig' (log100x): Simple correlation and regression coefficients for relationships with climatic or biotic indices. (69 sets of readings; n.s. = not statistically significant). Crosses, right hand side, mark indices selected for multiple regression analysis (Table 6.7).

Factor	Index	Correlation coefficient		Regression coefficient		
		r	$100r^2$	b	P	
	CLIMATIC					
Temperature	(1) Mean maximum during generation time	-0,645	41,7	-0,196	0,001	X
	(2) Mean minimum " " "	-0,569	32,4	-0,105	0,001	
	(3) $D^\circ > 30^\circ C$ " " " (log)	-0,426	18,1	-0,520	0,001	X
	(4) $D^\circ > 25^\circ C$ " " " (log)	-0,348	12,1	-0,658	0,01	
Saturation deficit	(5) Mean maximum " " "	-0,493	24,3	-0,098	0,001	X
Rainfall	(6) Total " " "	-0,189	3,6	-0,002	n.s.	
	(7) Total > long term mean in generation time	-0,072	0,5	-0,001	n.s.	
	BIOTIC					
L. lophantae intensity	(8) At 10000 h° beforehand (log100x)	0,655	42,9	0,755	0,001	X
Host intensity/dm^2	(9) Mean adult ♀ scale intensity in generation time (log)	0,720	51,8	0,719	0,001	X

10000h°. That is, the generation time was assumed to be the same as that estimated for *Aphytis*, although in fact it may have been rather longer. The various indices which were derived were therefore similar to those for *Aphytis*, but because of the uncertainty of the generation time, relationships were not sought between *L. lophantae* intensity and indices for each half of the generation time.

Relationships were sought first by simple regression and correlation (Table 6.6). The best index of temperature was (1), the mean maximum temperature during the generation time, and the coefficients were negative. This might indicate that *L. lophantae* was adversely affected by high temperatures, but in multiple regression the index for high temperature extremes, D°>30°C (index 3), was not statistically significant (Table 6.7). Predator numbers tended to increase slowly each season, reaching their maximum intensity between June and September (Fig. 6.1), when temperatures were at their minimum. Conversely predator intensities were at their minimum in summer. Abdelrahman (1974a) showed that *L. lophantae* adults were remarkably tolerant of high peak-temperatures (LD_{50} 42°C) but he did not test the immature stages. The conclusion here is that while the insect may have been sensitive to high summer temperatures in the orchard, the negative relationship with mean maximum temperature primarily indicates the insect's tendency to reach a peak in numbers during winter. This conclusion is supported by the strong negative correlation with mean minimum temperature (index 2, Table 6.6).

There was also a strong negative correlation with the mean maximum saturation deficit during the life cycle (index 5) but

Table 6.7 Adult *L. lophantae* intensity (log100x): Values of Student's t, and their probability levels, for the partial regression coefficients of intensity on five, four or three of the indices shown, taken from Table 6.6. Indices (3) and (5) were not significant (n.s.) and were dropped from the regression. (69 sets of readings).

Indices		No. of indices in regression					
		5		4		3	
		t	P	t	P	t	P
(1)	Mean maximum temperature in generation time	5,0	0,001	5,2	0,001	6,1	0,001
(3)	D° > 30°C in generation time	1,8	n.s.	1,9	n.s.	-	-
(5)	Mean maximum saturation deficit in generation time	0,3	n.s.	-	-	-	-
(8)	*L. lophantae* intensity 10000 h° beforehand (log100x)	3,7	0,001	3,7	0,001	4,5	0,001
(9)	Mean adult ♀ scale intensity/dm² in gen. time (log)	8,2	0,001	8,7	0,001	8,3	0,001

this index fell away in multiple regression analysis (Table 6.7).

Index (8), the (transformed) intensity of *L. lophantae* at a time 10000h° beforehand, was of interest only in multiple regression analysis where it accounted for some of the variation due to the intensity of the parental generation. There was a very strong correlation between the transformed intensity of *L. lophantae* and index (9), the log mean adult female scale intensity/dm² in the generation time. This index of host numbers was the average intensity / dm² of leaf, twig and fruit surface, but it was not an exact measure of the stages actually attacked.

Only three out of five of the indices selected from Table 6.6 were statistically significant in multiple regression analysis (Table 6.7), but these three described 79,9% of the variation in transformed intensity of *L. lophantae*. The regression coefficients were:

(8)	*L. lophantae* intensity 10000h° beforehand (log100x)	0,3390
(9)	Host adult female intensity/dm² in generation time (log)	0,5075
(1)	Mean maximum temperature in generation time	-0,1157
	Constant term in regression	0,3197

When index (8) was omitted, on the grounds that the generation time was not known and therefore the intensity at the end of the previous generation could not have been known, then indices (9) and (1) described 73,7% of the variation and the coefficients were:

(9)	Host adult female intensity/dm² in generation time (log)	0,5912
(1)	Mean maximum temperature in generation time	-0,1486
	Constant term in regression	0,4094

Table 6.8 Adult- *C. bifasciata* intensity per 'twig' (log10x): Simple correlation and regression coefficients for relationships with climatic or biotic indices (72 sets of readings; n.s. = not statistically significant). Crosses, right hand side, mark indices selected for multiple regression analysis.

Factor	Index	Correlation coefficient		Regression coefficient		
		r	100r²	b	P	
	CLIMATIC					
Temperature	(1) Mean maximum during generation time	0,171	2,9	0,051	n.s.	
	(2) Mean minimum " " "	0,269	7,3	0,043	0,05	X
	(3) D° > 30°C in generation time (log)	0,198	3,9	0,240	0,05	X
	(4) D° > 25°C in generation time (log)	0,056	0,3	0,231	n.s.	
Saturation deficit	(5) Mean maximum during generation time	0,062	0,4	0,010	n.s.	
Rainfall	(6) Total in generation time	0,124	1,5	0,010	n.s.	
	(7) Total > long term mean in generation time	0,086	0	0	n.s.	
	BIOTIC					
C. bifasciata intensity	(8) At 10000 h° beforehand (log10x)	0,540	29,2	0,565	0,001	X
Host intensity/dm²	(9) Adult ♀ scale intensity at time t'+1 (log)	0,563	31,7	0,529	0,001	X
M. javensis intensity	(10) At time t'+1 (log10x)	0,628	39,5	0,475	0,001	X

6.4 *Comperiella bifasciata*

This exotic species was the most important endoparasitoid in the orchard. There were seasonal trends in its intensity although they were not clear trends (Fig. 6.1), and the fluctuations in its intensity more closely followed those of the host than did the fluctuations in the intensity of *H. rouxi*. For example when host intensities/dm² fell in 1973/74 (Fig.2.5), so did intensities of *C. bifasciata* but not those of *H. rouxi* (Fig.6.1). The intensity of the hyperparasitoid, *M. javensis*, followed the intensity of *C. bifasciata* more closely than that of *H. rouxi* (Fig. 6.1).

The intensity per 'twig' of *C. bifasciata* was transformed by multiplying by ten and taking logarithms. The generation time was assumed to require 10000h°, so the indices were the same as those for *L. lophantae* except for the introduction of index (10), the intensity of the hyperparasitoid. Five of the indices were statistically significant in simple regression analysis (Table 6.8), but only four in multiple regression (Table 6.9).

In Table 6.8, the positive coefficients for index (2), mean minimum temperature in the generation time, suggested that there was some seasonal trend with temperature but this index fell away in multiple regression analysis (Table 6.9). The positive coefficients for index (3), the total D° > 30°C in the generation time, suggested that the insect tended to reach its maximum intensity under hot weather conditions, and that it was not sensitive to high summer temperatures. This conclusion agrees with the findings of Abdelrahman (1974a), who gave the LD_{50} peak temperature for the female as 43° - 44°C,

Table 6.9 Adult-C. *bifasciata* intensity (log100x): Values of Student's t, and their probability levels, for the partial regression coefficients of intensity on five or four of the indices shown, taken from Table 6.8. Index (2) was not significant (n.s.) and was dropped from the regression. (72 sets of readings).

Indices	No. of indices in regression			
	5		4	
	t	P	t	P
(2) Mean minimum temperature in generation time	0,1	n.s.	-	-
(3) D° $>$ 30°C in generation time (log)	2,0	0,05	2,6	0,02
(8) C. *bifasciata* intensity 10000 h° beforehand (log10x)	2,1	0,05	2,1	0,05
(9) Adult ♀ scale intensity/dm² at time $t+1$ (log)	2,9	0,01	2,9	0,01
(10) M. *javensis* intensity (log10x)	2,3	0,05	2,5	0,02

although that for the male was somewhat lower at 39°C. He did not test the immature stages, but the insect is apparently well adapted to high summer temperatures, as Messenger and van den Bosch (1971) concluded.

Index (9), the scale intensity/dm² at time t′+1, was a measure of the intensity/dm² of the host from which the parasitoids had emerged, rather than the intensity/dm² which was attacked. Index (8) the index for parental intensity, was again only of interest in explaining some of the variation in multiple regression analysis. There was a strong positive correlation with host intensity/dm² (index 9), which is not surprising except that the other endoparasitoid, *H. rouxi* showed a moderately strong negative correlation with host intensity/dm².

There was also a strong positive correlation (0,63) with the intensity of the hyperparasitoid at time t′+1. Since *M. javensis* parasitised mainly female *C. bifasciata*, the correlation with female-host intensity was even higher (0,74). This positive correlation is not surprising because the intensity of *M. javensis* adults at time t′+1 must have reflected the numbers of *M. javensis* which emerged from *C. bifasciata* hosts. However common sense dictates that *M. javensis* must have caused considerable mortality of its host; and that had it been possible to determine the mortality of *C. bifasciata* then there would have been a positive correlation between the mortality and *M. javensis* intensity. The result here illustrates the kind of misleading correlation which can arise when seeking relationships between environmental indices and insect numbers, rather than insect mortality.

In multiple regression analysis, four out of the five indices were statistically significant (Table 6.9), and they de-

Table 6.10 Adult-*H. rouxi* intensity per 'twig' (log10x): Simple correlation and regression coefficients for relationships with climatic or biotic indices (72 sets of readings; n.s. = not statistically significant). Crosses, right hand side, mark indices selected for multiple regression analysis (Table 6.11)

Factor	Index	Correlation coefficient		Regression coefficient		
		r	$100r^2$	b	P	
	CLIMATIC					
Temperature	(1) Mean maximum during generation time	-0,209	4,4	-0,052	n.s.	
	(2) Mean minimum " " "	-0,132	1,7	-0,019	n.s.	
	(3) D° > 30°C in generation time (log)	-0,310	9,6	-0,312	0,02	X
	(4) D° > 25°C in generation time (log)	-0,132	1,7	-0,455	n.s.	
Saturation deficit	(5) Mean maximum in generation time	-0,142	2,0	-0,023	n.s.	
Rainfall	(6) Total in generation time	0,151	2,3	0,009	n.s.	
	(7) Total > long term mean in generation time	0,210	4,4	0,116	n.s.	
	BIOTIC					
H. rouxi intensity	(8) At 10000 h° beforehand (log10x)	0,456	20,8	0,425	0,001	X
Host intensity/dm^2	(9) Adult ♀ scale intensity at time t′+1 (log)	-0,338	11,4	-0,266	0,01	X
M. javensis intensity	(10) At time t′+1 (log10x)	-0,141	2,0	-0,089	n.s.	
C. bifasciata intensity	(11) At time t′+1 (log10x)	-0,031	0,1	-0,026	n.s.	

scribed 53,4% of the variation in transformed intensity of *C. bifasciata*. The regression coefficients were:

(8)	*C. bifasciata* intensity at 10000h° beforehand (log 10x)	0,2239
(9)	Host adult female intensity/dm^2 at time $t'+1$ (log)	0,3127
(3)	Total $D^\circ > 30^\circ$C in generation time (log)	0,2768
(10)	*M. javensis* intensity at time $t'+1$ (log 10x)	0,2231
	Common term in regression	−0,4829

When index (8) was omitted, on the grounds that the generation time was not known, the remaining three variables described 50,3% of the variation, and the coefficients were:

(9)	Host adult female intensity/dm^2 at time $t'+1$ (log)	0,3418
(3)	Total $D^\circ > 30^\circ$C in generation time (log)	0,3226
(10)	*M. javensis* intensity at time $t'+1$ (log 10x)	0,2951
	Common term in regression	−0,5696

6.5 *Habrolepis rouxi*

This indigenous endoparasitoid appeared to be the least important natural enemy of red scale in the orchard. There was no discernable seasonal, or year-to-year, fluctuation in its intensity which corresponded to the fluctuations in the intensity/dm^2 of its host (compare Figs. 6.1 and 2.5).

Intensities per 'twig' were transformed by multiplying by ten and taking logarithms. The same indices were used as those for *L. lophantae* and *C. bifasciata*. Simple correlation and regression coefficients were calculated, and only three indices were statistically significant (Table 6.10). All three remained significant in multiple regression analysis (Table 6.11).

The insect appeared to be sensitive to high summer temperatures because there was a negative correlation with index (3),

Table 6.11 Adult-*H. rouxi* intensity (log10x): Values of Student's t and their probability levels for the partial regression coefficients of intensity on three of the indices taken from Table 6.10. (72 sets of readings)

Indices	t	P
(3) $D^\circ > 30^\circ C$ in generation time (log)	3,7	0,001
(8) *H. rouxi* intensity 10000 h° beforehand	3,0	0,01
(9) Adult ♀ scale intensity/dm^2 at time $t+1$ (log)	2,2	0,05

the total day-degrees above 30°C in the generation time. However there was no statistically significant relationship with measures of seasonal temperature changes, such as mean maximum or minimum temperature during the generation time (1 and 2).

There was a statistically significant negative relationship with host intensity/dm^2 (index 9). the negative relationship may have been because of competition with *C. bifasciata* in searching for suitable stages of the host to attack, or possibly because of an interaction of both primary parasitoids with each other and with the hyperparasitoid. However there was no significant relationship between the (transformed) intensity of *H. rouxi* and the intensities of either *C. bifasciata* or *M. javensis* (Table 6.10).

In multiple regression analysis (Table 6.11) the three indices described only 33,7% of the variation in transformed intensity of *H. rouxi*. The regression coefficients were:

(8)	*H. rouxi* intensity at 10000h° beforehand (log 10x)	0,3054
(9)	Host adult female intensity/dm^2 at time $t'+1$ (log)	-0,1909
(3)	Total D° > 30°C in generation time (log)	-0,3667
	Constant term in regression	0,3542

When index (8) was dropped, on the grounds that the generation time was not known, then the remaining two variables described 24,9% of the variation and the coefficients were:

(9)	Host adult female intensity/dm^2 at time $t'+1$ (log)	-0,3021
(3)	Total D°>30°C in generation time (log)	-0,3713
	Constant term in regression	0,3723 .

6.6 Conclusions

The effect on natural enemy numbers, of the numbers in the previous (parental) generation is obvious. Because of serial correlation in measures of insect abundance, the inclusion of a measure of the parental numbers as a variable in regression analysis, may not be strictly valid. For these reasons the numbers in the previous generation have not been considered in these final conclusions about the factors which affected natural enemy numbers in the orchard.

For each natural enemy, except *H. rouxi*, the numbers were related positively to host numbers. In the case of the predator, *L. lophantae*, the best measure of host abundance was the mean intensity/dm² during the generation time of the predator, but for *Aphytis* and *C. bifasciata* it was the intensity/dm² from which the parasitoids had emerged. No explanation can be offered for the negative relationship of *H. rouxi* numbers with those of the host, unless it was a consequence of competition between the two endoparasitoid species for a limited resource, the host.

The numbers of both *Aphytis* and *L. lophantae* were related to seasonal temperature changes. In the case of *Aphytis* seasonal temperature changes appeared to affect the immature stages (in the first half of the generation time), and the relationship was positive. Hence temperature probably influenced the rate of development, or mortality, of the immature stages. In the case of *L. lophantae* the effect of temperature, measured over the whole generation time, was not so clear because the relationship was a negative one. It is probable that the insect's numbers built-up relatively slowly so that maximum numbers each season were reached during winter, and minimum numbers occurred during summer. It seems unlikely that high summer temperatures were unfavourable for the insect because the adult, at least, has been shown to tolerate peak temperatures of over 40°C (Abdelrahman, 1974a); and here the index for high temperature extremes, day-degrees over 30°C accumulated in the generation time, was not statistically significant.

On the other hand, both *Aphytis* spp. and *H. rouxi* appeared to be sensitive to high summer temperatures because their intensities were negatively related to indices of day-degrees above 30°C. In the case of *Aphytis* the adults seemed to be less tolerant than the younger stages. The intensity of *C. bifasciata* was positively related to the day-degrees above 30°C accumulated in the generation time and it is concluded that, within reason, this insect thrived under hot conditions. In this respect it resembled its host.

There was a strong correlation between the intensities of *C. bifasciata* and the hyperparasitoid, *M. javensis*. There was an even stronger correlation between the numbers of female *C. bifasciata* and the numbers of the hyperparasitoid. Despite the positive relationships between the numbers of these two insects, it is concluded that a good deal of mortality of *C. bifasciata* was caused by *M. javensis*. This is a pity, because *C. bifasciata* not only tolerated the climate, but it was also more resistant to pesticides than the other scale parasitoids. (For example at Tambankulu Estate, where the orchard was continually treated with corrective applications of insecticides, *C. bifasciata* was the only natural enemy to survive, and it increased to high numbers there, with its host).

The correlation of fluctuations in insect numbers with environmental factors does not constitute formal proof of a causal relationship. Nevertheless, from such correlations hypotheses can be formed and verified by experiment (Williamson, 1972, p. 56). In the present case, the experiment came first. Abdelrahman (1974a) for example, demonstrated that *Aphytis* spp. were less tolerant of high peak temperatures (LD_{50} peak temperatures 38°C - 39°C) than were *C. bifasciata* or *L. lophantae* (LD_{50} peak temperatures 44°C and 42°C respectively). He also showed that adult *Aphytis* spp. were less tolerant than the younger stages. Both these conclusions are confirmed here under natural conditions.

Abdelrahman's (1974a) conclusions could not suggest which natural enemies were likely to be effective or ineffective, but the results given here can help to do so. *H. rouxi* for example is very unlikely to be effective, although the negative relationship with scale intensity is not a formal proof of inverse density dependence. *C. bifasciata* appears to have been severely limited by the hyperparasitoid, *M. javensis*, and it was also subject to encapsulation by its host (discussed in section 2.9). Furthermore, adult females parasitised by *C. bifasciata* had often begun to reproduce before dying, so this parasitoid is unlikely to have been effective despite its heat tolerance. *Aphytis* spp. and *L. lophantae* numbers were closely related to the numbers of their host (r = 0,61 and 0,72 respectively, compared to 0,56 for *C. bifasciata*) and there is no other reason to suppose they were ineffective natural enemies, except the sensitivity of *Aphytis* (mainly *A. africanus*) to high summer temperatures. *A. melinus* may be more tolerant and this should be investigated before making further attempts to get it well established in the lowveld.

CHAPTER 7

CONCLUSIONS

An attempt was made between 1972 and 1975 to re-introduce integrated control of citrus pests to orchards in the Swaziland lowveld. In integrated control, the key pest, red scale, is naturally controlled although corrective sprays may be necessary and which are usually of mineral oils. Other pests are scarce, reduced by fungicide applications, or are treated on a corrective basis. An exception is thrips which always necessitates a preventative spray, of low toxicity to natural enemies. The advantages of this approach are (i) cheapness and (ii) low pesticides residues in fruit; but in the lowveld the mean level of red scale populations is so high that it has not yet been possible to practice this form of control. However, it has recently become important to re-examine the question of integrated control in this region because of the evolution of resistance to organophosphates by red scale populations elsewhere in southern Africa. Should such resistance occur in the lowveld, it will be very difficult to achieve acceptable control by natural means or with the judicious use of oils.

During the attempt to re-introduce integrated control, data were collected from red scale populations in three lowveld orchards (at Swaziland Irrigation Scheme, Tambankulu and Ngonini estates), but in two of these orchards the scale infestations required spraying to prevent tree-damage. This work describes the analysis of the data from Swaziland Irrigation Scheme where the orchard did not need to be treated, and these data were also the most extensive. The object of the analysis has been to see if the factors affecting red scale abundance in the lowveld could be better understood. In particular, answers were sought to five questions:

(i) What factors caused the seasonal population fluctuation?

(ii) Was the population under natural regulation?

(iii) If so, which factors or natural enemies were most effective in regulating the population?

(iv) What factors limited natural enemy numbers?

(v) Why was the mean level of the population so high?

The conclusions are discussed under the headings of these five questions.

Stage durations and rates of reproduction, which were measured under almost natural conditions in an insectary, differed on leaves, twigs and fruit. Fruit were the most favourable type of site, leaves the least favourable. The proportion of females in each section of the population also differed, being highest on fruit and lowest on leaves (and increased in all three sections during spring and early summer). The various categories of mortality differed in extent on leaves, twigs and fruit. The three sections of the population were analysed separately because of these differences. The population on leaves was largely ignored because of its low intensity, although there was evidence that in absolute density it was equivalent to that on twigs.

7.1 The causes of the seasonal and between-years variation in the population

The residual section of the population in the tree was that on twigs. To some extent the population on leaves would have contributed to this because leaves remained on the tree for a year or more and there was an equal rate of exchange of crawlers between leaves and twigs. However, the high proportion of males together with the relatively slow rates of growth and reproduction made this section of the population less important than that on twigs.

(a) Variation on fruit. Crawlers immigrated to fruit from October onwards, first maturing as adult females early in December. The intensity/dm^2 of scales on fruit was very variable from year-to-year and largely depended on the rate of immigration from twigs between October and December. Immigration after December seemed to make little difference to the maximum intensity /dm^2 reached in a season. There was evidence that dry years rather than hot years contributed to high infestations on fruit and mortality on fruit was negatively related to the mean saturation deficit during the life cycle.

(b) Variation on twigs. The section of the population on twigs was the most important one for understanding the dynamics of the whole population. The mortality of scales on twigs was investigated in two ways in order to identify the causes of seasonal and between-years variation: (i) by assessing the relative importance of the various categories of mortality in percentage mortality data, (ii) by regression analysis of the generation mortality with climatic and biotic indices. The first way indicated that death from undefined causes was the most important category of mortality. There were several possible causes of this mortality but since the method was not quantitative, only tentative conclusions can be drawn. Undefined mortality probably consisted of unrecognised predation (for example by Chrysopidae), the effects of overcrowding and the death of host-plant cells being tapped by scales . It is unlikely that high summer temperatures caused much direct mortality, but low winter temperatures probably did. Some of the effect of seasonal temperature changes may have been mediated by changes in the host-plant's physiology.

In the second way of identifying the causes of the population variation, values of K, the log generation mortality, were estimated from Moran diagrams. The objections to this method (as used here) are (i) that the data were arbitrarily divided into cohorts which were assumed to correspond to generations, (ii) that the intensity of adult females in samples was assumed to represent the total number of individuals reaching adulthood in each generation. When a continuously breeding population is sampled at more or less extended intervals, the census data are in discrete units anyway, and there are examples of animal ecologists and of demographers having used discrete mathematics for the analysis of such data. The Rogers/Moran method was a simple way of estimating the mortality in a population in which the generations almost completely overlapped and in which stable stage distributions could rarely have occurred. In order to circumvent the second objection, the population would have had to be sampled at very short intervals so that the recruitment distribution of each cohort could have been integrated in some way. A possible third objection to the use of Moran plots for this kind of continuously breeding population, where seasonal or other delayed-mortality effects occur, is that the delay must be of about one generation which seems to have been the case here.

Indices of three factors were associated with the variation in mortality on twigs: (i) temperature, (ii) predator numbers, (iii) excess rainfall.

The relation of mortality with predators is discussed in 7.3. Here, it is concluded that the seasonal temperature changes caused the cycling in scale intensity on twigs and that similar cycling in predator numbers may have contributed to it. [However, there was no evidence of any interaction between temperature and predator numbers in their relationships with scale mortality (Appendix 3).]

During 1973/74, the seasonal cycle on twigs was missing; while spring and early summer rainfall were well above average. The conclusion is that the excess rainfall in spring caused high mortality of scales on twigs; probably by affecting the physiology of the trees because excess rainfall at other times did not have this effect. Although the excess rainfall in 1973/74 affected the internal quality of the fruit, it could not be shown to affect scale mortality on fruit because the cohorts for which mortality was estimated occurred too late in the season.

The demonstration of relationships between climatic indices and scale mortality does not constitute rigorous proof of cause and effect but, as Williamson (1972) pointed out, the existence of such relationships can generate hypotheses for which tests could be devised. The relationship between high rainfall and mortality is a tenuous one and it has been suggested that the effect was mediated via changes induced in the physiology of the host-plants. There is little information about the way in which tree-quality affects red scale populations, in particular on how fertilisation, irrigation and climate alter the quality of the tree to the insect. Work on this topic could be of special interest in regions where red scale is very troublesome.

7.2 The question of population regulation

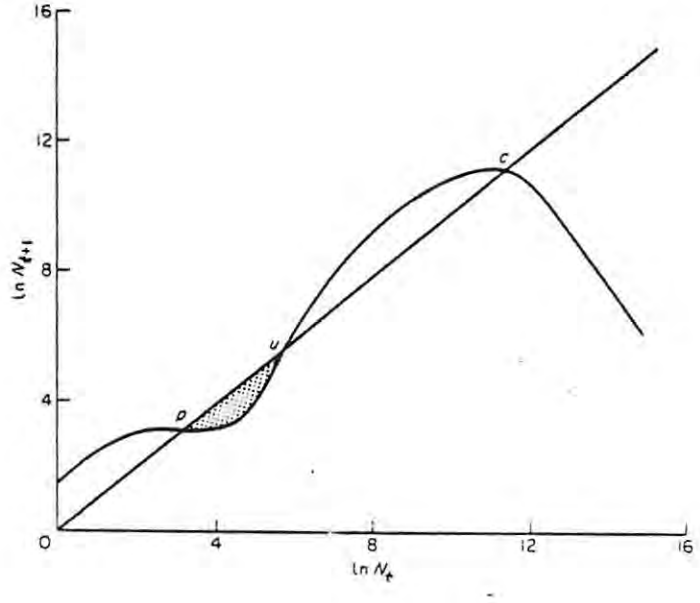
It is now generally accepted that for a population to be naturally regulated there must be density dependent mortality acting on it. The existence of density dependent mortality is difficult to demonstrate, especially in the kind of population which has been examined here.

Density dependence can be deduced from the shape of the graph when either the percentage of survivors from a source of mortality, or the k-value of that mortality, is plotted against the initial density before the mortality had acted (Varley, Gradwell and Hassell, 1973; Bellows, 1981). In the present instance several mortality factors acted contemporaneously and the number of survivors could not be calculated. Furthermore, the evidence for much of the mortality accumulated so that the initial density was unknown.

Although Rogers (1979) distinguished between density dependent and density independent mortality in Moran plots, his method was subjective to apply and assumed that density dependence was direct. In the present case, there may have been delayed density dependence and this could not have been separated from the delayed seasonal temperature effect which acted on the population. Delayed density dependence could have been of the Nicholson (1933) kind, defined by Varley (1947), in which a delay of one generation results from the time-lag between a change in host density and a numerical response by the parasitoids. Alternatively, delayed density dependence may have arisen if the fecundity of adult female scales was affected by their own density, resulting in fewer adult females one generation later. For the reasons advanced in this and the preceding paragraph, density dependence could not be demonstrated.

Two facts suggested that the red scale population was in fact regulated, albeit at an equilibrium level which was unacceptably high. Firstly, the population reached similar maximum log intensities in three years out of four. Secondly, it returned to this maximum level after being reduced to a low level in 1974/75 (see Fig. 2.5). The population was presumably regulated by natural enemies, rather than by its food supply, because tree-damage was not evident. However, if scale intensity affected fecundity, the food supply could have been limiting. One of the natural enemy exclusion methods described by DeBach and Huffaker (1971) would have shown if natural enemies were regulating the population but would not have shown which species was the most important (the latter point is discussed in 7.3).

Southwood and Comins (1976) described a synoptic model of population growth. In the model, organisms not adapted either for very rapid increase (not r-selected) or for maintaining a stable equilibrium (not K-selected), but which were intermediate between these extremes, were shown to have more than one possible equilibrium:



At the point P, the population is regulated by natural enemies. Should the population increase for some reason (different climate, better food) above point U, then it escapes from natural enemy control and is limited at C by competition for food (or another resource). The inference seems to be that while a population may escape above U relatively easily, it would be difficult to get it down again to P; or to lower the level of P, for example by introducing new natural enemies.

7.3 The question of which natural enemies were the most effective

It is assumed that natural enemies at least helped to regulate the population, although no evidence can be produced for this assumption.

The assessments of the relative importance of each category of mortality indicated that predators were the most effective natural enemies on twigs, and *Aphytis* spp. on fruit. The assessment of mortality on fruit included an approximation of host-mutilation by *Aphytis* which, if it was realistic, suggested that *Aphytis*-activity was almost as important as undefined mortality. Endoparasitoids were the least effective natural enemies on both twigs and fruit. There was other evidence that endoparasitoids were ineffective:

(i) Some adult female scales which had been endoparasitised showed evidence that they had begun to reproduce before being killed.

(ii) A proportion of endoparasitoids, probably *C. bifasciata*, were encapsulated by the host.

(iii) A high proportion of endoparasitised scales were hyperparasitised. The endoparasite involved was probably *C. bifasciata*.

(iv) The numbers of *H. rouxi* were negatively related to those of its host.

The effectiveness of each kind of natural enemy could not be assessed by regression analysis of red scale generation mortality with indices of natural enemy numbers. This approach was more in the nature of a key-factor analysis and would not detect the fine adjustments made to the generation mortality by regulating factors. Nevertheless, scale mortality on twigs was closely related to predator numbers measured over the generation time. There are three possible conclusions which can be drawn from this correlation of mortality with predators:

(i) The scale variation on twigs was caused by temperature (and possibly rainfall) and predators merely responded to their host's variation.

(ii) Predators, varying in number with temperature, helped to cause their host's variation; that is, they acted as a key-factor.

(iii) Predators helped to cause the variation but regulated the population when it reached high intensity; that is, predators acted as a key and a regulating factor.

Whatever the conclusion, predators seem to hold more promise for exploitation than do parasitoids in any future attempts at biological control of red scale in the lowveld. New endoparasitoids in particular, do not seem to be worth importing; for example *Prospaltella* spp.

7.4 Factors which limited the numbers of natural enemies

With the existing data it was not possible to estimate the mortality of the various natural enemies. There was no certainty that Moran plots would be suited to the analysis of the natural enemy populations, nor were there any data for the generation times of the insects. A kind of key-factor analysis was therefore made by regression analyses of the intensity of each natural enemy with indices of weather and host intensity/dm^2.

The predator, *Lindorus lophantae* was probably the most important natural enemy. Its intensity fluctuated seasonally, following its host's intensity, but was negatively related to temperature. This relationship with temperature is attributed to the slow seasonal increase of the insect, which reached maximum intensity in winter and vice versa. There was no evidence that the insect was sensitive to the high summer-temperatures which prevailed in the lowveld.

Aphytis spp., mainly *A. africanus*, fluctuated seasonally in relation to temperature. It was sensitive to high summer-temperature and there was evidence that the adults were more affected than the sheltered immature stages; which agrees with the pattern of susceptibility to peak temperatures found by Abdelrahman (1974a), and with the conclusions of others (Catling; 1971a,b; DeBach *et al.*, 1955; and DeBach *et al.*, 1971) on the general susceptibility of *Aphytis* to high temperature. If *A. melinus* is more tolerant of high temperature than *A. africanus*, but there seems to be no evidence of this, then it would be worth getting the exotic species well established in the lowveld.

The exotic species of endoparasitoid, *C. bifasciata*, also fluctuated seasonally and its intensity was related to that of its host, but it was positively related to indices of high temperatures. This suggested that far from being limited by summer temperatures in the lowveld, it was well suited to them. Unfortunately it was limited by the indigenous hyperparasitoid, 117a

Fig 7.1. Values of the log finite rate of increase, log R, calculated from McLaren (1971) (crosses), Willard (1972a) (dots), and Wentzel (1970) (open circles), plotted against constant temperature.

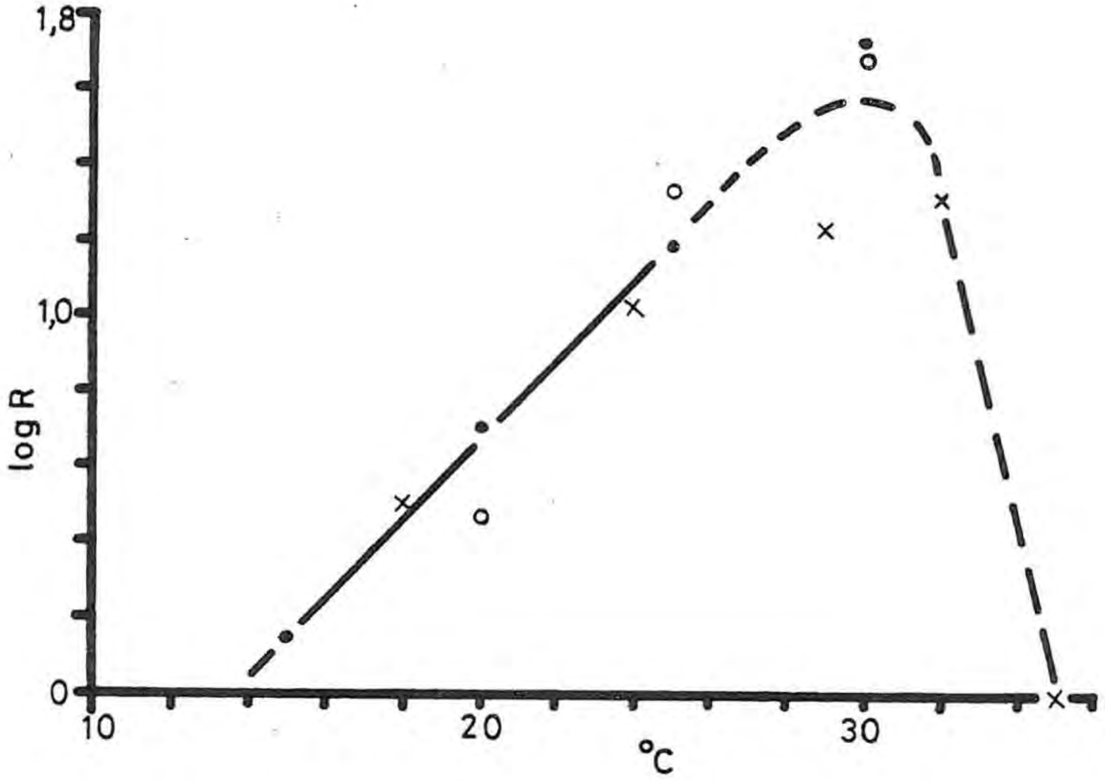
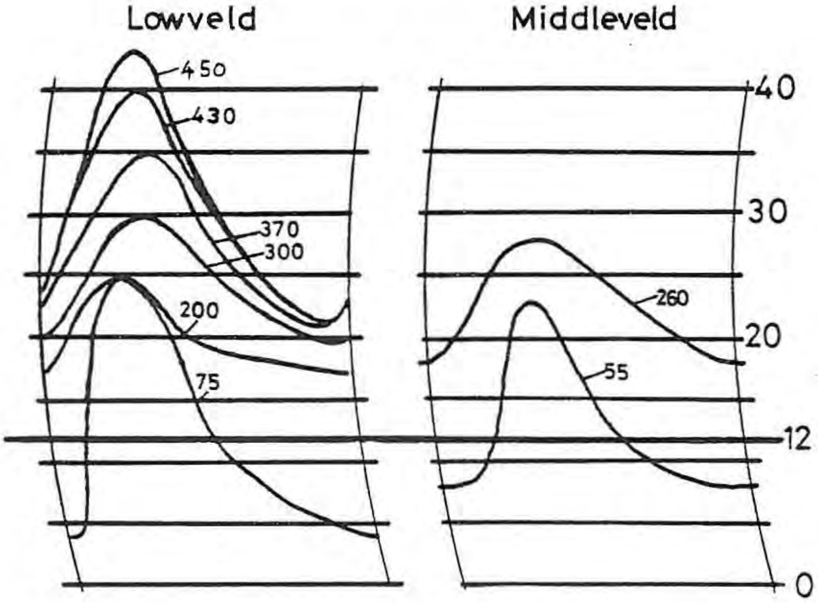


Fig 7.2. Typical reconstructed thermograph traces from the lowveld and middleveld, with h°.



M. javensis, which particularly attacked females.

The indigenous endoparasitoid, *H. rouxi*, was not only sensitive to high summer-temperatures but its intensity was negatively related to host intensity. Possibly this was a result of competition with *C. bifasciata*, but in any event it suggests that *H. rouxi* was ineffective. Messenger and van den Bosch concluded that *H. rouxi* was ineffective in California because of its sensitivity to high temperature while *C. bifasciata* was ineffective despite its tolerance of high temperature.

7.5 Why was the mean level of the scale population so high in the lowveld?

The finite rate of increase, R, is the multiplicative growth factor of the population per generation. For red scale, values of R are shown in Fig. 7.1, calculated from measurements of age-specific mortality and fertility made at constant temperatures. The optimum temperature is $\leq$30°C, and R falls rapidly above this. In the field, the optimum maximum daily temperature might be higher than 30°C because the high temperature is sustained for only a short time (Fig. 7.2) compared to constant temperature regimes.

The optimum number of hour-degrees per day for reproduction was calculated from the predictive model given in Chapter 4. On twigs, the optimum is 335 h°/day (Table 7.1) and corresponds to maximum daily temperatures, under lowveld conditions, of about 33°C (see Fig. 7.2). On fruit, the optimum for reproduction is 300 h°/day, corresponding to maximum daily temperatures of about 30°C. (At constant temperatures of 30°C or more, the h°/day exceed the optimum indicated by the model, see Table 7.1).

Table 7.1 Daily maximum temperatures and their corresponding h°/day, with the predicted crawler production per female in each case. Optima (underlined) are 335 h°/day on twigs and 300 h°/day on fruit. (s = summer, w = winter)

		Constant temperatures			Fluctuating temperatures (see Fig. 7.2)						
Daily Max. Temp.		40	35	30	43	40	35	$\underline{33}$	$\underline{30}$	25(s)	25(w)
h°/day		672	552	432	450	430	360	$\underline{335}$	$\underline{300}$	200	75
crawlers/♀/day:	Twigs	1,27	2,23	3,10	3,00	3,11	3,36	$\underline{3,38}$	$\underline{3,35}$	2,85	1,49
	Fruit	0,59	1,63	3,07	2,86	3,09	3,74	$\underline{3,87}$	$\underline{3,95}$	3,48	1,87

Table 7.2 Predicted daily crawler production per female in summer in the principal citrus-growing regions of Swaziland. (Tambankulu is similar to Big Bend, climatically).

Climatic region	Place name	Mean Max. Temp. Dec./Jan.	Corresponding h°/day	Crawlers/♀/day	
				Twigs	Fruit
Lowveld	Big Bend	31,6 (1)	320 (4)	3,38	3,92
	S.I.S.	30,2 (2)	313 (2)	3,37	3,94
Intermediate	Ngonini	29,9 (3)	304 (3)	3,36	3,94
Middleveld	Malkerns	27,1 (1)	210 (4)	2,93	3,57

(1) Means of 9 years, 1968 - 1976

(2) Measured in orchard over 4 years

(3) " " " " 2 "

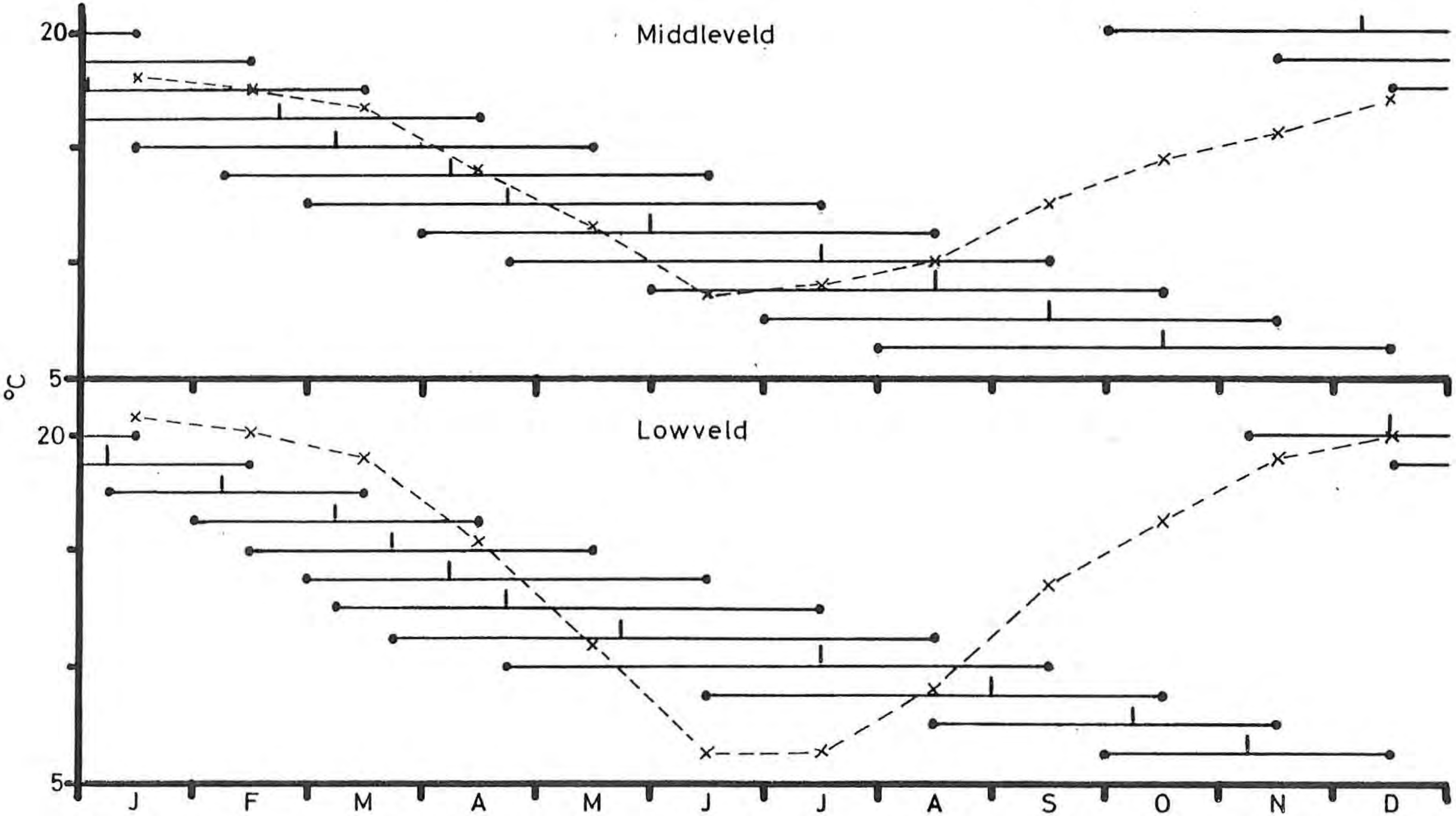
(4) Estimated from (1).

1189

The conditions for reproduction in the middleveld and lowveld are compared in Table 7.2. Malkerns is the site of most of the citrus grown in the middleveld and Catling (1971a,b) was able to introduce biological control of red scale there. However the trees are subject to greening disease in that region. Big Bend and Tambankulu are slightly hotter than Swaziland Irrigation Scheme (where the present data were collected) and all three places constitute the bulk of Swaziland's citrus. Ngonini, a large citrus estate intermediate in altitude between middleveld and lowveld, was the third site where biological control was attempted during the present study.

In Table 7.2, the predicted rates of crawler production in summer on twigs are considerably higher in the lowveld (Big Bend and S.I.S.) than in the middleveld (Malkerns). Although the rates of crawler production on fruit are comparable in both regions, the level of infestation on fruit seems to depend more on the rate of immigration from twigs in early summer than on any other factor. The conclusion is that while conditions on the lowveld in summer are very close to the optimum for reproduction, in the middleveld they are rather below optimum, especially for the all-important section of the population on twigs.

According to Catling (1971a,b), at Ngonini it should be easier to introduce biological control than in the lowveld. This was not the experience during the present attempts at biological control, and the Ngonini orchard required many corrective sprays to prevent tree-damage. The scale population never approached a steady-state like the one at S.I.S. (but it might have done so in time). The predicted daily rates of crawler production are as high at Ngonini in summer as they are at S.I.S. (Table 7.2), Fig 7.3. Approximate durations of generation times (thermal constant 20 000 h°) of adult female scales maturing in the middle of each month under average middleveld and lowveld conditions. Crosses, connected by broken lines, denote mean minimum monthly temperatures. (Vertical bars in centre of each duration show time to accumulate 10 000 h°)



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indicating that conditions are just about as favourable for the seasonal increase as they are in the true lowveld.

The predictive model for mortality on twigs is

$K = 1{,}064 - 0{,}059t + 0{,}872p + 0{,}0027r$ (see section 5.3.2 and Appendix 3)

where t is the mean minimum temperature, p the mean predator intensity and r the excess rainfall above the long term mean, all measured over the generation time. This equation is applicable only to the conditions under which p, predator intensity, and r, excess rainfall, were measured. However, the relation between K and mean minimum temperature, t, is

$$K = 2{,}815 - 0{,}115t$$

which explained 39,5% of the variation in K, and which can be used to predict mortality from seasonal temperature differences in the lowveld and middleveld. Such mortality has been labelled k'.

The approximate durations of the generation times of adult females maturing in the middle of each month are shown in Fig. 7.3, for average middleveld and lowveld conditions. In Fig. 7.3, the mean minimum monthly temperatures are nine-year averages, 1968 - 1976. Mean minimum daily temperatures were averaged over the indicated generation times and the predicted values of k' are plotted in Fig. 7.4. During winter and spring, the predicted values of k' are similar in both regions because although maximum temperatures are lower in the middleveld, minimum temperatures are higher. (Daily h° values are comparable in both regions in winter ; see Fig. 7.2.) However for 6 - 7 months of the year, the predicted mortality due to temperature differences is much higher in the middleveld.

Fig 7.4. Predicted mortality on twigs of adult females maturing in the middle of each month, as a result of the average seasonal temperature changes in the middleveld and lowveld.

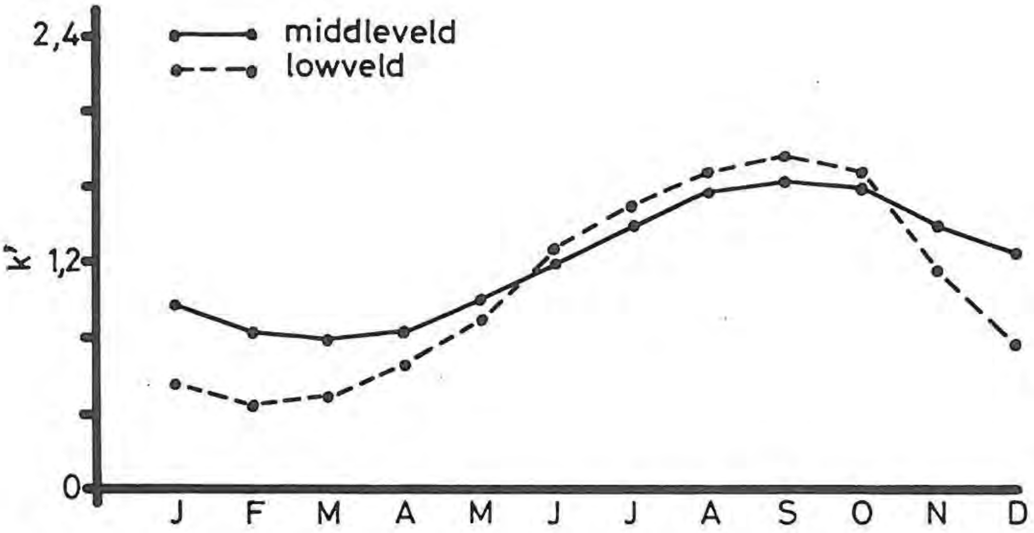
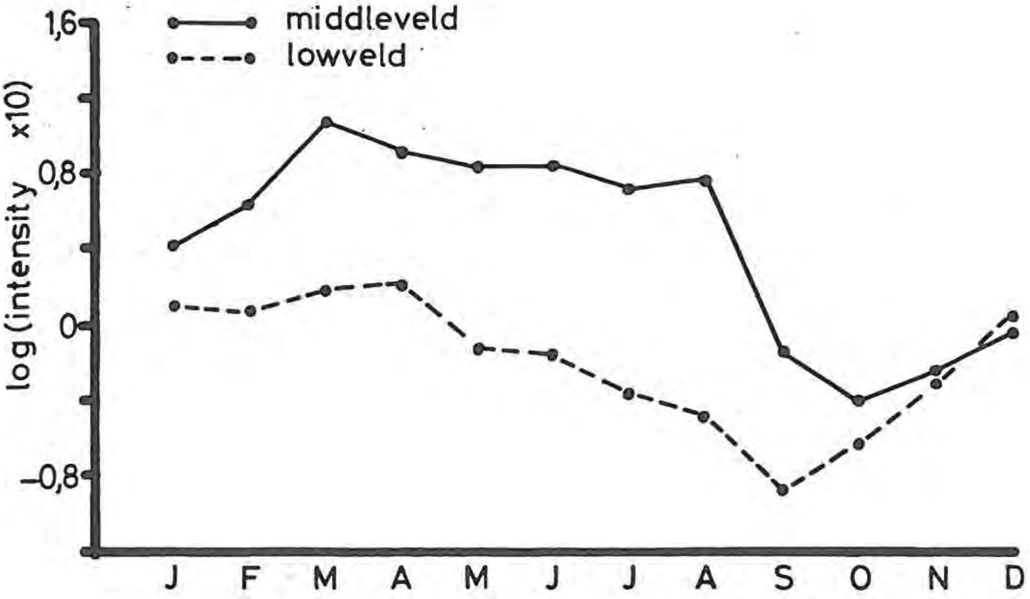


Fig 7.5. Predicted relative intensity of *Aphytis* in the middleveld and lowveld.



Slower rates of reproduction in the middleveld would account for much of the higher mortality in that region but some natural enemies might be relatively more numerous in the middleveld and might account for part of the difference in mortality. Although *Lindorus lophantae* was not affected by high temperatures in the lowveld, *Aphytis* was. Average day-degrees per month for the four hottest months (October - January) were 85D° in the lowveld but only 20D° in the middleveld (September - December). The relationship between *Aphytis* intensity per 'twig' and indices of temperature was:

$$\log(\text{intensity x10}) = -0{,}298 - 1{,}136D + 0{,}132t$$

where D is the number of day-degrees above 30°C and t the mean minimum temperature, both measured over the approximate generation time (thermal constant c 10.000h°). Approximate generation times are shown in Fig. 7.3 (vertical bars) for *Aphytis* adults emerging in the middle of each month. Values of D and t were computed over the indicated generation times. Predicted relative intensities of *Aphytis* are shown in Fig. 7.5, and show that the parasitoid would be more numerous in the middleveld <u>relative to the intensity/dm² of scale</u>. The parasitoid's <u>total</u> numbers would tend to be higher in the lowveld because of the high intensity/dm² of its host, with which *Aphytis* intensity was closely related (r = 0,606, Table 6.4).

7.6 Recommendations

Lowveld conditions in Swaziland appear to be close to the optimum for red scale but below optimum for at least one natural enemy, *Aphytis*, which is regarded elsewhere as one of the most effective biological control agents.

Suggestions for any future work on the biological or integrated control of red scale in this region are:

(i) to study the effects of cultural practices, especially the frequency and amount of irrigation, on red scale abundance;

(ii) to more fully investigate, and if possible augment, the rôle of predation in the scale population.

(iii) to get A. *melinus* well established in lowveld orchards.

ACKNOWLEDGEMENTS

The data used in this study were collected whilst I was employed by the Swaziland Citrus Board, Mbabane, and stationed for most of the time at Swaziland Irrigation Scheme, Tshaneni. Experimental orchards were provided by S.I.S., Ngonini Estate and Tambankulu Estate. To all these organisations I am most grateful.

I thank Prof. B.R. Allanson, Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa for the opportunity to present this work, and for discussion.

It is a pleasure to express my thanks to Mr M.G. Murdoch, South African Sugar Association Experiment Station, Mount Edgecombe, for programming the temperature summations, running multiple regressions of more than three variables and for discussion. I am grateful for the use of the computer of the South African Sugar Association.

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APPENDIX 1

1	2	3			4	5	6	7	8	9
Sample Date	Adult ♀ intensity (N)	Cohort spacing, with no. of h° separating the readings			logN	$_1K_T$	Crawler recruitment to cohort	$_2K_T$	$_3K_T$	$\frac{N_{t+1}}{N_t}$
		Set 1	Set 2	Set 3						
15/2/72	2.87				0,458	-		-	-	
9/ 3	8.36				0,922	-		-	-	
22/ 3	14.65				1,166	-		-	-	
5/ 4	5.53	18673								
19/ 4	11.65		17359							
3/ 5	14.54				1,166	0,21	563	1,59	1,15	5,07
30/ 5	17.13			20443	1,234	0,61	701	1,61	1,15	2,05
21/ 6	10.20									
7/ 7	11.01									
21/ 7	8.26	18326								
4/ 8	8.63				0,936	1,15	1082	2,10	1,43	0,59
18/ 8	8.96		19914							
5/ 9	6.00									
19/ 9	2.06				0,313	1,78	1258	2,79	2,13	0,14
2/10	3.94			21718						
12/10	4.75				0,677	1,47	1174	2,39	2,48	0,28
30/10	3.32	18778								
15/11	2.91		20798		0,464	1,40	803	2,44	2,87	0,34
4/12	1.67				0,224	1,01	601	2,56	3,38	0,81
28/12	1.96			18973	0,292	1,31	439	2,35	3,76	0,41
18/1/73	2.57	20218			0,411	0,97	320	2,09	3,32	0,88
6/ 2	3.32		25717		0,520	0,62	216	1,81	3,22	1,99
27/ 2	6.38			19532						
20/ 3	11.21	19851			1,049	{0,16	136	1,08	2,18	5,72
10/ 4	6.34				0,802	0,28} 0,64	210	1,52	2,26	1,91
30/ 4	8.98									
21/ 5	11.15		19523							
12/ 6	5.54	19523		22462						
3/ 7	6.85				0,836	1,13	488	1,85	2,30	0,61
30/ 7	4.62				0,665	1,31	597	2,11	2,26	0,41
20/ 8	2.13				0,329	1,39	665	2,49	2,46	0,34
7/ 9	2.84		19270							
3/10	.58			21134						
24/10	.44	23946			-0,359	2,12	604	3,14	3,85	0,06
13/11	.22		18500		-0,663	2,25	430	3,30	4,64	0,05
5/12	.55				-0,264	1,51	286	2,72	5,28	0,26
31/12	.99			18960	-0,005	0,57	147	2,17	4,64	2,25
16/1/74	.85	18518			-0,070	0,33	56	1,82	4,10	3,86
31/1	.32		21763		-0,496	1,16	40	2,10	3,27	0,58
21/2	.14			22978						
8/3	.49	22024			-0,308	1,23	54	2,04	2,75	0,49
5/4	.58				-0,239	1,09	39	1,83	2,95	0,68
25/4	.21				-0,672	1,09	32	2,18	2,87	0,66
9/5	.31		19382							
28/5	.15									
13/6	.29			20820						
24/6	.32	20456			-0,493	1,11	21	1,81	2,68	0,65
17/7	.36									
2/9	.31				-0,514	1,19	14	1,65	2,62	0,53
23/9	.50		19529		-0,301	0,56	14	1,45	2,67	2,38
8/10	.40									
21/10	.63			18452	-0,199	0,63	15	1,38	2,32	1,97
4/11	1.21	18670								
21/11	.73				-0,140	0,55	20	1,44	2,03	2,35
4/12	1.75		19082		0,242	0,38	27	1,18	1,79	3,50
17/12	3.73									
30/12	4.72				0,674	0,06	61	1,11	1,60	7,49
17/1/75	5.45			20090						
21/1	6.00	18789								
24/1	5.80									
27/1	6.17				0,790	0	177	1,34	1,13	8,45
31/1	8.78		16653							
4/2	9.99									
7/2	11.95				1,077	0,08	239	1,30	0,98	6,83
11/2	7.33									
19/2	7.29			18766						
26/2	17.73				1,249	0,34	339	1,28	0,86	3,76
5/3	13.59									
17/3	12.24									
27/3	9,23									
1/4	12.03	18635								
14/4	10.14				1,006	0,70	696	1,84	0,89	1,64
23/4	6.49		19871							
29/4	8.49				0,929	1,12	858	2,00	1,01	0,71
13/5	7.48									
26/5	5.78									
5/6	4.71									
18/6	6.63				0,821	1,35	1159	2,24	1,49	0,37
n = 38 cohorts		mean cohort spacing = 19952,2h° s.d. = 1790,3								

APPENDIX 2

1	2	3					4	5	6
Sample date	Adult ♀ intensity (N)	Cohort spacing with no. of h° separating the readings					LogN	K_F	$\frac{N_{t+1}}{N_t}$
		Set 1	Set 2	Set 3	Set 4	Set 5			
15/2/72	2,16	18673					0,335	-	
8/ 3	2,34		17359				0,369	-	
22/ 3	4,34			20443			0,637	-	
5/ 4	2,58				19027		0,414	-	
19/ 4	11,48					18468	1,060	-	
3/ 5	9,10	18326					0,959	1,03	4,21
30/ 5	11,10						1,045	0,98	4,74
21/ 6	12/12								
7/ 7	8,87								
21/ 7	8,29								
4/ 8	5,73						0,758	1,53	1,32
18/ 8	9,81						0,992	1,07	3,80
5/ 9	5,55						0,745	1,97	0,48
19/ 9	5,75						0,760	1,85	0,63
4/12	0,12	20218					-0,917		
28/12	5,94		25715				0,773	-	
18/1/73	6,91			19532			0,839	-	
6/ 2	5,46	19851					0,737	0	45,50
27/ 2	7,19				20136		0,856	$\bar{1}$,31}	2,19}
20/3	13,00		19522	22462			1,114	1,38}	1,88}
10/ 4	10,55						1,023	1,37	1,93
30/ 4	26,75								
21/ 5	17,13						1,234	1,28	2,38
12/ 6	23,61								
3/ 7	17,31						1,238	1,53	1,33
30/ 7	20,18						1,305	1,46	1,55
5/12	0,18	18518					-0,747	-	
31/12	0,17		21763				-0,775	-	
6/1/74	0,27			22978			-0,575	-	
31/1	0,08	22024					-1,103	1,66	0,44
21/ 2	0,06				20915		-1,192	-	
8/ 3	0,15		19382				-0,818	1,71	0,88
5/ 4	0,15						-0,836	1,27	0,56
25/ 4	0,10						-0,991	1,55	1,25
9/ 5	0,04								
28/ 5	0,08						-1,101	1,57	1,33
13/ 6	0,29								
24/ 6	0,11						-0,943	1,78	0,73
17/ 7	0,07								
4/12	0,11	18789					-0,971	-	
17/12	0,64		18503				-0,193	-	
30/12	0,62			16653			-0,205	-	
17/1/75	0,38				19060		-0,417	-	
21/ 1	0,93								
24/ 1	1,45								
27/ 1	0,86								
31/ 1	1,73								
4/ 2	1,49					20953	0,172	-	
7/ 2	1,55	18635					0,190	0,50	14,09
11/ 2	0,84								
19/ 2	0,73		20181				-0,137	1,61	1,14
26/ 2	2,12			19871			0,327	1,12	3,42
5/ 3	2,38								
17/ 3	0,95								
27/ 3	0,98								
1/ 4	0,56						-0,253	1,49	1,47
14/4	0,54								
23/ 4	0,59								
29/ 4	0,70						-0,155	2,00	0,45
13/ 5	0,37						-0,434	2,26	0,25
26/ 5	0,58						-0,240	1,76	0,79
5/ 6	0,35								
18/ 6	0,90						-0,046	2,03	0,42
n = 27 cohorts		mean cohort spacing = 19924,3 s.d. = 1883,5							

APPENDIX 3

CHECKING FOR POLYNOMIAL EFFECTS IN THE FACTORS WHICH AFFECTED MORTALITY ON TWIGS

Indices of three factors were associated with scale mortality on twigs (${}_1K_T$). These factors were mean minimum temperature, excess rainfall, and predator numbers (section 5.3.2, p.86). Moreover the scale infestations on fruit each year depended largely on the size of the population on twigs in spring (section 2.7, p.28), so these three factors were fundamental ones which influenced the changes in the whole population in the tree. In order to see whether these factors interacted with each other, or acted independently, interaction terms were investigated by multiple regression analysis. Quadratic terms were also introduced to see whether any of the relationships were curvilinear. The procedure was similar to surface-response analysis, described for example by Newell (1979*).

The results are given in the accompanying table. In the first step of the analysis, quadratic and interaction terms were introduced for all the possible interactions. None of the terms was statistically significant. In succeeding steps the interaction terms and then the quadratic terms were eliminated until the remaining terms became significant. Although the analysis programme did not cover all the possible combinations of terms, the conclusions are:

(i) the interactions were not significant indicating that mortality was affected independently by each factor,

(ii) the relationship between mortality and each factor was rectilinear. (In the case of rainfall, the quadratic term was significant but the linear term was not (steps 3 and 4) and so the former term was not included in the regression in the absence of the latter).

The object of the analysis described in section 5.3.2 (p.86) was to identify the main factors affecting scale mortality on twigs. The object of the analysis described in this appendix was to see if these factors acted independently or if there were interactions. In neither case was the object to develop a predictive model for mortality, or to define optimum zones of the environment, for the following reasons:

(i) Although meteorological data is available for many citrus-growing regions of the world, it would not be possible to define 'excess' rainfall, particularly where irrigation is practised.

(ii) Measures of predator numbers would, similarly, not be available.

Nevertheless, were a model required, it would be the simple rectilinear relationship:

$$K = 1{,}064 - 0{,}059t + 0{,}872p - 0{,}0027r$$

where K is the total mortality and t, p and r are as defined in section 5.3.2.

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* Newell, R.C. (1979). Biology of intertidal animals. pp. 185-196. Marine Ecological Surveys Ltd., Kent, England.

AP 3a

Stepwise multiple regression analysis to check for polynomial effects in the three environmental indices associated with scale mortality on twigs. The table gives the value of Student's t and the corresponding probability level for the partial regression coefficient of each term in the regression (n.s. = not significant). No. of observations, 38.

Step	Terms in regression	t	P
1	Temp	0,47	n.s.
	Pred	1,39	n.s.
	Rain	0,24	n.s.
	$Temp^2$	0,04	n.s.
	$Pred^2$	1,71	n.s.
	$Rain^2$	1,21	n.s.
	Temp x Pred	1,56	n.s.
	Temp x Rain	0,14	n.s.
	Pred x Rain	0,54	n.s.
	Temp x Pred x Rain	0,50	n.s.
(Coeff. Detn., R^2, = 0,842)			
2	Temp	0,40	n.s.
	Pred	1,33	n.s.
	Rain	0,76	n.s.
	$Temp^2$	0,08	n.s.
	$Pred^2$	1,66	n.s.
	$Rain^2$	1,13	n.s.
	Temp x Pred	1,52	n.s.
	Temp x Rain	1,56	n.s.
	Pred x Rain	0,33	n.s.
(Coeff. Detn., R^2 = 0,840)			
3	Temp	1,09	n.s.
	Pred	0,64	n.s.
	Rain	1,21	n.s.
	$Temp^2$	1,26	n.s.
	$Pred^2$	0,81	n.s.
	$Rain^2$	2,41	0,05
(Coeff. Detn., R^2, = 0,788)			
4	Temp	1,06	n.s.
	Pred	5,21	0,001
	Rain	1,20	n.s.
	$Temp^2$	1,25	n.s.
	$Rain^2$	2,34	0,05
(Coeff. Detn., R^2, = 0,783)			
5	Temp	2,82	0,01
	Pred	4,59	0,001
	Rain	4,34	0,002
(Coeff. Detn., R^2, = 0,728)			
6	Temp	4,85	0,001
(Coeff. Detn., R^2, = 0,397)			
7	Pred	6,31	0,001
(Coeff. Detn., R^2, = 0,518)			
8	Rain	2,41	0,05
(Coeff. Detn., R^2, = 0,137)			