ATOLL RESEARCH BULLETIN

No. 291

CHANGES IN THE DISTRIBUTION OF THE COCCID *ICERYA SEYCHELLARUM* WESTW. ON ALDABRA ATOLL IN RELATION TO VEGETATION DENSITY

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Issued By

THE SMITHSONIAN INSTITUTION

Washington, D. C., U.S.A.

May 1985

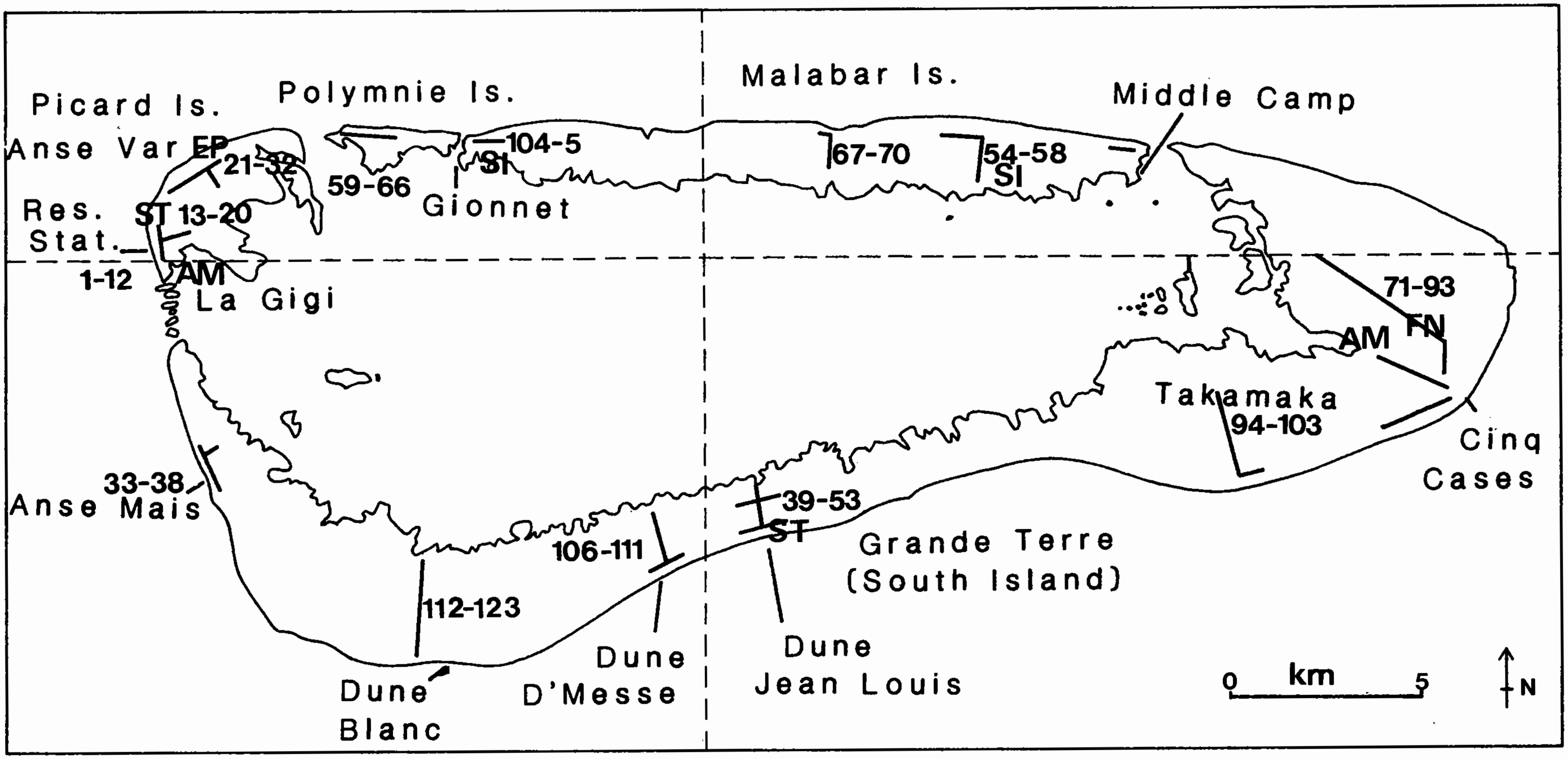

Fig. 1. Aldabra Atoll showing the areas sampled in the 1983 resurvey and the locations of monitoring sites for the species: AM, Avicennia marina, EP, Euphorbia pyrifolia, FN, Ficus nautarum, SI, Sideroxylon inerme, ST, Scaevola taccada. Numbers refer to the number of sampling points.

CHANGES IN THE DISTRIBUTION OF THE COCCID *ICERYA SEYCHELLARUM* WESTW. ON ALDABRA ATOLL IN RELATION TO VEGETATION DENSITY

BY

D. McC. NEWBERY[1] AND M. G. HILL[2]

ABSTRACT

1. The overall abundance of *Icerya seychellarum* Westw. (Margarodidae : Homoptera), on Aldabra Atoll in the Western Indian Ocean, has changed little between 1978 and 1983 but its spatial distribution over the atoll has altered markedly. 2. Several susceptible host tree species showed ten-fold or more higher median infestation levels in the SE than the NW quadrant of the atoll. These differences were not evident in 1978. 3. The results of the 1983 survey are supported by biannual monitoring of five species of host trees from 1980 to 1983. 4. Since 1978 the level of coccid infestation has risen in the SE, where tree mortality is largely density independent, but has remained low in the NW, where tree mortality is more density dependent.

Keywords: Coccids Aldabra Atoll Distribution Hosts Vegetation Density.

INTRODUCTION

Two surveys of the distribution of the coccid, *Icerya seychellarum*, Westw. (Margarodidae : Homoptera), in 1976/77 and in 1978 on Aldabra Atoll, showed an overall low abundance (Hill and Newbery, 1980) compared with the peak infestations of 1975 (Renvoize, 1975). Host tree species differed considerably in their susceptibility to coccids (Hill and Newbery, 1980; Newbery, Hill and Waterman, 1983) but the abundance of coccids on any host species varied insignificantly between different areas of the atoll. Thus, by late 1978, the outbreak which had started c. 1968 (Hill and Newbery, 1982) appeared to have settled down to an even and residual level. In this paper we report the results of a resurvey of the status of *I. seychellarum* on Aldabra in 1983 and monitoring of the coccid on five tree species between 1980 and 1983.

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METHODS

Survey of coccid distribution and abundance

Between July and August 1983, we recorded the abundance of *I. seychellarum* on the woody flora of Aldabra in the areas shown in Figure 1. Apart from the recently-opened long transect in the south-west, these areas were approximately the same as those sampled in the 1976/77 and 1978 surveys by Hill and Newbery (1980).

The woodlands and shrub vegetation were sampled by a plotless method. In each area sampling points were chosen either in a pseudo-random, representative manner, or evenly at intervals of c. 100m along transect lines. At each sampling point the nearest thirty trees were identified and the coccid infestation scored as a composite value for each individual tree and on the same scale used in 1976/77 and 1978, viz: 0, no coccids found after searching; 1, few coccids found after searching; 2, numerous coccids evident without searching; 3, vast numbers of coccids; 4, coccid infestation devastating. Our hundred and twenty-three sampling points were all in 'mixed-scrub' vegetation (Newbery and Hill, 1981; Gibson and Phillipson, 1983) and these were supplemented by observations on all individuals of susceptible species when encountered in walking between sampling points. In this context a susceptible species was one which had a median infestation score of 1.0 or more in the 1976/77 or 1978 surveys. Mangrove, *Pemphis acidula*-dominated, and coastal scrub communities were sampled in a similar but less intensive manner. (Authorities for plant species are included in Table 1.) Time was not available to comprehensively search for rare tree species.

The results of the late 1983 monitoring (referred to below) were added to our sample. Excluding seven uncommon host-tree species, each of which had less than ten individuals, 5137 trees and woody shrubs were sampled from thirty-six species.

Monitoring

In the light of the earlier surveys (Hill and Newbery, 1980) and detailed studies on highly susceptible species (Newbery, 1980a,b,c and Hill, 1980), thirty individuals of each of five heavily infested tree species were randomly selected and tagged along transects in areas of the atoll where they were locally abundant and highly infested in 1980 : *Scaevola sericea* (near the Research Station, Picard Island, and near Dune Jean Louis, Grande Terre); *Euphorbia pyrifolia* (Anse Var, Picard Island); *Ficus nautarum* (Cinq Cases, Grande Terre); *Sideroxylon inerme* (Gionnet and Middle Camps, Malabar Island) and *Avicennia marina* (La Gigi, Picard Island, and Cinq Cases creek, Grande Terre).

Trees were scored for coccid abundance biannually from 1980 to 1983 using the survey scoring scale of 0 to 4. Where an individual tree died between the sampling times the number of replicates were fewer at the time of measurement and these numbers were made up by randomly selecting and tagging new individuals. (E. pyrifolia was not sampled in the first six months of 1980: In one case, S. sericea near Dune Jean Louis, the number of replicate bushes was twenty-three; and in twelve other of the sixty-four species-site-time combinations this number was between twenty-six and twenty-nine.)

RESULTS

Comparison with previous surveys

The median infestation scores of the thirty-six species are shown in Table 1 for the whole atoll and for its four quadrants (Fig. 1). Thirty-two species had median infestation scores greater than nil in either the 1983 survey or one of the 1976/77 or 1978 surveys (Table 1, Hill and Newbery, 1980). Spearman rank correlations between the scores in 1983 and scores in 1976/77, and in 1978, were highly significant ($P < 0.01$, $r=0.773$ and 0.864 respectively), indicating that those species which were highly and lowly infested in 1976/77 and 1978 remained so in 1983.

For the whole atoll the changes in median infestation for these thirty-two species between 1976/77 and 1983 and between 1978 and 1983 were not significant by sign tests (15+, 17- ; 18+, 10- , 4 nil differences respectively, $P > 0.05$). Of the ten most heavily infested species in 1983 (Table 1), between 1976/77 and 1983 five increased and five decreased in infestation and the same occurred between 1978 and 1983.

Variation in infestation across the atoll (1983)

Ficus nautarum, Sideroxylon inerme and Apodytes dimidiata show approximately ten-fold higher mean infestation scores in the SE quadrant than in the NW quadrant, and Avicennia marina shows a sixteen-fold difference in the same direction. For Pemphis acidula the infestation in the SE is about sixty times that in the NW, though it must be noted that this is coastal and mixed-scrub P. acidula and not the main P. acidula dominated vegetation zone in which individuals are rarely infested. Scaevola sericea and Polysphaeria multiflora differed little in infestation between the SE and NW quadrants : many other species in Table 1 had either sample sizes that were too small for analysis or median infestations that were too low to make comparisons across the atoll. The NE, like the NW, quadrant had comparatively low infestation scores, even on the generally more susceptible species; but in the SW quadrant (most of which was not accessible for sampling in 1976/77 and 1978) Sideroxylon inerme, Scaevola sericea and Polysphaeria multiflora had notably high and similar levels of infestation to those the SE quadrant.

Clearly, in the SE quadrant the susceptible host species support higher median infestation levels than in the NW quadrant with the SW and NE quadrants being intermediate. Comparing the median infestation scores in the NW quadrant (1983) with those over the whole atoll in

1976/77, and in 1978, shows no significant change ($P > 0.05$) by sign tests (8+, 9-, 2 nil ; 7+, 11-, 1 nil differences, respectively). Similarily, for the SE quadrant the sign tests show an overall rise, but this is significant at only $P \leq 0.1$ (10+, 4-, 1 nil differences in both cases).

Differences in weighted abundance of coccids across the atoll

In 1976/77 Newbery and Hill (1981) recorded the percentage cover abundance of trees and woody shrubs in sixty-five, mostly 20 x 20 m plots, during the course of that coccid survey. The 1983 coccid data were collected from the same areas (comparing Fig. 1 in Hill and Newbery, 1980 with Fig. 1 here) and there has been little visible change in the vegetation and its composition in that time interval (excepting unusually damaged vegetation inland of Dune Jean Louis - Newbery personal observation 1983). Those vegetation data may be used to calculate weighted vegetation coccid scores for the 'mixed-scrub' areas in the NW and SE quadrants. The NE was less intensively sampled for coccids, both earlier and in 1983, and the flora of the SW has, in its widest part, only been recently investigated (C. Peet and D. Cowx unpublished) and not with comparable plot records. The thirty-three commonest species were used : fourteen rarer (less than 1% cover) and very infrequently infested species were excluded. The mean percentage cover abundance for each species was calculated for thirteen NW quadrant plots and twenty-eight SE quadrant plots. (Of these latter, one was of coastal *Scaevola sericea* dominated scrub and two others lay in the *Thepesia populneoides* - *Lumnitzera racemosa* association inland of Cinq Cases creek). The coccid score for each host species in the two quadrants was weighted by the hosts' mean cover abundance and the overall weighted mean found. For the NW quadrant this mean (still on the 0 to 4 coccid scoring scale) was 0.120 and in the SE quadrant was 0.363 - a three-fold difference across the atoll.

Changes in infestation over four years

Coccid infestations on monitored tree species generally continued to decline on Aldabra between 1980 and 1983, except for the SE monitored *Avicennia marina* and *Ficus nautarum* (Fig. 2) which appeared to increase. Infestations have been high on *Scaevola sericea*, *Avicennia marina* and *Ficus nautarum* to a similar level shown in the 1976/77, 1978 and 1983 surveys. The most obvious decline from moderate infestations in 1980 to near zero levels in 1983 were for *Sideroxylon inerme* (Malabar Island) and *Avicennia marina* (Picard Island).

DISCUSSION

The two previous surveys of 1976/77 and 1978 were conducted in Aldabra's wet season whilst access to the atoll was only possible at the end of the wet season and the start of the dry season in 1983. It is unlikely that differences between the 1983 and previous results were due to meteorological changes because, apart from species like

Euphorbia pyrifolia which are deciduous (Newbery, 1980b), phenology was not a significant factor in host tree susceptibility (Newbery, Hill and Waterman, 1983) and monitoring over the four years (Fig. 2) did not show periodic changes in infestation levels from dry to wet season. Overall, there has been little qualitative change (in the terms of numbers of host species increasing and decreasing) in the status of I. seychellarum on Aldabra between 1976 and 1983, and this is supported by the monitoring results. Within the atoll there have developed marked differences between the NW and SE quadrants with indications of serious local increases in the SE between 1976 and 1983.

Aldabra has become drier in recent years. Stoddart (1984) has analysed eight years of atoll rainfall patterns based on a rain-gauge circuit of thirteen stations around the atoll (1974-1981). Grouping the yearly total rainfall results for stations within each of the four quadrants (and excluding that for Ile Esprit) for the years 1976 to 1981, the NW quadrant decreased by 41% from 1695 mm to 999 mm. Similarily, for the NE, SE and SW quadrants respectively the changes were: 1209 to 798 (34%); 1229 to 856 (30%); and 1273 to 855 (33%). The SE is consistently drier than the NW, though suffered a slightly smaller decrease in rainfall than the NW between 1976 and 1981.

It seems unlikely that the infestation in the NW was lower because an agent of biological control has taken effect in these recent years. In 1983 no coccinellid beetles were seen and in 1976-1978 Hill and Blackmore (1980) found only a few beetles after searching. Parasites were not found in 1976-1978 and in 1983 there was no evidence of dead colonies which could have been a result of these or of a pathogen.

There are large differences in habitat between the NW and SE quadrants of the atoll. In geomorphology, the NW has a rough, dissected terrain of pavé and champignon coral whilst in the SE the predominant form is flat platin limestone (Stoddart et al., 1971) except for the areas just inland of the south coast. As a consequence soils fill wide shallow basins in the SE whereas in the NE trees are rooted in much smaller, often deeper pockets (Trudgill, 1979a,b). The vegetation in the NW is a species-rich closed canopy (average percentage cover of woody species 131%, Newbery and Hill, 1981) compared with the relatively species-poor and more open (85% cover) canopy in the SW (see also Hnatiuk and Merton, 1979a,b and Gibson and Phillipson, 1983). The vegetation in the SE is more exposed than in the NW to SE trade winds during the dry season (Hnatiuk, 1979). These factors suggest that decreased rainfall will be more deleterious to the vegetation in the SE than in the NW, and greater water stress may, in part, explain the higher levels of coccid investation in the SE (Newbery, 1980a,c).

Against this hypothesis is the observation that the mangrove Avicennia marina will not be short of water in dry season yet this species shows one of the greatest differences in infestation between the NW and SE quadrants. Newbery (1980a) has suggested that one of the controlling factors of infestation on A. marina is the build-up of excreted salt on the younger leaves and therefore frequent rain may keep leaves more receptive to coccid settlement. Possibly increased immigration onto A. marina from other stressed plants led to high levels in the SE.

An alternative, but not isolated, hypothesis follows from Hill and Newbery (1980). The peak infestation levels in 1975 (Renvoize, 1975) were at levels far greater than those we recorded in 1976/77 and 1978 and may have caused the death of some susceptible trees (Newbery 1980b,c). These deaths would have thinned the vegetation and left young, more resilient, individuals. Could this have happened faster in the NW than in the SE? In the SE the trees are more widely spaced and mortality is probably density independent in the main due to environmental factors (Stoddart and Wright, 1967) and to grazing (feral goats, Gould, 1979; and tortoises, Merton, Bourn and Hnatiuk, 1976) which predominates in the SE. In contrast, tree mortality in the denser luxuriant vegetation of the NW is likely to be more density dependent.

In the NW there is ample evidence of tree regeneration (Newbery pers. obs.), whereas in the SE the grazers reduce seedling survival and hence regeneration, especially in the areas where grazers and coccids are both abundant. Removal of phloem sap by coccids in dense vegetation will mean that an infested, and therefore weakened, tree (Newbery 1980b,c) is less able to compete with its non-infested neighbours and would be rapidly thinned from the vegetation. Where there is sufficient rainfall, trees could maintain a rapid leaf turnover rate leading to high rates of leaf mortality for a sedentary stylet feeder such as I. seychellarum, (Hill, 1980). Conversely, in the SE the same species, less affected by tree-tree competition, although debilitated by coccids, would be expected to survive longer and to either have a slower leaf turnover rate or become deciduous as a result of the drier environment.

Evidence from several species supports this role of vegetation density in the population regulation of I. seychellarum:

1. The highly infested fig trees (Ficus nautarum) in the SE are large, imposing trees whilst in the NW they tend to be smaller, growing in amongst other shrub and tree species. Similarily, the heavily infested Guettarda speciosa trees in the SE are well separated from neighbours and therefore probably suffer less competition as a result. Apodytes dimidiata, commonly infested in the SE, does grow in small clumps of trees and shrubs though not infrequently as separated individuals. Lastly, Avicennia marina stands sampled at La Gigi, Picard Island (Newbery, 1980a) and at Cinq Case creek are structurally different : The NW site shows colonization on a sand bar with young growth and competition, whereas the trees in the SE are larger and more spaced in coral pockets at the upper limit of the tide and where the zone of brackish pools begins.

2. Species such as Scaevola sericea that tend to grow as monospecific stands of similar density in the NW and SE, suffer intraspecific competition between similarly infested individuals and showed little difference in infestation levels between these quadrants (Table 1).

Polysphaeria multiflora is a small tree species of dense mixed-scrub and woodland over most of the atoll (Newbery and Hill, 1981; Gibson and Phillipson, 1983) and, rarely being found as an isolated individual, also showed similar infestation levels in the NW and SE.

3. Lumnitzera racemosa and Thespesia populneoides do not afford a NW - SE comparison as they form a special community type only in the SE. Calophyllum inophyllum dominates an isolated grove in the SE, and Casuarina equisetifolia occurs in the NW and NE. However, for T. populneoides (much less so L. racemosa which lines brackish pools), it was common to find well spaced individuals which were frequently heavily infested (Table 1).

4. Pemphis acidula mainly occurs as an almost monospecific band of vegetation around the atoll inland of the lagoon mangroves (Gibson and Phillipson, 1983), and there it is very lightly infested. In the sparser vegetation along the SE coast it had moderate infestation levels. Sideroxylon inerme provides an interesting case, because it also had higher infestation levels in the SE than in the NW. In the NW this species is commonly found in either dense P. acidula stands or in mixed-scrub, whereas in the SE it occurs as isolated trees.

Our findings and hypothesis illustrate an important ecological principle. This new immigrant insect to the island ecosystem of Aldabra is still settling into its fundamental niche (MacArthur & Wilson, 1967; Pianka, 1978). The extent to which this niche is developed differs in different vegetation types. In the parts of the atoll (NW) where the vegetation appears to be near equilibrium we suggest that the original outbreak has been dampened to a residual level by a process of negative feedback (thinning and the capacity for vegetation regrowth) whereas in the non-equilibrium parts (SE) which are subject to stronger environmental stresses enforcing the effects of increasing large herbivore pressures on the vegetation, a recent positive feedback has occurred in the form of a small upward oscillation in coccid abundance. On this basis, we predict that coccid abundance will fall back to a residual level in the SE once the susceptible host trees have all died out. And, since the regeneration of these host species is limited in the SE, this residual level may well be lower than that in NW, not precluding the possibility that in a few decades present young individuals of susceptible species will have aged and become more infested in the NW.

ACKNOWLEDGMENT

We thank past wardens of Aldabra, C. Peet, J. Stevenson, and R. Pimm for recording monitoring data; the Carnegie Trust for the Universities of Scotland for travel funds (for D.McC.N); the Royal Society and the Seychelles Islands Foundation for permission to revisit the atoll; and D. R. Stoddart and L. U. Mole for encouragement in all matters Aldabran.

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Table 1 Median infestation scores of *Icerya seychellarum* on the tree flora of Aldabra Atoll in 1983. (n is the sample size)

	QUADRANT								WHOLE ATOLL	
	NW	n	SW	n	NE	n	SE	n		
Lumnitzera racemosa Willd. var. *racemosa*	--	0	--	0	--	0	2.41	59	2.41	59
Thespesia populneoides (Roxb.) Kostel.	--	1	--	0	--	0	1.85	169	1.85	170
Ficus nautarum Baker	0.32	18	--	3	0.06	19	3.00	58	1.65	98
Avicennia marina (Forsk.) Vierh.	0.11	29	--	0	--	0	1.61	59	1.06	88
Allophyllus aldabricus Radlk.	0.97	50	--	2	--	0	--	3	1.03	55
Casuarina equisetifolia L.	1.13	94	--	0	0.92	66	--	0	1.03	160
Sideroxylon inerme L. ssp. *cryptophlebia* (Baker) Hemsley	0.25	145	1.68	215	0.54	116	2.50	17	0.90	493
Scaevola sericea Vahl	0.72	46	2.50	8	0.04	25	0.90	121	0.74	200
Calophyllum inophyllum L. var. *takamaka* Fosb.	--	0	--	0	--	0	0.70	14	0.70	14
Guettarda speciosa L.	--	0	0.73	68	--	4	1.17	116	0.68	188
Euphorbia pyrifolia Lam.	0.59	51	--	3	--	0	0.00	8	0.50	62
Ficus reflexa Thunb.	0.83	14	--	1	0.23	16	--	1	0.44	32
Azima tetracantha Lam.	0.50	31	0.07	8	--	5	--	2	0.38	46
Dichrostachys microcephala Renvoize	0.38	42	--	0	--	0	--	0	0.38	42
Polysphaeria multiflora Hiern.	0.31	210	0.62	226	0.00	70	0.44	345	0.36	851
Ficus avi-avi Bl.	0.50	8	--	2	0.30	34	--	0	0.35	44
Pemphis acidula Forst.	0.02	22	--	5	0.00	8	1.21	38	0.27	73
Apodytes dimidiata E. Mey. ex Arn.	0.04	39	0.04	71	0.06	20	0.40	267	0.24	397
Maytenus senegalensis (Lam.) Exell	0.02	106	0.03	110	--	2	0.01	163	0.18	381
Erythoxylon acranthum Hemsl.	0.11	22	--	1	--	3	--	5	0.08	31
Clerodendrum glabrum E. Mey. var. *minutiflorum* (Bak.) Fosb.	0.00	10	--	5	--	0	--	3	0.06	18
Flacourtia ramontchii L'Hér. var. *renvoizei* Fosb.	0.00	12	0.05	32	--	3	0.07	42	0.04	89
Tarenna tricantha (Bak.) Brem.	0.04	26	0.00	16	0.00	8	0.03	54	0.02	104

Footing to Table 1.

Species with infestation of 0.01 (n) : *Dracaena reflexa* Lam. var. *angustifolia* Baker (42), *Jasminum elegans* Knobl. (36), *Mystroxylon aethiopicum* (Thunb.) Loes (398), *Tricalysia sonderana* Hiern. (68), *Tarenna supra-axillaris* (Hemsl.) Bremek (168).

Species with infestation of 0.00 : *Acalypha claoxyloides* Hutch. (91) Brong.(33) *Canthum bibracteatum* (Bak.) Hiern. (93), *Colubrina asiatica* (L.) Brong.(33), *Cordia subcordata* Lam. (14), *Ochna ciliaris* Lam. (373), *Tournefortia argentea* L.f. (15), *Terminalia boivinii* Tul. (71), *Tarenna verdcourtiana* Fosb. (40).

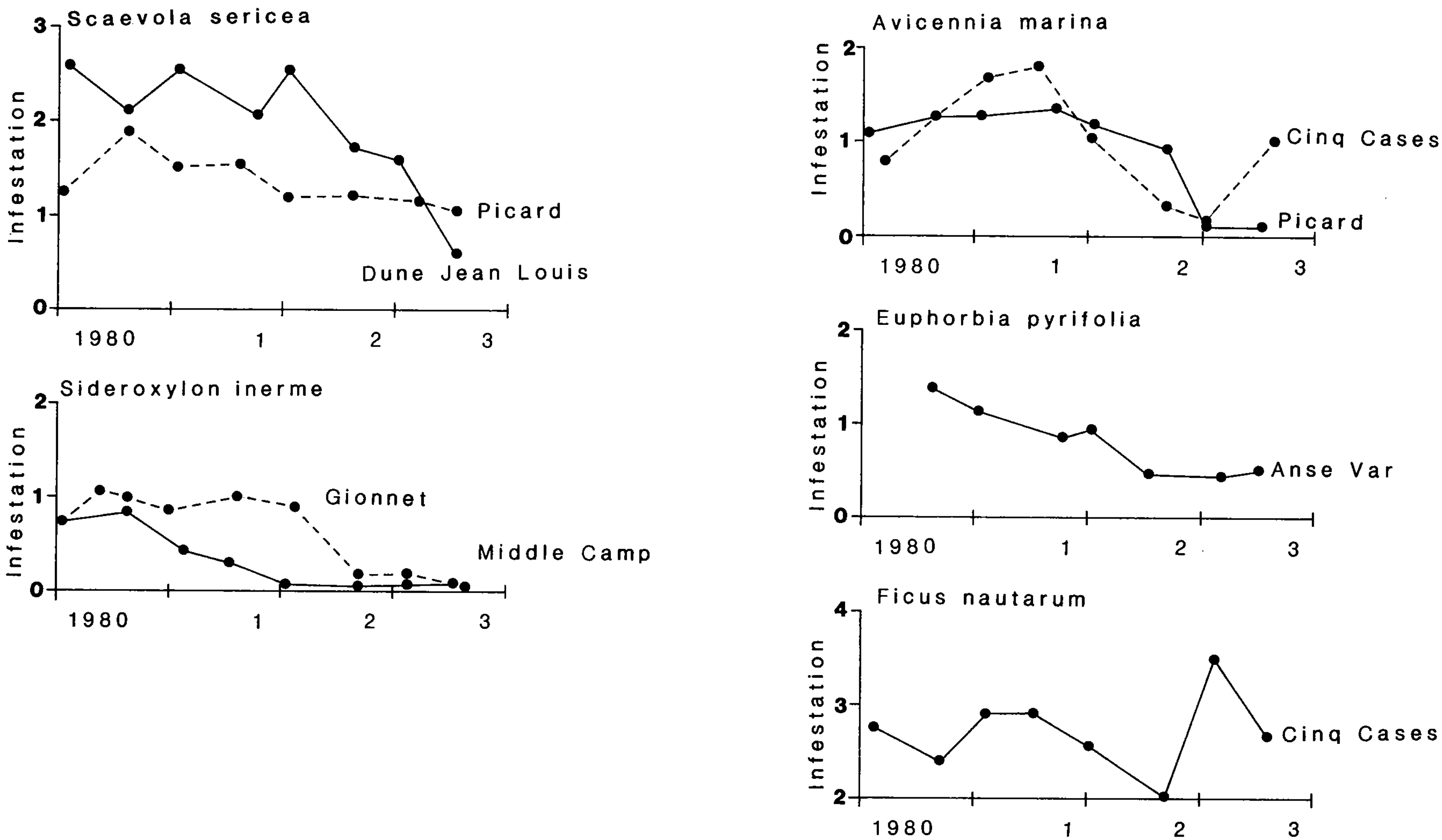

Fig. 2. The change in median coccid infestation on five susceptible species at eight locations on Aldabra Atoll monitored biannually, 1980-1983.