

Relationship between red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae), and its natural enemies in the upper and lower parts of citrus trees in South Africa

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Abstract

In mature Valencia orange trees at three sites in the Transvaal lowveld, there was a variable differential between levels of *Aonidiella aurantii* (Maskell) in the upper and lower parts of the trees. At one site there were high scale levels in the crowns of the trees as a result of past poor chemical spray procedure. In recent years, pest management has maximized on the use of natural enemies, especially *Aphytis* spp. However, the natural enemies have not been able to ameliorate the crown problem. At generally high levels of *Aonidiella aurantii*, the natural enemies were able only, more or less, to maintain the average overall level of the scale from one year to the next; they could not bring it down. This arose each year from too many scales escaping parasitism and reaching the relatively invincible adult stage early in the season. As the behaviour of the parasitoids was inversely density-dependent at these relatively high scale levels, this led to a greater increase in scale numbers, leading eventually to up to 90% of the population (excluding crawlers) being composed of adult females. The inverse density dependence was also partly because the majority of single scales escaped parasitoid attack. In the lowveld, it is a prerequisite that the density of *A. aurantii* first be lowered by an introduced natural enemy (e.g. the coccinellid *Chilocorus nigritus* (F.)) that attacks the adult stage and/or by chemical means before maximal use is made of the regulatory influence of the existing natural enemies, particularly *Aphytis* spp.

Introduction

There has been a renewed interest in the biological control of red scale, *Aonidiella aurantii* (Maskell), on all varieties of citrus in southern Africa since the pest became resistant to organophosphate insecticides (Georgala, 1975; Nel *et al.*, 1979). Although biological control has worked well on the highveld (Bedford, 1968), it has not been so successful in the lowveld (Catling, 1971; Atkinson, 1977, 1983*a,b*). The reasons given include a high rate of scale population increase and a sensitivity by existing parasitoids to high summer temperatures.

Although Atkinson (1977) in his thorough biological studies sampled both the tops and bottoms of the trees, he did not investigate any differences that might have occurred in natural enemy behaviour at the two heights in the tree. Similarly, in recommendations for biological control in the lowveld (e.g. Bedford, 1981), although emphasis is laid on the appropriate pesticides that can be used for the pest complex so that there will be the

minimum impact upon the natural enemies of *A. aurantii*, no mention is made of the differences that can exist with height in the tree. Part of the reason is that there has been a belief that the existing natural enemies even out any differences in the numbers of *A. aurantii*.

The purpose of the present study was to quantify the differences in *A. aurantii* levels on certain trees in the lowveld where it has not been under satisfactory commercial control since the implementation of an integrated control programme. Further, the ability of natural enemies to alter the age-distribution of the scale was examined, and the findings are used as a pointer for improving pest management in citrus.

Sites and methods

Sites

The main orchard used was at Mataffin, near Nelspruit, South Africa, mostly of 50- to 60-year-old Valencia orange trees (4–6 m tall) which had been under integrated control from the 1977–78 season onwards. Under such a programme, *A. aurantii* is controlled by natural enemies (particularly *Aphytis* spp.) and so far as possible, treatments for other pests are selected for minimal impact upon these natural enemies. The trees were pruned on a three-year basis, which tends to give them a flat-topped appearance. Excessively high densities of psylla, *Trioza erythrae* (Del Guercio), and *Aonidiella aurantii* necessitated the application of a mixture of 0.06% phenthoate and 1.4% narrow distillation range oil by 'Eagle' mistblower on 10 December 1982. At this site, study was made of mature fruit at the end of a first season (August 1982) and of developing and maturing fruit throughout a second season (December 1982–July 1983).

Supplementary results for comparison of infestations in the tops and bottoms of Valencia trees were obtained only at the end of the first season (August 1982) on mature fruit at Plaston (35 km north-east of Nelspruit) which was similar to the first site except that the trees had been under integrated control for over seven years (instead of four).

The second major site was an orchard of Valencia trees at Tenbosch near Komatipoort, 130 km east of Nelspruit. It was lower-lying and hotter than the first site. Pest management was similar to that at Nelspruit, except that sprays against *T. erythrae* were never required, the trees were not top-pruned and the integrated control programme was instigated only in 1980–81. Results were obtained only throughout the second growing season (January–July 1983).

Infestations of *A. aurantii* on mature fruit

At the end of the first season at Nelspruit (18–25 August 1982), 20 trees were used for assessing *A. aurantii* levels on ripe fruit in the four fruit and tree quadrants. Ten fruit from a height of 1.5 to 2.0 m were randomly selected from each quadrant of each tree. The scale was sampled in a 30 × 30-mm area at the four compass points around the equator of the fruit. The total number of samples from each of the 20 trees was therefore 160 (4 per fruit, 10 per quadrant and 4 quadrants per tree). For comparison of tops of trees with bottoms, ten trees were used. From each tree, four fruit were taken from the crown and four from around the bottom of the canopy (height 1.5–2.0 m), making a total sample size of 40. All living immobile stages (i.e. all stages except the crawler and whitecap) of the scale, both unparasitized and parasitized, were counted.

Distribution of *A. aurantii* on twigs and young fruit

At the beginning of the second season at Nelspruit (7 December 1982), ten trees were used for assessing scale levels on twigs and small immature fruit. Two twigs, 150 mm long and with one terminal fruit, were taken from each of the four quadrants at a height of 1.5–2.0 m. This gave 80 twigs and 80 young fruit from the lower half of the trees. Additionally, the same number of twigs and fruit were taken from the crowns of the same

ten trees. All living examples of the scale, first moult and older, both parasitized and unparasitized, were counted on each whole fruit and twig.

Seasonal changes in scale and parasitoid levels

Twigs and fruit were sampled monthly throughout the second season at both the main sites. From randomly-selected trees, one fruit and one twig (150 mm long) were taken from each of the four quadrants of ten trees at a height of 1.5–2.0 m. A further four samples of fruit plus twigs were taken from the crowns of each tree, giving 40 samples from the top and 40 from the bottom each month. All living examples of *A. aurantii*, first moult and older, parasitized and unparasitized, were counted on whole fruit and twigs. The fruit and twigs were then transferred to emergence boxes, where they remained for 20–25 days, to obtain monthly absolute numbers for parasitoids.

Percentage parasitism

Monthly samples of 40 fruit from the tree crowns and 40 from the tree bottoms at the two main sites were also taken for direct observation under the stereo-microscope. The viewpoint of McLaren & Buchanan (1973), who emphasized the value of studying only the live stages of the scale, was strongly supported here. It is misleading to include dead individuals as these remain on the fruit for varying and sometimes long periods of time depending on weather conditions. At the beginning and end of the season, all scales on the fruit were counted and their covers lifted. In the middle of the season, when scale density was high, only a representative sample was taken from each fruit, so that the total number of scales examined was at least 500 (but well over 1000 mid-season) from each batch of 40 fruit. To avoid bias, these representative samples involved examining every living scale within whole microscope fields of view at 60× magnification. After studying all the scales in the first field, the fruit was turned and all the scales in the next field examined, and so on to achieve a satisfactory scale sample size of at least 500 from all the fruit.

In the discussions below, the minimum arbitrary patch size is one microscope field. Where groups or single scales are mentioned, the density is also per microscope field.

Scales were categorized into developmental stages which were parasitizable by the existing parasitoid complex: second instar (sex indistinguishable) (2e), second instar (male) (2♂), second instar (female) (2♀), virgin adult or grey stage (A⁻), and mature adult female (A⁺). A record was made of the numbers of eggs, larvae or pupae of *Aphytis* spp.; the species was identified in the case of older pupae. Counts were also made of pupae of *Comperiella bifasciata* Howard and, where possible, scales eaten by *Rhyzobius lophanthae* (Blaisdell). The mature adult female is only rarely attacked by *C. bifasciata* (Atkinson, 1981).

Transformation of raw data

As the variances were proportional to the squares of the sample means both for the fruit quadrants ($r = 0.56$, $P < 0.02$) and for the tree quadrants ($r = 0.96$, $P < 0.001$), and as *Aonidiella aurantii* has a contagious distribution (Spiller, 1948, 1952), all raw data were transformed using $\log(x + 1)$.

Results

Infestation of mature fruit and twigs according to quadrant

In the northern and western sections of the trees at the Nelspruit site, there were significant differences in mean levels of *A. aurantii* on the four faces of the fruit (Table 1). In particular, the northern faces of fruit from the northern and western sides of the trees had fewer scales than the other faces.

TABLE I. Mean number ($\log x + 1$) of *Aonidiella aurantii* on the four faces of fruit picked from points around the tree (top), and on fruit from the four quadrants of the tree (bottom)

Quadrant of tree	Sample size	Quadrant of fruit			
		North	West	South	East
North	800	0.3395 ^a	0.4851 ^b	0.5900 ^c	0.4829 ^b
West	800	0.6910 ^a	0.7432 ^b	0.8062 ^c	0.8141 ^c
South	800	0.5090 ^a	0.4594 ^a	0.4677 ^a	0.4521 ^a
East	800	0.6943 ^a	0.7830 ^a	0.7615 ^a	0.6912 ^a

Sample size	Quadrant of tree	Mean
2000	North	0.4738 ^a
2000	West	0.7258 ^b
2000	South	0.5042 ^a
2000	East	0.8010 ^b

Numbers followed by the same letter down the column are not significantly different at $P < 0.05$ by Duncan's multiple range test. In view of recent discussions and criticisms of multiple-range tests (e.g. Jones, 1984), this analysis is provided only as a guide and not as an absolute criterion on which to accept or reject a particular hypothesis.

When the level of *A. aurantii* on the north face of the fruit on the north side of the tree ($n = 200$, $\bar{x} \pm 1$ s.e. = 0.3395 ± 0.0699) was compared with level on the south face of the fruit on the south side ($n = 200$, $\bar{x} \pm 1$ s.e. = 0.4677 ± 0.0492) they differed significantly ($t = 2.503$, $P = 0.012$).

When the data from the four faces of the fruit were combined, there were significant differences in *A. aurantii* infestation levels (ANOVA, $F = 25.54$, $P < 0.0001$) between fruits from the four quadrants of the tree. Fruit on the north side of the tree had similar overall scale levels to those on the south, and those on the west to those on the east (Table I). However, those on both the north and south differed significantly from those from both west and east.

There were no significant differences in levels of the scale on twigs taken from the four compass points in the lower half of the tree.

TABLE II. Percentage parasitism of *Aonidiella aurantii* by species of *Aphytis* in the tops and bottoms of trees at two sites

	Tops of trees				Bottoms of trees					
	<i>n</i>	<i>Aphytis</i> spp.*	<i>A. melinus</i>	<i>A. africanus</i>	<i>Aphytis</i> sp.**	<i>n</i>	<i>Aphytis</i> spp.*	<i>A. melinus</i>	<i>A. africanus</i>	<i>Aphytis</i> sp.**
Nelspruit 1982-83										
December	1	0	0	100	0	0	0	0	0	0
January	0	0	0	0	0	0	0	0	0	0
February	1	0	0	100	0	1	100	0	0	0
March	234	76.1	0.4	21.8	1.7	73	100	0	0	0
April	457	70.2	0.9	28.9	0	296	66.2	0	33.8	0
May	43	88.4	2.3	7.0	2.3	108	73.1	2.8	24.1	0
June	37	70.0	0	30.0	0	44	72.7	0	27.3	0
July	28	67.9	14.2	17.9	0	27	74.1	3.7	22.2	0
Komatipoort 1983										
January	1	100	0	0	0	3	33.3	66.7	0	0
February	44	86.4	6.8	6.8	0	68	82.4	2.9	14.7	0
March	221	62.4	37.6	0	0	109	58.7	40.4	0	0.9
April	57	93.0	1.8	0	5.2	18	94.4	0	5.6	0
May	69	89.9	8.7	1.4	0	47	93.6	2.1	4.3	0
June	22	77.3	18.2	4.5	0	12	75.0	25.0	0	0
July	0	0	0	0	0	2	100	0	0	0

* Unidentifiable eggs, larvae or young pupae of all species.

** Wholly dark pupae, i.e. *Aphytis* sp. nr. *A. lingnanensis*.

General variation within and between trees

The total log-transformed data base from the four tree quadrants at the Nelspruit site was used to assess within- and between-tree variation. The 20 means for the 20 within-tree samples ranged from 0.129 to 1.27. Coefficients of variation (c.v.) of individual trees ranged from 0.27 to 97.8%. Between-tree variation ranged from 0.340 to 0.846. The coefficients of variation ranged from 37.6% through 50 and 60% for most quadrants, to a single high value of 92.1% for the north side of the fruit on the north side of the tree.

Comparison of scale density at tops and bottoms

The density of the scale on mature fruit at the tops of the trees at Nelspruit was significantly different from that at the bottoms ($t = 6.39$, $P < 0.001$), the untransformed means (± 1 s.e.) being 34.1 (± 0.1916) and 3.95 (± 0.3467), respectively, a ratio of 8.6:1. At Plaston, the mean (± 1 s.e.) for the tops was 7.88 (± 0.1889) and for the bottoms it was 1.88 (± 0.1678), a ratio of 4.2:1. These means were significantly different ($t = 3.52$, $P < 0.01$).

The number of scales per whole young fruit at Nelspruit was not significantly higher at the tops of the trees than at the bottom on 7 December (Fig. 1). The lack of significance partly results from the high sample to sample variation in scale levels (c.v. at top = 91.1%, c.v. at bottom = 72.4%) and a low top:bottom ratio of only 1.5:1.

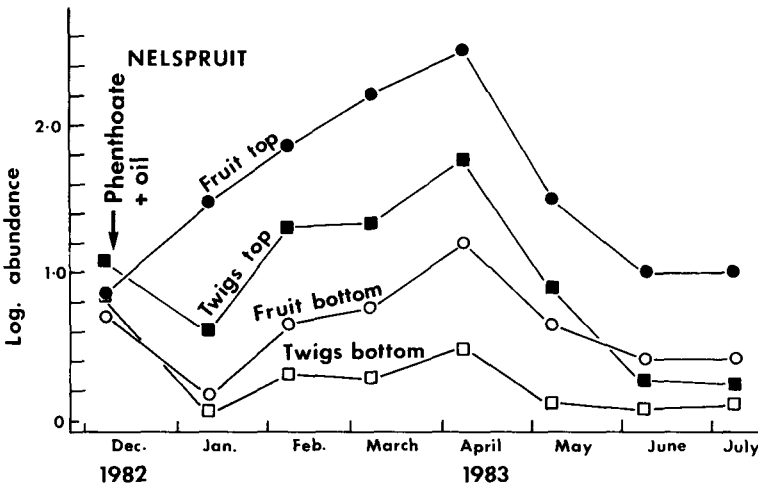


Fig. 1.—Abundance of second-instar nymphs and older individuals of *Aonidiella aurantii* on 40 whole fruit and 40 twigs from the tops and bottoms of citrus trees at the cooler Nelspruit site. Standard errors are omitted for sake of clarity.

By 11 January, the density of *A. aurantii* on maturing fruit at the top of the trees at Nelspruit had become much higher than at the bottom ($P < 0.001$) (Fig. 1). The difference remained significant at under the 0.1% level for the rest of the season.

After harvesting the fruit in the first cropping season (August 1982), the remaining twigs at the top of the trees at Nelspruit supported more scales than those at the bottom ($P < 0.05$) (Fig. 1). The untransformed means (± 1 s.e.) were 48.7 (± 0.3223) and 9.67 (± 0.2323) respectively, a ratio of 5.04:1. At the beginning of the second cropping season (7 December 1982), the difference between tree tops and bottoms was still significant ($P < 0.01$). The difference in subsequent months became even greater, with a significance level of less than 0.1% for the remainder of the season (Fig. 1).

In contrast to the situation at Nelspruit, the number of *A. aurantii* on fruit at Komatipoort was higher in tree bottoms than the tops (Fig. 2). On 13 January 1983, the untransformed mean number of scales per fruit (± 1 s.e.) was 39.8 ± 7.85 at the top and almost double at the bottom (77.3 ± 13.3), these means being significantly ($t = 3.10$, $P < 0.01$). After January, the differences were not so great, being non-significant in February and significant only at the 2% level in March, and 5% in April and May (Fig. 2).

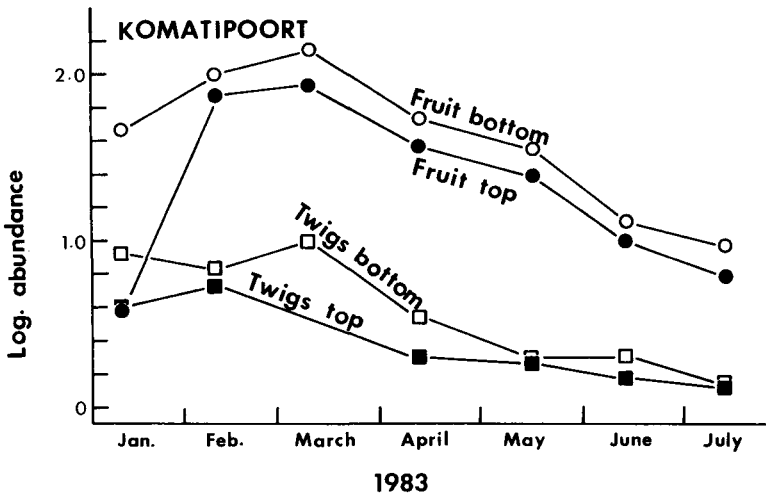


Fig. 2.—Abundance of second-instar nymphs and older individuals of *Aonidiella aurantii* on 40 whole fruit and 40 twigs from the tops and bottoms of citrus trees at the hotter Komatipoort site. Standard errors are omitted for sake of clarity.

As with the fruit, twigs in January at Komatipoort supported more scales at the bottom of the trees ($\bar{x} \pm 1$ s.e. = 10.4 ± 1.41) than at the tops (6.15 ± 1.72), the difference being significant ($t = 3.68$, $P < 0.001$). The difference was non-significant in February, but throughout the rest of the season increased again with bottom twigs constantly supporting greater levels than top twigs ($P < 0.02$) (Fig. 2).

A regression analysis comparing scale levels on mature fruit at the tops of the trees with those at the bottom at Nelspruit was not significant at the 5% level ($r = 0.397$). Similarly, the regressions for both young fruit and twigs were also non-significant ($r = 0.345$ and 0.016 , respectively). Thus, although there was a tendency for trees with higher scale levels at the tops also to have higher scale levels at the bottoms (all correlations were positive), the relationship was nevertheless too weak to be significant.

Predation of pre-adult scales

Various predators of *A. aurantii* were present, including the phytoseiids *Amblyseius citri* van der Merwe & Ryke and, to a lesser, extent *A. tamatavensis* Blommers, which fed on host crawlers. *R. lophanthae* was conspicuous feeding on various stages from first instars through to grey adults, but not on mature adults. Its exact impact was difficult to assess owing to the accumulation of dead scales, although at the beginning of the season at Nelspruit 8.9% and 15.8% of *Aonidiella aurantii* in the tops and bottoms of the trees, respectively, had been eaten by this predator. At Komatipoort, the abundance of this beetle suggested considerable impact and on 12 April apparently 88% of young scales had been eaten by *R. lophanthae* on fruit at the tops of the trees.

Parasitism of pre-adult scales

The species composition of parasitoids, after dissection of scales on fruit, in the tops and bottoms of trees at the two major sites is shown in Table II. The high values for *Aphytis* spp. is because eggs, larvae and young pupae could not be identified to species. From March to June at Nelspruit, *A. africanus* Quednau was by far the most abundant species. It was present at similar levels both in the tops and bottoms of the trees. *Aphytis* sp. nr *A. lingnanensis* Compere was only recorded at the tops of the trees, while *A. melinus* DeBach tended to be more abundant at the tops than the bottoms.

At Komatipoort, *A. africanus* was as common as (tree tops) or more common than (bottoms) *A. melinus* in February. From March onwards in the tops of the trees, *A. melinus* was the dominant species. In the bottoms, *A. melinus* was dominant only in March and June, with *A. africanus* being dominant in April and May.

Interaction between scales and *Aphytis* spp.

Data from Nelspruit (Figs. 1 & 3) can all be divided into halves, with events up to April being different from April onwards, particularly in the tops of the trees. The increases in scale population levels (Fig. 1) were followed by sharp rises in the levels of *Aphytis* captured in the emergence boxes (Fig. 3a). This parasitoid increase took place earlier in the tree tops than in the bottoms. When *Aphytis* increased, it depleted its resources, resulting in a steady decline in the percentage of scales available to it (Fig. 3b). Concurrent

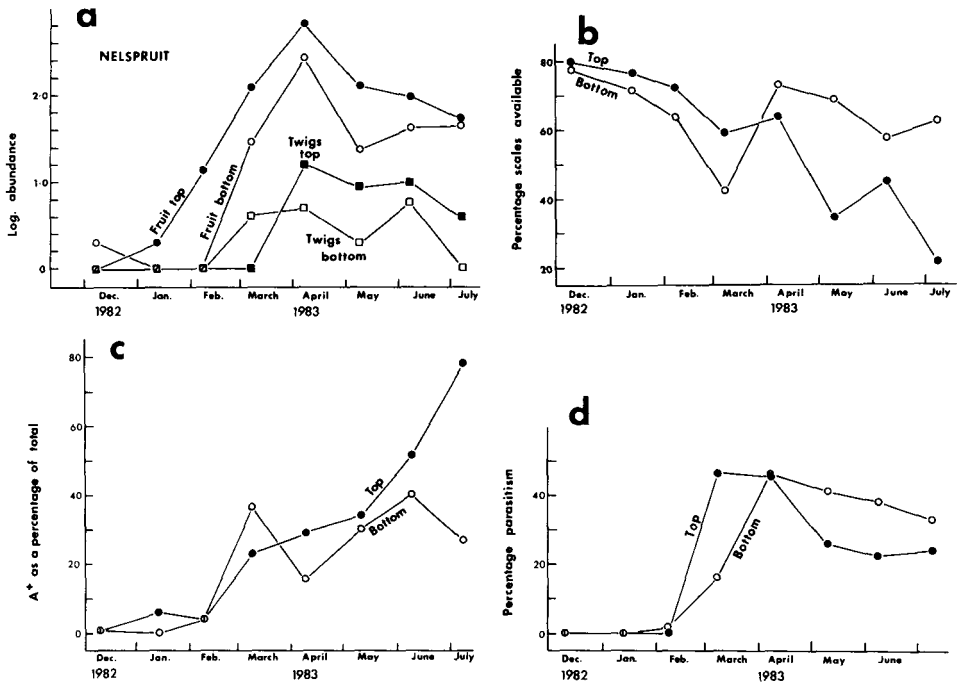


Fig. 3.—Aspects of the relationship between *Aphytis* spp. and *Aonidiella aurantii* on fruit and twigs from the upper and lower parts of citrus trees at the cooler Nelspruit site throughout one growing season; a, abundance of *Aphytis* spp. emerging from *Aonidiella aurantii*; b, percentage of the total living population of *A. aurantii* of the right age for parasitism by *Aphytis* spp.; c, the percentage of reproducing adult females of *Aonidiella aurantii* among the total living population (excluding crawlers); d, percentage parasitism by *Aphytis* spp. of parasitizable living individuals of *Aonidiella aurantii*.

with this was an increase in the percentage of A^+ adults as a percentage of the total number of scales, first moult and older (Fig. 3c). In other words, *Aphytis*, and to a lesser extent the other natural enemies, caused a shift in the age-distribution of the scale population. In doing so, it deprived itself of resources, causing an increase in the percentage parasitism of parasitizable stages of scales up to and including April (Fig. 3d). This sequence of events was most acute in the tree crowns.

From April onwards in the tops of the trees, the percentage of scales available to *Aphytis* decreased (Fig. 3b), and this was associated with an increase in the A^+ adult percentage (Fig. 3c). This late-season decline in resources for *Aphytis* apparently changed its behaviour, because the percentage parasitism by *Aphytis* actually decreased from April onwards (Fig. 3d).

At the bottoms of the trees, the situation was different. The percentage of scales available to *Aphytis* actually increased in April and then remained high (Fig. 3b). It did not decrease as in the crowns. Concurrent with this was a levelling out of the percentage of A^+ adults at about 30% of the total number of scales (Fig. 3c). As at the tops, however, at the bottoms after April, there was a gradual decline in percentage parasitism by *Aphytis* (Fig. 3d).

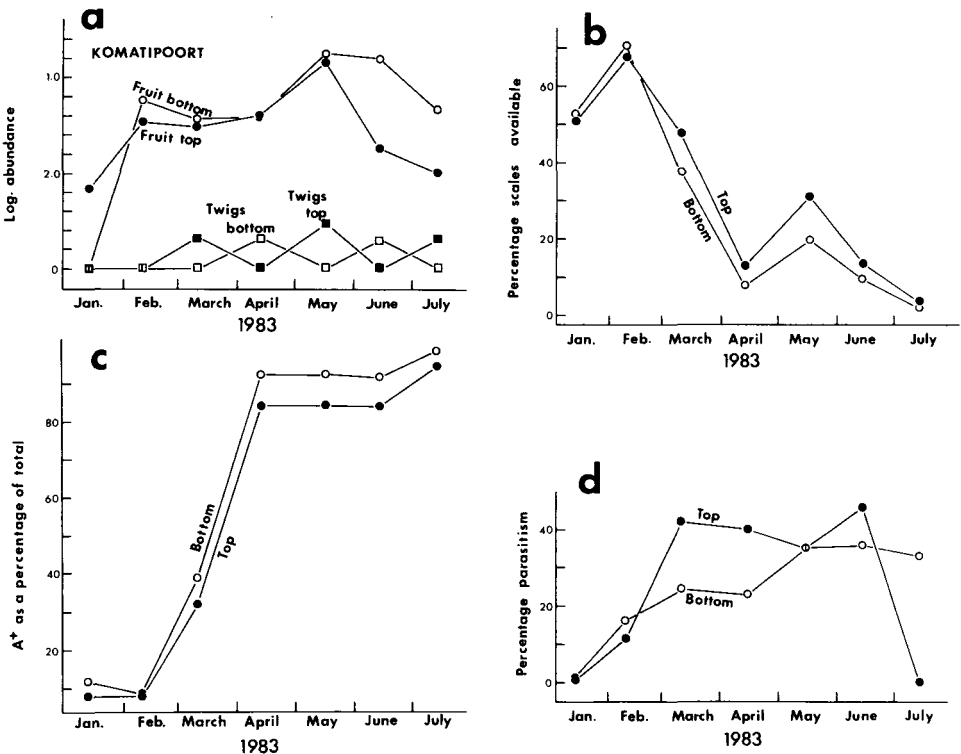


Fig. 4.—Aspects of the relationship between *Aphytis* spp. and *Aonidiella aurantii* on fruit and twigs from the upper and lower parts of citrus trees at the hotter Komatipoort site throughout one growing season; a, abundance of *Aphytis* spp. emerging from *Aonidiella aurantii*; b, percentage of the total living population of *A. aurantii* of the right age for parasitism by *Aphytis* spp.; c, the percentage of reproducing adult females of *Aonidiella aurantii* among the total living population (excluding crawlers); d, percentage parasitism by *Aphytis* spp. of parasitizable living individuals of *Aonidiella aurantii*.

These percentage changes through the season were closely associated with changes in absolute numbers. There was a clear decrease in numbers of living male and female scales on fruit and twigs from April onwards (Fig. 1). Similarly, there was a decline in the absolute number of *Aphytis*, particularly on fruit (Fig. 3a).

The data from Komatipoort (Figs. 2 & 4) do not show a distinct pre-April and April onwards division as did the results from Nelspruit. There was a generally higher level of scales in tree bottoms than in the tops (Fig. 2), the converse of the situation at Nelspruit. On fruit in particular, *Aphytis* numbers reached a peak in February and remained high for more or less the whole season, with a second peak in May (Fig. 4a). The numbers in the tops and bottoms of the trees overall were about the same, although in June and July they were highest at the bottom (Fig. 4a).

In contrast to Nelspruit, at Komatipoort, the age-distribution of *Aonidiella aurantii* in tree tops was similar to that in tree bottoms (Fig. 4b), and further was similar to that in the tops of trees at Nelspruit. From February to April, there was a rapid decline in the percentage of scales available to *Aphytis* (Fig. 4b). At the same time, there was a dramatic shift in the age-distribution of the scale, with a massive depletion of immature instars (excluding crawlers), resulting in a population composed mostly of mature adult females (Fig. 4c). This depletion was caused by both the mortality of immature instars, especially through the activity of *Aphytis* and *R. lophanthae*, and by their maturation to adult females.

During the first part of the decline in the percentage of scales available to *Aphytis* (February–March) (Fig. 4b), percentage parasitism increased in both the tops and the bottoms of trees (Fig. 4d). However, after March, the percentage parasitism levelled off but was generally higher at the tops than at the bottoms (Fig. 4d), despite the fact that *Aphytis* numbers were approximately the same at both heights (Fig. 4a). The apparent drop in percentage parasitism at the top of the trees in July is largely experimental error associated with the small sample size for this last month.

Activity of Aphytis africanus in relation to density

At Nelspruit, parasitism by *A. africanus* was patchy. In March, at the bottom of the trees, correlation between density and arcsin-transformed percentage parasitism of parasitizable scales was positive and significant ($r = 0.402$, $P < 0.02$). However, during this relatively early period of *A. africanus* activity, this correlation was weighted and made significant by the relatively large number of single scales (29.4%). Without these single scales, the correlation was negative and non-significant ($r = -0.00422$, n.s.). During April, the percentage of single scales decreased to 13.3 and the correlation including them was again positive and significant ($r = 0.356$, $P < 0.05$) while without them it was still positive but not significant ($r = 0.288$, n.s.). In May, the situation was similar, with a higher correlation when single scales were included ($r = 0.386$) than when they were not ($r = 0.263$), although neither value was significant at the 5% level. In summary, there was a strong tendency for single scales to escape parasitism. This was emphasized by the fact that for every month from February to July, except May, the percentage parasitism of single scales was zero. In May, it was 37.5%, apparently due to the presence of a peak number of adults of *A. africanus* searching for diminished resources.

Where the density was higher than one parasitizable scale per microscope field, there was generally a slight increase in percentage parasitism with density, but the correlation was not statistically significant. This statistical weakness principally arose out of the patchiness of *A. africanus* activity. During April, for example, this parasitoid showed between 0 and 78.0% parasitism of parasitizable scales where groups of two or more scales were present.

At Komatipoort, both *A. africanus* and *A. melinus* were abundant in the lower parts of the tree canopies (Table II). In March, the correlation between density and arcsin-transformed percentage parasitism of parasitizable scales was positive and significant ($r = 0.481$, $P < 0.02$). This correlation included many zero percentages but no single scales.

In other words, none of the fruit had only one parasitizable scale, but many had several parasitizable scales free of parasitoids. However, the percentage number of fruit with single scales increased from zero to 52.2% in April, 35.7% in May and 65.2% in June. These large percentages involving many zeros made further correlations (for May and June) statistically weak and ecologically uninformative. However, one further trend was clear. In April, the first month in which single scales were recorded, all of them were unparasitized. In May, 20% were parasitized and in June 33.3%. In other words, the diminishing resources as the season progressed put pressure on *Aphytis* spp. to attack more isolated scales.

Throughout the season at both sites there were no significant differences in percentage parasitism of parasitizable scales on fruit from the four quadrants of the tree.

Percentage parasitism by *Comperiella bifasciata*

The *Aphytis* species recorded here only attacked certain of the nymphal stages. On moulting to a young non-reproducing adult (A^-), the scale was susceptible to parasitism by *C. bifasciata*. Although at times this parasitoid was common, it was always heavily hyperparasitized by *Marietta javensis* (Howard). At Nelspruit during February, percentage parasitism (including by parasitoids supporting hyperparasitoids) of living A^- scales was zero, but in March it was 13.1% in tree tops and 4.0% in the bottoms. Later it dropped dramatically, with 0% being recorded both for tops and bottoms in May.

At Komatipoort, events were similar, only they occurred earlier in the season. In February, 1.54% of the A^- adults in tree tops and 11.0% of those in the bottoms were parasitized. In March, the figures were 4.86% in the tops and 7.08% in the bottoms. After March, *C. bifasciata* activity dropped considerably as the percentage of A^- adults decreased in comparison with those at the A^+ stage (Fig. 9). During April, despite the large drop in the abundance of suitable hosts, parasitism by *C. bifasciata* at tree tops was 6.06%, although at the bottoms it had already dropped to zero. In May, the percentage parasitism in both the tops and bottoms was zero.

Seasonal variation in *Comperiella bifasciata* activity

The emergence results clearly show a peak in *C. bifasciata* activity in March and April at Nelspruit (Fig. 5). The higher values recorded in the tops of the trees are a reflection of high scale levels there. There was a high level of hyperparasitism by *M. javensis* on the

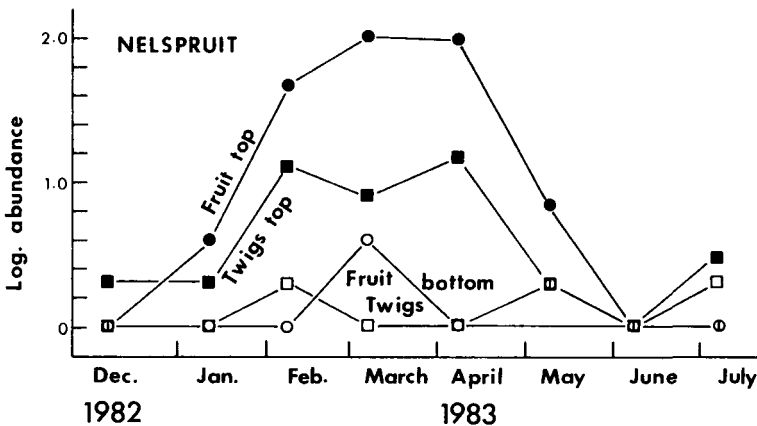


Fig. 5.—Abundance of the primary parasitoid *Comperiella bifasciata* emerging from *Aonidiella aurantii* on fruit and twigs from the upper and lower parts of citrus trees at the cooler Nelspruit site throughout one growing season.

fruit (Fig. 6). Similarly, the fairly high number of *M. javensis* on the twigs at the top is a response to the high number of *C. bifasciata* in that part of the tree.

There was a peak in *C. bifasciata* activity at Komatipoort in February and March (Fig. 7), values for tree tops and bottoms being similar and a reflection of scale levels in those parts (Fig. 2). As at Nelspruit, hyperparasitism on the fruit was extremely high (Fig. 8), but as the numbers of *C. bifasciata* on the twigs were relatively low (Fig. 7), it follows that hyperparasitism on the twigs was also low (Fig. 8).

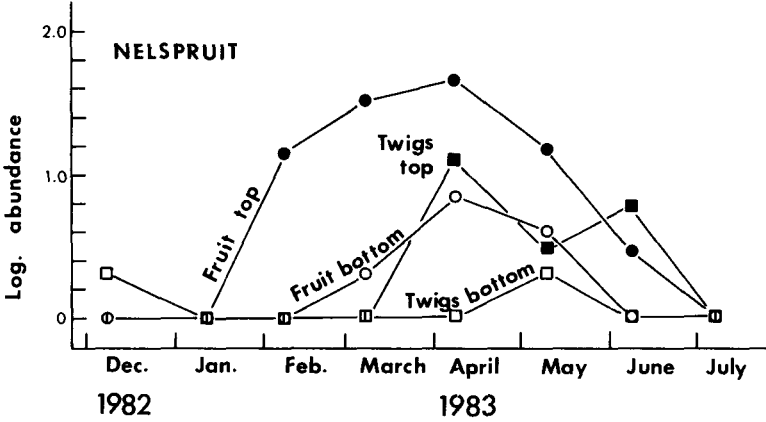


Fig. 6.—Abundance of the hyperparasitoid *Marietta javensis* emerging from *Aonidiella aurantii* on fruit and twigs from the upper and lower parts of citrus trees at the cooler Nelspruit site throughout one growing season.

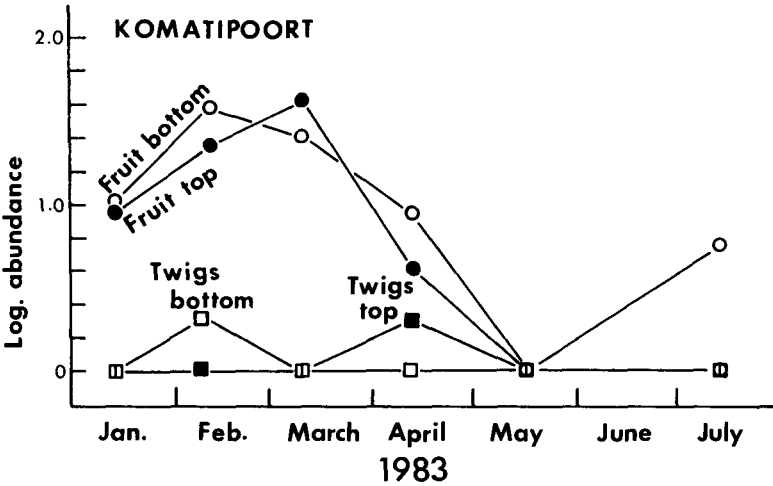


Fig. 7.—Abundance of the primary parasitoid *Comperiella bifasciata* emerging from *Aonidiella aurantii* on fruit and twigs from the upper and lower parts of citrus trees at the hotter Komatipoort site throughout one growing season.

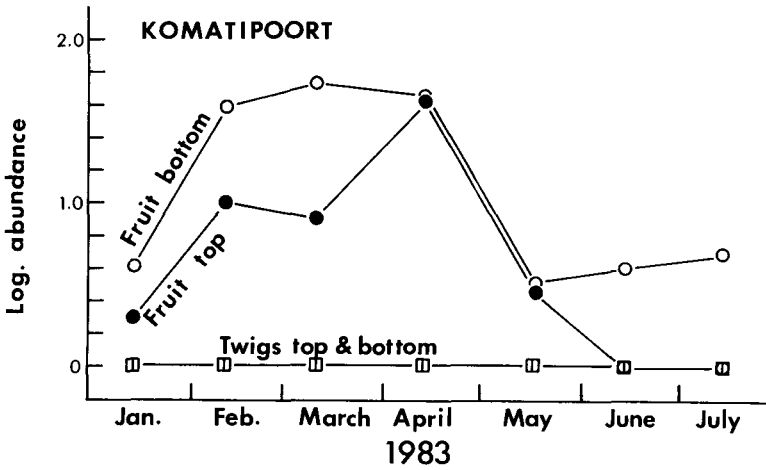


Fig. 8.—Abundance of the hyperparasitoid *Marietta javensis* emerging from *Aonidiella aurantii* on fruit and twigs from the upper and lower parts of citrus trees at the hotter Komatipoort site throughout one growing season.

Discussion

Aonidiella aurantii densities in the fruit and tree quadrants

There were no significant differences in scale density in any of the fruit quadrants of mature fruit taken from the south or east sides of the tree. On the north and west sides of the tree, however, scale levels did vary. On these sides of the tree, the north face had fewer scales than the others. This points to the degree of exposure to sunlight having had some influence and causing higher than average scale mortality. Had pesticide application been mainly responsible, then scale density on this north face on the north side of the tree would have been the same as that on the south face on the south side of the tree. Carroll & Luck (1984) have also recently suggested that the low numbers of *A. aurantii* on the south side of trees in California in the northern hemisphere were the result of exposure to direct sunlight.

When all the quadrants of the mature fruit were combined and the overall scale levels for the four quadrants of the tree compared, west and east supported more scales than the other sides. The reason for this is uncertain, but the triazophos sprays applied for control of thrips (*Scirtothrips aurantii* Faure) early in the season may have been partly responsible, particularly as this product is known to be toxic to immature scales (Nel *et al.*, 1979).

Aonidiella aurantii densities in the tops and bottoms of trees

Differences in the numbers of scales between the tops and bottoms of trees were much clearer than those between quadrants. In addition, these differences were highly variable from one site to another (Figs. 1 and 2). At two of the sites, scale density was much higher in the tree crowns than at the bottom of the trees. Although this is not unusual when the insect is primarily controlled with pesticides (Carman, 1977; Georgala, 1979), the interesting point here is that *Aphytis* spp. did not on their own even out these differentials and suppress *Aonidiella aurantii* in the tree crowns.

Microhabitat preferences of the natural enemies

Although occurring on the same tree, *Aphytis africanus* and *A. melinus* showed slightly different but overlapping microhabitat preferences. At the cooler Nelspruit site, *A.*

africanus was by far the most abundant species, and *A. melinus* was present only occasionally in the tops of the trees. At the hotter Komatipoort site, *A. africanus* was dominant at the beginning of the season, particularly at the bottoms of the trees. Later, *A. melinus* was dominant in the tree tops while in the bottoms *A. melinus* or *A. africanus* was dominant depending on the month.

The other natural enemies of *Aonidiella aurantii* did not show such definite microhabitat preferences. The numbers of *C. bifasciata* and *R. lophanthae* seemed to be associated more with host numbers than with host position. At the geographical level, however, *C. bifasciata* was more heavily hyperparasitized at Komatipoort than at Nelspruit.

In contrast to the major differences in *Aphytis* activity between the tops and bottoms of trees, there was no indication that natural enemy activity was greater or lesser in one or other quadrant within the lower part of the tree.

Changes in age-distribution of Aonidiella aurantii

Catling (1971) and Atkinson (1977, 1981, 1983*b*) invoked weather and climate as being responsible for relatively high scale increase and relatively low natural enemy activity in the lowveld, resulting in poor biological control. The results here additionally show behavioural phenomena as playing a role.

Looking at the life stages of scale relative to time suggests a reason why the natural enemies were unable to bring down the high scale levels. The mature adult female (A^+) is virtually invincible to attack from the existing natural enemy complex. Further, many of the first-generation scale reached maturity before natural enemies were abundant. This early increase in the numbers of adult females resulted in the production of many young in the next generation. This new generation, in contrast, suffered extremely high mortality from natural enemies, which by this time had also built up, but because scales had reached such high numbers early in the season, even a low percentage survival of late generations meant a large number of scales.

Means by which A. aurantii escaped natural enemy attack

The mechanism behind survival of *A. aurantii* to maturity in the face of high natural enemy activity in mid-season is intriguing; where scales were present singly, they remained almost entirely unparasitized or uneaten, but where they were in groups on the fruit, parasitism (and predation) was high.

At Nelspruit, when two or more scales were present within the arbitrary minimum patch size of at least one microscope field, there was no statistically significant density dependence. The statistical weakness arose partly out of the extreme patchiness of natural enemy activity, with percentage parasitism of parasitizable scales ranging from 0 to 78%.

At Komatipoort, no single scales were recorded early in the season and, unlike the situation at Nelspruit, the percentage parasitism did increase with density. Soon after, however, the position changed dramatically, with more than half the samples being of single scales. This change was the direct result of the initial high parasitism and predation leaving behind a patchwork of isolated scales. On maturing, these single scales were responsible for a major shift in age-distribution of the scale population, with the majority of these hosts then being unparasitizable adult females (Fig. 4*c*). Later in the season, this change in host age-distribution appeared to put the parasitoids under pressure for the diminished resources as suggested by the increase in percentage parasitism (Fig. 4*d*).

It is interesting that at Nelspruit the shift in scale age-distribution was more dramatic in the tops than the bottoms of trees (Fig. 3*c*). Indeed, tree tops at Nelspruit showed similar trends and a similar proportion of *Aphytis* species to tree bottoms at Komatipoort, suggesting that the top pruning at the cooler first site was creating a hot microclimate in the crowns similar to that in the tree bottoms at the hotter second site.

Percentage parasitism throughout the season

At Nelspruit, where scale density was much higher in the tree tops than in the bottoms, seasonal variation played an important role. Percentage parasitism of parasitizable scales was highest in the tops early in the season and higher in the bottoms later on. This seemed to arise from tree bottoms early in the season having many single scales on fruit (especially the occasional survivors from the phenthoate plus oil application) and these were rarely parasitized. These then produced groups of offspring later in the season, many individuals of which became parasitized. The situation in the tops of the trees was quite different, with a lower percentage parasitism than in the bottoms later in the season.

At Komatipoort, scale levels were lowest and percentage parasitism highest in the tops of trees (Fig. 4d). The converse was the case in the bottoms. Thus, in general terms at both sites, although there was patchiness of parasitoid activity between groups of scales, there was an overall trend at both sites towards lower parasitism with higher scale levels i.e. a weak inverse density-dependent relationship. This run-away situation would partly explain why the parasitoids did not bring scale density down from a high level to a low one. It also goes some way to explaining why the scale did not become evenly spread over the tree, and why it became increasingly severe in the crowns at Nelspruit.

Implications of the inverse density-dependent relationship

Looking at these results from the applied point of view, they emphasize the importance of bringing the scale density down to a level at which *Aphytis* can regulate the population as it has done in other districts (Bedford, 1968). However, it appears doubtful, in view of the inverse density-dependent relationship recorded at high scale levels, whether the scale, at least in the lowveld, can be kept under permanent biological control by *Aphytis* alone without periodic lowering of scale levels by other means. This emphasizes the point made by Ullyett (1946), Catling (1971) and Atkinson (1981, 1983b), with increasing scientific justification over the years, that it is important to establish a *complex* of natural enemies (particularly new predators) to effect good control.

Conclusions and implications for Aonidiella aurantii management

The existing natural enemies at both sites can to some extent contain *A. aurantii*. However, once the average scale level has become high, the natural enemies do not seem to be able to bring it down. Further, where there is a differential in scale density between the tops and bottoms of the trees, these natural enemies do not even it out. Large numbers of mature adult females at the beginning of the season present a risk for biological control, because they are rarely attacked by natural enemies and can produce large numbers of offspring. The principal aim of an integrated programme hinging on biological control of scale therefore, is to start when this key pest is at a low level. Reduction to this level within the context of integrated control can be achieved with chemical treatments such as narrow-range petroleum oils (Georgala & Stephen, 1983) or with a voracious predator of the adult scale such as *Chilocorus nigritus* (F.) (Samways & Mapp, 1983; Samways, 1984). Although the merits and disadvantages of chemical suppression have been well-assessed, those of *C. nigritus* await further studies.

Acknowledgements

Messrs P. van Dijk (H. L. Hall & Sons) and W. Smith (Transvaalse Suikerkorporasie Bpk. Tenbosch) kindly made sites available. Dr E. Uëckerman named the mites, and Drs P. Newton and M. Georgala made valuable comments on an earlier version of the manuscript.

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(Received 21 August, revised 5 November 1984)

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