THE ECOLOGY AND CONTROL OF

OPUNTIA AURANTIACA IN SOUTH AFRICA IN

RELATION TO THE COCHINEAL INSECT

DACTYLOPIUS AUSTRINUS


BY

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CONTENTS

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# 1. RESUME

The cochineal insect Dactylopius austrinus De Lotto, which was released on
jointed cactus, Opuntia aurantiaca Lindley, in South Africa in 1932, failed
to bring the weed under an acceptable level of control in spite of the
encouraging results during the first few years after release. The reasons
for this apparent failure were never clearly understood. In 1957 the State
embarked on an intensive herbicidal control programme which is still in
force today. This sustained and expensive programme has undoubtedly
reduced the density of the weed in most areas but has failed to solve the
problem and the plant continues to expand its range. The biological control
of O. aurantiaca in South Africa has been fundamentally influenced by this
chemical control campaign. The relationship between chemical and biological
control methods is reported in this study.

One primary aim, however, was to evaluate the effectiveness of D. austrinus
as a biological control agent against O. aurantiaca. A prerequisite of the
study was an understanding of the population dynamics of the host plant.
Consequently considerable emphasis is placed on sampling of O. aurantiaca
and D. austrinus populations.

Surveys of cohorts consisting of plants in randomly selected permanent
transects gave best estimates of jointed cactus and cochineal populations.
These surveys showed that the distribution of O. aurantiaca in the veld is
highly aggregated and all population samples conformed to the negative
binomial distribution. This has important consequences for both chemical
and biological control.

Firstly, efficiency of herbicidal spot spraying of jointed cactus is highly
correlated with the aggregation of the target plant, and because the
distribution of the cochineal is also correlated with the aggregation level
of its host, spraying eliminates cochineal from infestations. This explains
the low cochineal population levels in herbicidally-treated infestations of
jointed cactus in the eastern Cape.

Secondly, cochineal population increases remain low in "post-spray" infesta-
tions which consist of evenly dispersed small plants and isolated cladodes.
The increase of cochineal in these "endemic populations" was low until the
jointed cactus infestations become dense and aggregated, when again there is

a high correlation between cochineal abundance and aggregation of the weed. Under favourable conditions, and provided the jointed cactus infestation is dense, this may lead to the "epidemic level" where the relationship between host plant density, cochineal colonization rate and the aggregation level of the weed becomes obscure. Few plants escape cochineal attack under "epidemic" conditions, but because of the intensive chemical spraying of jointed cactus this seldom eventuates.

There is a high mortality of isolated cladodes and small plants in all jointed cactus populations. The key-mortality factor, however, is abiotic, with desiccation of small plants and isolated cladodes during hot and dry summer periods the main contributor to this mortality. Mortality caused by D. austrinus became significant only during rare "epidemic" phases.

In essence, D. austrinus was found to be only partially successful as a biological control agent of jointed cactus. Besides herbicides and desiccation of the host plant other factors such as poor dispersal and inadequate colonization limit the effectiveness of D. austrinus. The latter part of this thesis therefore deals with these factors and also reports on methods to improve the impact of this insect on jointed cactus.

## 2. INTRODUCTION

A comprehensive review on the origin, introduction and biological control of
Opuntia aurantiaca Lindley (fig. 1) in South Africa is given by Moran and
Annecke (1979). To provide the reader with a background to this study, an
account is given here on (i) the plant, (ii) its prime natural insect enemy,
Dactylopius austrinus De Lotto, (iii) the history of control, particularly
of biological control and (iv) on the efficiency of control measures in
South Africa.



Fig. 1.    Opuntia aurantiaca.    The fruit is indicated by an arrow.

The Jointed Cactus, Opuntia aurantiaca

Jointed cactus is an inconspicuous, perennial succulent which seldom exceeds
0,5m in height in open veld (fig. 2). The plant consists of up to 100 or
more spiny elongated fleshy joints or cladodes. Each cladode is 5 to 20 cm
long, 1 to 3 cm wide and contains numerous 1 to 3 cm long, barbed spines
(fig. 3). Young cladodes are slightly flattened and have a bright green
colour while older cladodes become cylindrical with a corky surface. Rooted
cladodes from which plants originate may become buried and develop into a
tuber which functions as a storage organ (Zimmermann & van de Venter 1981).
The length of the cladodes is much influenced by habitat and climate.

Fig. 2.    Heavy infestation of O. aurantiaca in False Karroid Broken
           veld.

The spines, and the minute barbed glochids at the base of the spines, arise
in groups from areoles.    The areole is the preferred feeding site of
D. austrinus, possibly because of better accessibility to vascular tissue
near the surface (B Whiting, pers. comm.).

The plant flowers between November and January.    The flowers are bright
yellow, not orange as the name implies   (see Moran et al. 1976).    Small
green to reddish club-like fruits are formed (fig. 1) containing infertile
and aborted seeds.    Archibald (1936) reported 99,95% seed sterility.
Approximately 1% of the fruit is large and swollen containing many large
but empty seeds.    Jointed cactus propagates exclusively by vegetative means.
Cladodes become easily detached from the plant, especially during periods of
drought and during winter.    Cladodes are also disseminated by water and
adhere to stock, wild animals and vehicles and are thus spread over large
distances.    Remote infestations often originate from cultivation in pots
and rockeries from where cladodes invariably find their way into the
surrounding veld (Serfontein 1961).    Most of the detached cladodes however,
fall and root in the vicinity of the mother plant (fig. 1 ).

O. aurantiaca is native to East Argentina and Uruguay where it is found in
small numbers along the riverrine bush of the Parana and Uruguay Rivers

(Moran et al. 1976). Although the origin of the type specimen was Chile and the colour of its flower was orange, this is in error (Moran et al. 1976; Moran & Annecke 1979). It has been suggested that the plant could be of hybrid origin based on seed sterility, pollen morphology and plant morphology (Arnold 1977). This theory is now generally accepted (Moran & Annecke 1979) and O. salmiana is thought to be one of the parents. Sterility, however, is very common among similar low growing Platyopuntiae e.g. in O. discolor, O. tayapayensis, O. pascoensis, O. pestifer, O. curassavica and O. pubescens and this suggests that O. aurantiaca may not necessarily be a recent hybrid. Three forms of O. aurantiaca are distinguished in South America but only one of these is present in South Africa. This form has 2n = 44 chromosomes (Arnold 1977).
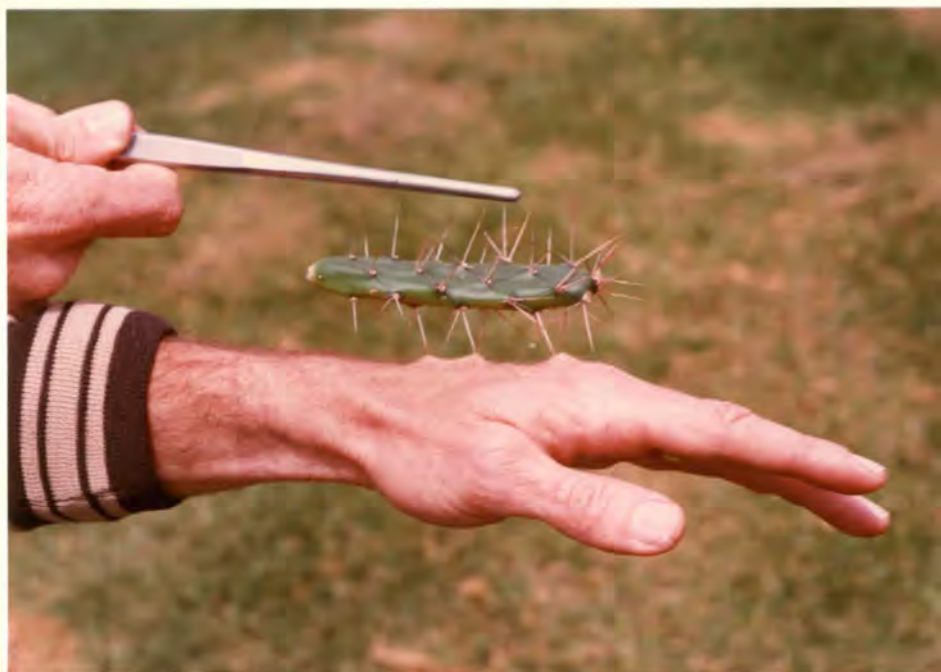


Fig. 3.    Jointed cactus cladode.  The spines are barbed.

Moran et al (1976) and Moran and Annecke (1979) give a detailed account of how the plant could have arrived in South Africa (Cape Town) in 1843, via England. The plant was then carried to the East Cape by travellers, collectors and missionaries who planted it as an ornamental shrub (Phillips 1938; Pettey 1948; Serfontein 1961; Moran & Annecke 1979).

Today O. aurantiaca is South Africa's most important and costly weed (Serfontein 1961; Slabber 1964; Neser & Annecke 1973; Zimmermann & van de Venter 1981). Infestations limit the grazing potential of pastures because

nutritive plants are replaced or prevented from being fully utilized. Grazing animals are injured by spiny cladodes that can also become lodged in hair and wool, resulting in inconvenience to handlers and degrading of wool. O. aurantiaca is also a serious problem plant in Australia where it is known as tiger pear (Mann 1970; Anon. 1980; Hosking & Deighton 1981a) and there are many parallels in attempts by the two countries at control of the weed.

## The Cochineal Insect Dactylopius austrinus

This insect, one of nine species in the genus, (De Lotto 1974), was previously referred to as D. sp. near confusus (Dodd 1940; Pettey 1948; Mann 1969, 1970; Neser & Annecke 1973), and as species 'J' by Karny (1972). It is native to the dry areas of central, north and western Argentina where it has been recorded from other low growing opuntias namely O. retrorsa, O. discolor, O. canina, O. kiska-loro, O. palmadora (from Pernambuco, Brazil), O. sulphurea, O. brunnescens and Opuntia (Austrocylindropuntia) salmiana (Zimmermann et al. 1979). The record on O. russellii (Mann 1969) mentioned by Gunn (1979) probably referred to a similar species now known as D. zimmermanni De Lotto which was found on Tephrocactus ovatus. Its original native host is unknown, but according to H E Erb (pers. comm.) it is most likely to be O. utkilio, O. brunnescens or O. vulpina from Catamarca because these species agree more or less with Dodd's (1940) description of "an unidentified prickly-pear with rather long narrow tuberculate joints, possibly a relation of O. sulphurea". In South America, D. austrinus does not occur on O. aurantiaca because the insect and plant are allopatric.

The entire genetic stock of D. austrinus in South Africa originated from four or five females that were intercepted at Cape Town en route to Australia (Smit 1964). D. austrinus under natural (field) conditions in South Africa, will not develop on any plants other than on O. aurantiaca.

The females of D. austrinus are covered by a characteristic woolly substance, consisting of compacted wax filaments (fig. 4). Females are ovoviviparous and lay small (0,5 mm long) eggs that hatch in less than a minute or up to several hours after laying (Gunn 1979). Newly emerged first instar crawlers can be sexed by the distribution and length of the wax filaments on the body which are an adaptation for wind dispersal (Gunn 1978, 1979). First instar crawlers are long-lived (10 days) thereby enhancing their chances of locating new hosts. Gunn (1978, 1979) gave detailed accounts of dispersal behaviours of the crawlers. He suggested that the small size and low height of O. aurantiaca makes it a small target for wind blown crawlers and limits effective colonization.

Moran and Cobby (1979) and Gunn (1979) give a detailed account of the life history and biology of D. austrinus. Fecundity averaged 1 145 crawlers per female with a ratio of 2 males:1 female. After the female has located a suitable feeding spot it inserts the mouthparts and begins to feed and becomes sedentary. There are three instars in the female, and mating occurs shortly after moulting to the third instar. The life span of a cochineal female is about 106 days under summer conditions (Gunn 1979 from Moran & Cobby 1979).

The male crawler settles near the protective wax covering of the parent female where it feeds intermittently : it is not well adapted for dispersal (Gunn 1979). The male cochineal forms a cocoon in the second instar and there are three further moults inside the cocoon. The winged adult male lives for three days during which period it mates once. The entire male life cycle lasts about 40 days under summer conditions.

There are no discrete generations in the field and all instars can be found at any time.

Presumably salivary toxins cause the death of cladodes and plants (Pettey 1948; Mann 1969; Gunn 1979; Moran 1981). Feeding sites become swollen and discoloured whereafter the cladode shrivels and dies. These toxins are also produced by other cochineals used for the biological control of other cacti in South Africa e.g. D. opuntiae, D. ceylonicus and D. tomentosus (Pettey 1948; Karny 1972; Neser & Annecke 1973) but must be lacking from D. coccus which is the commercially cultivated species on O. ficus-indica and Nopalea sp. because cladodes can support very dense infestations without being harmed.

No parasitoids have been reared from any of the known cochineal species (Mann 1969; Goeden 1967; Zimmermann et al. 1979). It is possible that carminic acid which is an anthraquinone (Baranyovits 1978) and which gives the characteristic red colour to the body contents, functions as a deterrent to ants (Eisner et al. 1980) and possibly also to parasitoids (Moran 1980).

Cactoblastis cactorum (Berg) is an additional but insignificant biological control agent on jointed cactus in South Africa. Its occurrence on jointed cactus is sporadic and only deserves passing mention in this thesis.

Fig. 4. Dactylopius austrinus on jointed cactus cladodes.

History of Control in South Africa

Jointed cactus was possibly first planted in the eastern Cape and Karoo regions between 1850 and 1860 (Phillips 1938) and a schematic representation of the history of control of the weed is given in fig. 5.

First mention of control was made by MacDonald (1892) when plants were collected and burnt by some landowners. Since 1928 control of jointed cactus became compulsory and control was then partly the responsibility of local authorities. It was with the passing of the Weeds Act No 52 of 1934 that the responsibility of control was completely taken over by the State Department of Agriculture. From 1934 to 1938 jointed cactus was controlled by labourers using mechanical control methods and spraying with an inorganic arsenical herbicide. According to Slabber (1964) the years 1934 to 1938 saw much activity but little real progress.
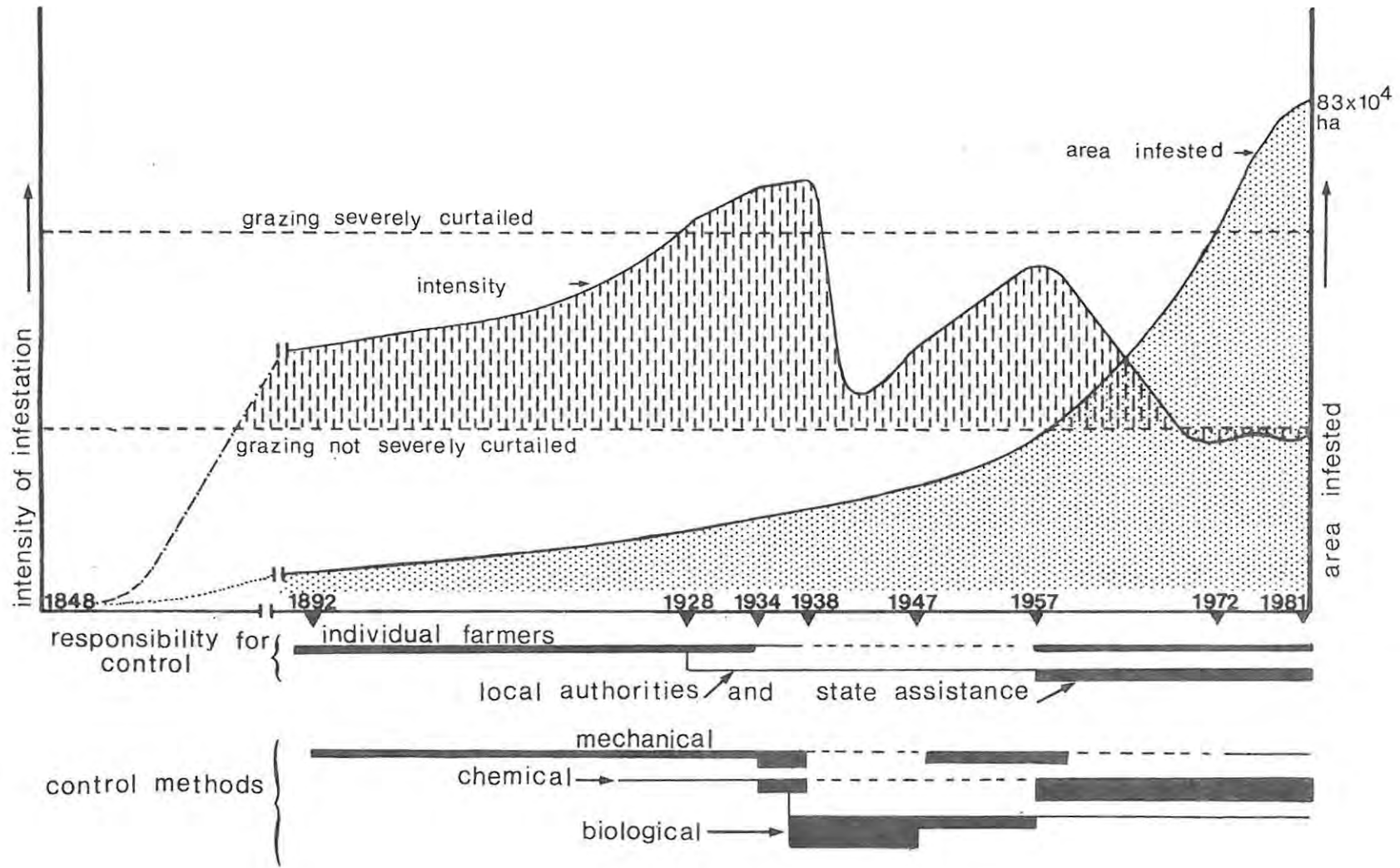
Fig. 5. Schematic representation of the history of jointed cactus control in South Africa.

A crisis was reached in the early 1920's where in some areas jointed cactus infestations were so heavy (fig. 6 ) that grazing by stock was completely inhibited.



Fig. 6.    Veld completely invaded by O. aurantiaca preventing any form
           of grazing.  These dense infestations have been cleared
           chemically.   (Photo from Slabber 1964).

Real progress, however, was recorded 12 to 18 months after releases of the first cochineal insects (D. austrinus) in 1935 (Pettey 1948).  It was in view of these first spectacular collapses of dense infestations of jointed cactus that the Department decided to discontinue the expensive mechanical and chemical control methods and to rely fully on biological control. Cochineal was manually distributed on jointed cactus cladodes throughout the East Cape and Karoo from 1938 to 1946 (Pettey 1948).

After the first successes with cochineal insects, extensive regrowth from surviving plants (see fig. 7 ) alarmed Departmental officials.  In many cases insufficient numbers or none of the cochineal insects survived and were consequently unable to cope with the cactus regrowth.  Redistribution of cochineal insects to the healthy regrowth was not carried out at that crucial time, and mechanical and chemical control methods did not follow on biological control as advocated by Petty (1948).  It is of course open to debate whether such practice would have improved the present situation in any way.

Fig. 7.     Regrowth from a jointed cactus clump which was almost
            killed by D. austrinus attack.

It was, however, generally accepted (Serfontein 1961; Slabber 1964) that
biological control had failed and mechanical control was then reintroduced
from 1947.   Unfortunately little quantitative data or any other pre- and
post-release reports from this important phase in the biological control of
jointed cactus are available.

Large areas were cleared again mechanically from 1947 to 1957.   A new phase
in the increasing efforts to control jointed cactus commenced in 1957 when
2,4,5-T in paraffin was introduced as a herbicide spray.   The general
practice today, as it was in the past, is that the herbicide is issued free
to the landowner as a ready mixed solution.   The landowner must then apply
it at his own expense as a spot spray (fig. 27 ).   In 1972, however, 2,4,5-T
was replaced with the iso-octyl ester of picloram and this is now (1981)
replaced with water-based MSMA (Zimmermann et al. 1981).

Efficiency of Control

Figure 5 indicates how the intensity of the jointed cactus infestations could
have been affected by the different control measures applied since 1892.
The only significant impact on infestations was caused by D. austrinus and
later by the intensive but very expensive chemical control campaign.
Chemical control since 1957 has cleared dense infestations (see fig. 6) and
is now maintaining the weed more or less below a tolerable threshold level
but at a cost of R2 million (i.e. $US 2,4 million) per annum (G. Burger,

pers. comm.). This continued annual investment cannot be relaxed for fear that the weed may again increase above the manageable level with possible disastrous consequences to the farming community.

In spite of all these efforts which resulted in a significant reduction of the infestation intensity, the weed has continuted to spread at a steady rate of approximately 8 000 ha per year (G. burger, pers. comm. and Burger in Moran & Annecke 1979, fig. 3). The present distribution of jointed cactus in southern Africa is shown in fig. 8.

Releases of D. austrinus in dense infestations in the North West Cape (near Barkly West) were extremely successful and indications are that an acceptable level of biological control can be maintained by the insect. This level of efficiency appears to be the same as experienced in Queensland, Australia (Mann 1970). Alarmingly dense infestations of jointed cactus exist in Natal where the impact of D. austrinus is unsatisfactory (H. de Mik, pers. comm.). Similar conditions exist in New South Wales where the cochineal insect does not achieve a satisfactory level of control in the cool and higher rainfall areas (Hosking & Deighton 1981a).
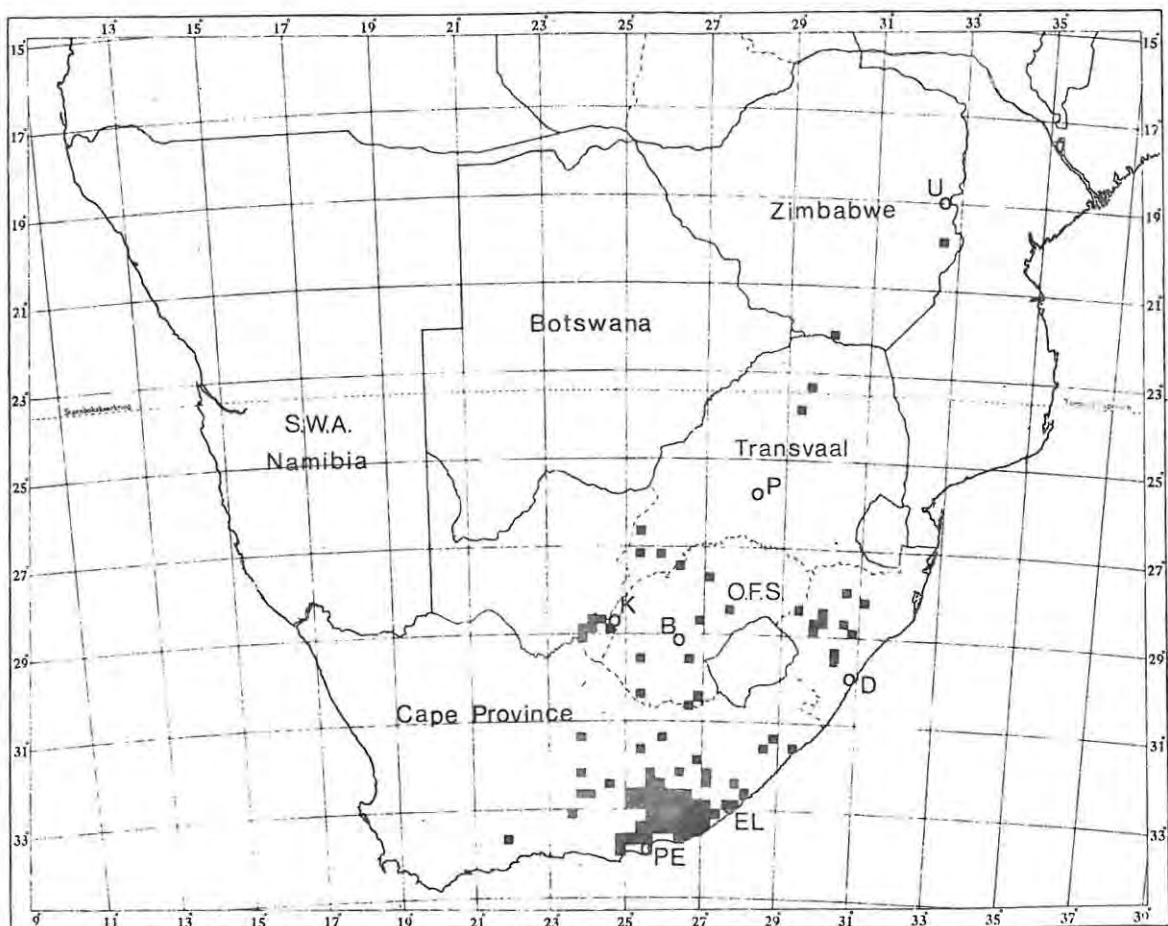


Fig. 8. Distribution of O. aurantiaca in southern Africa on a ¼° scale. PE = Port Elizabeth, EL = East London, B = Bloemfontein, P = Pretoria, K = Kimberley, U = Umtali and D = Durban.

Two points related to biological control of jointed cactus need to be highlighted :

(1)   At the start of the biological control phase (1938) farmers were asked to stop all other means of control in order to enhance the spread and multiplication of the cochineal insect. This was a serious tactical error, for farmers then believed that the State had assumed complete responsibility for jointed cactus control, a belief which is still strongly entrenched to this day.   All blame for subsequent problems with jointed cactus was put on the State and on biological control.

(2)   Many reasons were given to explain why $\underline{D}$. $\underline{austrinus}$ had failed to give satisfactory control of jointed cactus :

(a)   It was common belief that cochineal lost its "toxicity" but Pettey (1948) and Zimmermann $\underline{et}$ $\underline{al}$. (1974) showed this to be false, and this has again been demonstrated in the present study.

(b)   The general belief that the fungus $\underline{Empusa}$ $\underline{lecanii}$ was the cause of heavy cochineal mortality was supported by Pettey (1948) and Karny (1965).   Zimmermann $\underline{et}$ $\underline{al}$. (1974) denied this however, and supported the findings of H. Prinsloo (unpublished data) who reported that cochineal crawlers die (drown) during persistent rains and that the fungus may attack the cochineal $\underline{post}$ $\underline{mortem}$ (Greathead 1971; Moran & Annecke 1979).   These findings are however mainly based on observations of $\underline{D}$. $\underline{opuntiae}$ feeding on $\underline{O}$. $\underline{ficus-indica}$.

(c)   Predatory ants, namely $\underline{Anoplolepis}$ $\underline{steingroveri}$ Forel, were blamed for removing young cochineal insects (Pettey 1948). Zimmermann $\underline{et}$. $\underline{al}$. (1974), supported by later personal observations, do not see this as an important mortality factor.

(d)   Two coccinellids, $\underline{Exochomus}$ $\underline{flaviventris}$ Mader and $\underline{Cryptolaemus}$ $\underline{montrouzieri}$ Mulsant, have been reported to be important predators of $\underline{D}$. $\underline{austrinus}$ (Geyer 1947; Pettey 1948).   This cannot be supported because after years of extensive surveys on jointed cactus, only one occasion (lower Fish River Valley) can be recalled where coccinellids, mainly $\underline{C}$. $\underline{montrouzieri}$, were observed in small numbers on dense jointed cactus thickets, infested with $\underline{D}$. $\underline{austrinus}$.   These beetles,

however, are important predators on D. opuntiae (Pettey 1948; Annecke et al. 1969) and it could be that in the aftermath of the prickly pear campaign ($\pm$ 1946) the beetles were forced to feed on D. austrinus after the collapse of the large prickly pear infestations (Annecke & Moran 1978). The observations by Geyer (1947) and Pettey (1948) coincided with the peak of this prickly pear campaign. Walter (1977) showed that E. flaviventris adults starved to death in the laboratory if confined with D. austrinus adult females but that they do prey on the early stages of the cochineal which are inadequately protected by woolly wax coverings.

(e) Geyer (in Pettey 1948) reported that rodents were the sole cause of failure of D. austrinus in certain places and that considerable quantities of the cochineal insects were found in stomach contents. He also demonstrated that control of the rodents led to the increased effectiveness of cochineal against jointed cactus. No evidence of rodent predation was observed during this study.

(f) Pettey (1948), Zimmermann et al. (1974) and Gunn (1979) reported that the inaccessibility of the underground tuber to the insects and the difficulties of the insects to locate and establish on small and scattered plants must be regarded as a main reason for the failure of the cochineal insects.

The primary purpose of this study was to evaluate the role of D. austrinus as a natural enemy of jointed cactus in South Africa in relation to the distribution of the plant and to chemical control in order to pave the way for a more realistic control strategy, making optimum use of biological, mechanical and chemical control methods.

The following chapter reports on exclusion experiments designed to determine the effects of D. austrinus on jointed cactus plants. These studies show clearly that jointed cactus plants colonized by cochineal insects are usually killed. But these simple exclusion experiments provide limited information about the plant and the insect and have many other shortcomings. However, they highlighted the need for detailed quantitative field data on host plant and insect populations. Chapters 4 to 7 deal with methods used to measure distribution, age structure and dynamics of D. austrinus popula-tions and of its host plant. These methods are utilized to assess biological

and chemical control of the weed and the results are reported in chapters 8 to 11. The implications of these studies for the control of jointed cactus in South Africa are discussed in the final chapter.

## 3. THE EFFECT OF D. AUSTRINUS ON INDIVIDUALLY INOCULATED O. AURANTIACA PLANTS

After 1944, when it became evident that the efficiency of D. austrinus was declining, for reasons which have just been discussed, some poorly documented trials were started to evaluate D. austrinus in 7 different areas in the eastern Cape by placing cochineal insects amongst pre-selected jointed cactus infestations (Pettey 1948). No details of the trial plots and no quantitative data were given. The results based on visual inspection of these trial plots were disappointing with "satisfactory control" reported from only one of the plots.

When renewed interest was shown in the possibilities of biological control of jointed cactus in the early seventies, evaluation was initiated by D P Annecke and W A Burger in 1972 and these experiments were continued by me from 1973 onward.

The insect exclusion method was followed to demonstrate the impact of D. austrinus on individually selected jointed cactus plants. According to De Bach et al. (1976) this involves the elimination and subsequent exclusion of natural enemies from a number of plants (controls) which can then be compared with comparable plants where the natural enemies are not disturbed. The equilibrium levels of the two population densities then serve as a direct measure of the effectiveness of the natural enemies.

Four experimental plots were selected in 4 different ecological regions in the eastern Cape and Karoo. For details of the plots at Westondale and Glen Ovis see Table 4, and for the sites at Hankey and Fort Beaufort see Table 1. The size of the plots varied between 400 and 1 000 m². The plots were fenced. Between 50 and 80 medium to large jointed cactus plants were selected and numbered in each plot (= 265 in total for all 4 plots). Approximately half of the plants in each plot were kept free of cochineal insects and C. cactorum Berg by spraying with methidathion (5g/10 1 water of 40% wp) whenever necessary and by removing C. cactorum eggsticks during October/November and again February/March (Annecke et al. 1976). The other plants were inoculated with cochineal insects by placing a cladode colonized by D. austrinus at the base of each plant at the start of the experiment. All experimental plants became colonized except at Westondale where plants had to be reinoculated 6 months later : the severe drought during the second half of 1972 desiccated the infested cladodes before the cochineal could spread to the treated plants.

Table 1. Details of experimental plots.

|  | Fort Beaufort | Hankey |
|---|---|---|
| Location | 32° 50' S<br>26° 36' E | 33° 52' S<br>24° 51' E |
| Veld type<br>(Acocks 1975) | Valley bushveld | Valley bushveld |
| Mean annual<br>rainfall | 492 mm | 418 mm |
| For details on other sites see Table 4 | | |

The cladode was used as the unit for measuring growth and mortality, and results are therefore expressed as the number of cladodes per plant. The following records were taken : (i) the total number of cladodes on each plant; (ii) the number of cladodes that had become dislodged from the mother plant and that had rooted to form new plants, and (iii) the number of plants that had died from cochineal attack.

All plots were evaluated monthly until February 1974 when records were only taken every second or third month. The trial was started in August 1972 and was terminated five years later. A small area around each plant was regularly weeded to improve the accuracy of counts. This practice probably decreased interspecific density stress and consequently slightly increased the number of dislodged cladodes that rooted successfully.

Monthly counts of cladodes on insect-free plants over a three year period also provided some insight into the phenology of jointed cactus in the four diverse ecological regions. This included time of cladode formation, abscission of cladodes and root formation from cladodes that have dislodged from the mother plant. Information on the phenology of jointed cactus helps to explain the behaviour (e.g. feeding colonization and reproduction) of the cochineal insects in relation to the life history pattern of the plant. The phenology of jointed cactus is graphically represented in fig. 9 for two of the four localities.
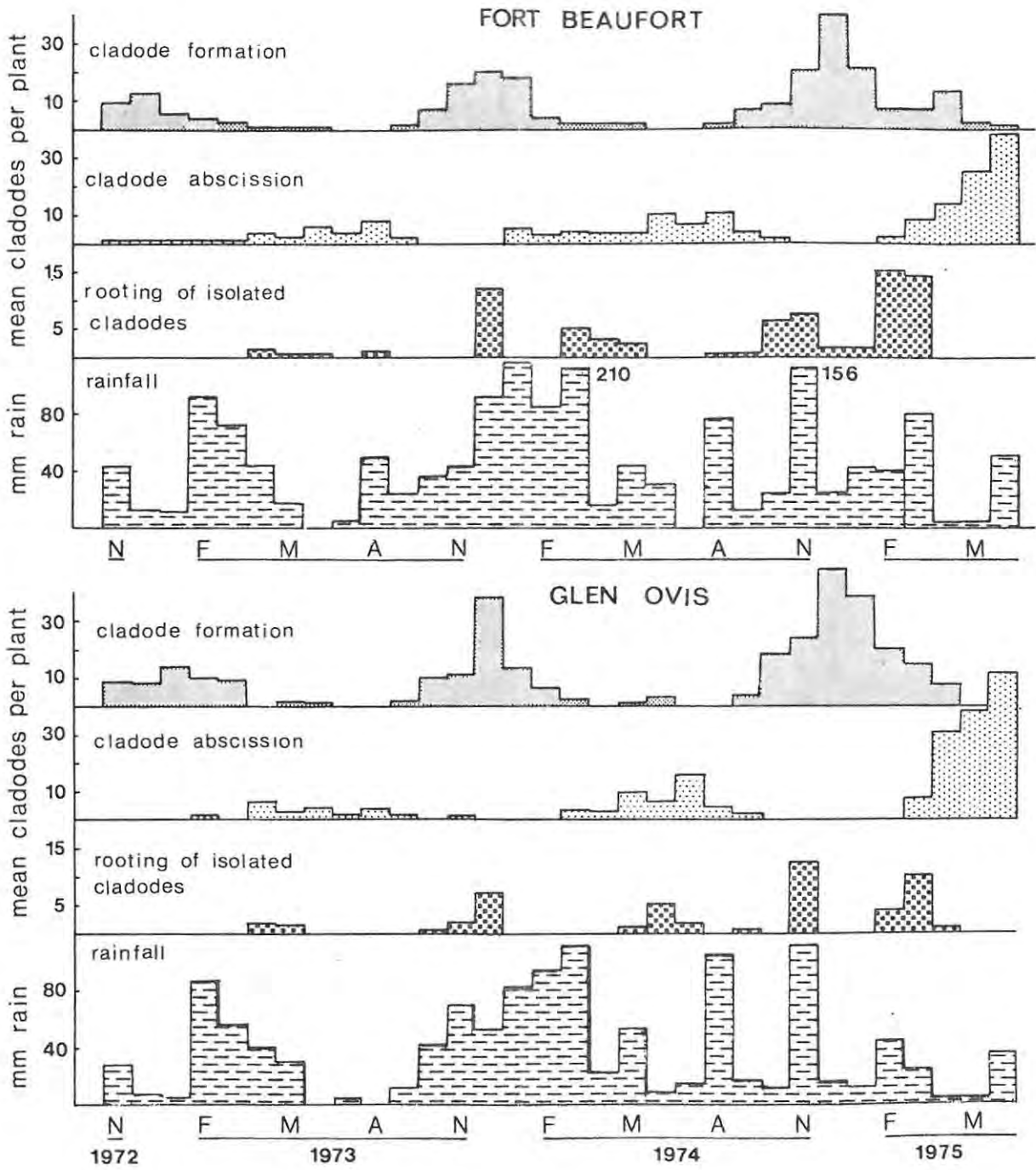
Fig. 9.    Phenology of <u>O</u>. <u>aurantiaca</u> at Glen Ovis and Fort Beaufort.
F = February; M = May; A = August; N = November.

New growth is limited to the months of September to April, always reaching
a peak in December, irrespective of rainfall. This peak also coincided with
a sharp increase in cochineal populations on infested plants (see also
chapter 11). Cladode abscission was generally limited to the winter months
ceasing during September and this coincides with cladode formation which
commenced at approximately the same time. Commencement of cladode abscission
however, overlapped considerably with cladode formation in the late summer,
generally starting during January and February. No abscission was recorded
for the months November and December.

Formation of new plants from rooted cladodes roughly corresponds to rainfall
peaks of 50 mm or more. The higher number of plants formed during 1974 was
the result of higher numbers of dislodged cladodes that had accumulated since
the start of the trial.

Unhindered growth of insect-free plants reached an upper asymptote approxi-
mately three years after the trials were started i.e. 1975 (fig. 10) :
thereafter the change in the number of cladodes per plant followed a strict
seasonal pattern. The maximum plant size of free standing plants varied
between ca. 160 cladodes per plant at Glen Ovis and ca. 40 cladodes per plant
at Hankey.

Although the numerical increase of cochineal insects on infested plants was
never measured it was noted that all cochineal populations increased dramati-
cally after the start of the experiment.

This increase in cochineal insects at all sites resulted in the collapse of
many plants from 12 to 18 months after release (figs 10 and 11).

Ignoring the seasonal fluctuations in cochineal-colonized plants the decline
in cladode numbers continued slowly after the initial collapse until the
experiment was terminated (fig. 11). Westondale is exceptional in this regard.
The initial collapse of colonized plants was manifested by a sharp decrease
in the total number of cladodes for the first 12 months while plant mortality
(figures next to open circles in fig. 11) only set in after 12 months and
continued somewhat less dramatically until the experiment was terminated. In
contrast, the number of cladodes on the insect-free plants increased
dramatically (fig. 10). Table 2 is a balance sheet of plant numbers showing
the fate of the originally inoculated plants after 5 years. Only a relatively
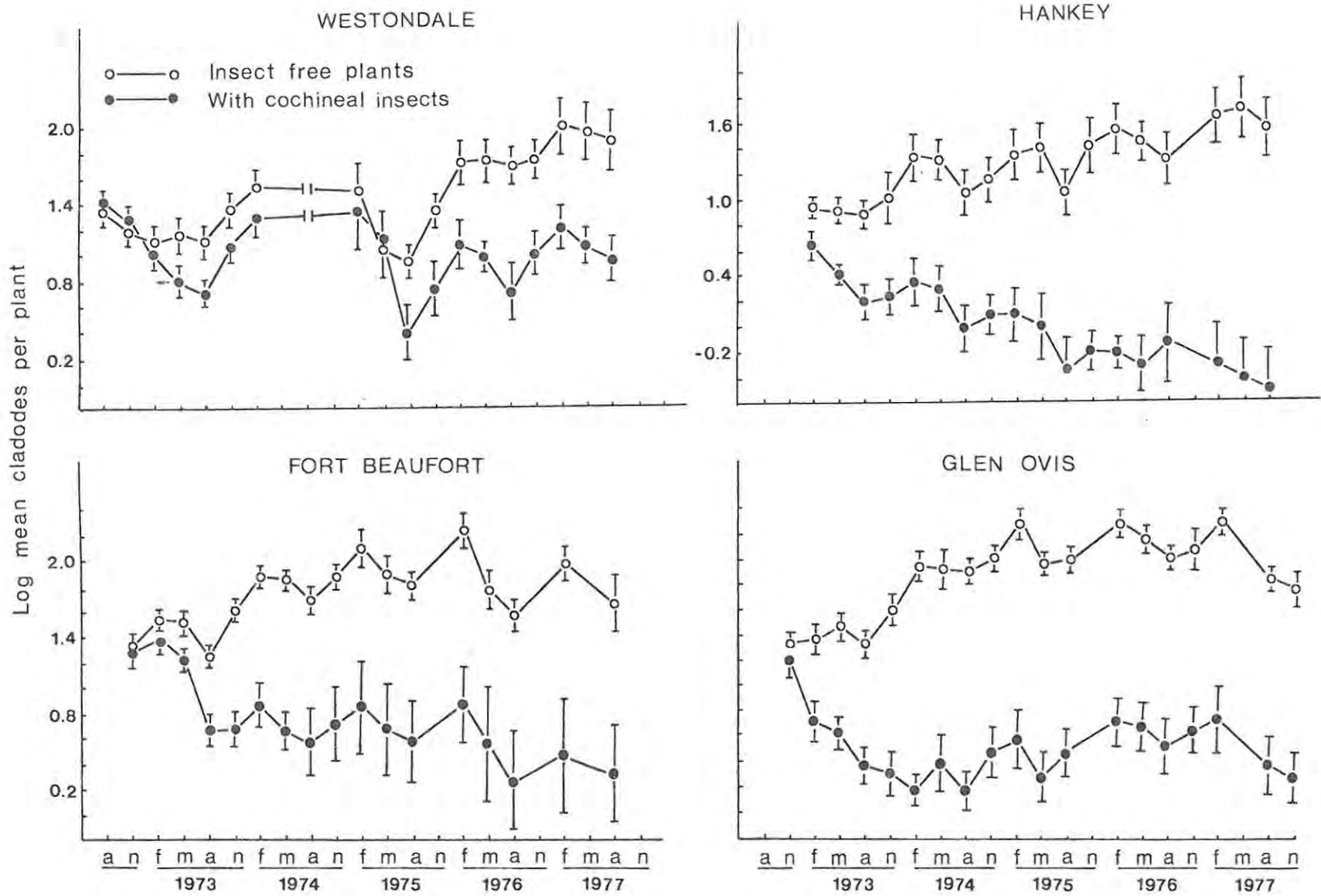
Fig. 10.  Log mean number of cladodes for 20 jointed cactus plants with 95% confidence levels at four localities in the East Cape, with (solid circles) and without (open circles) cochineal insects. F = February; M = May; A = August; N = November.
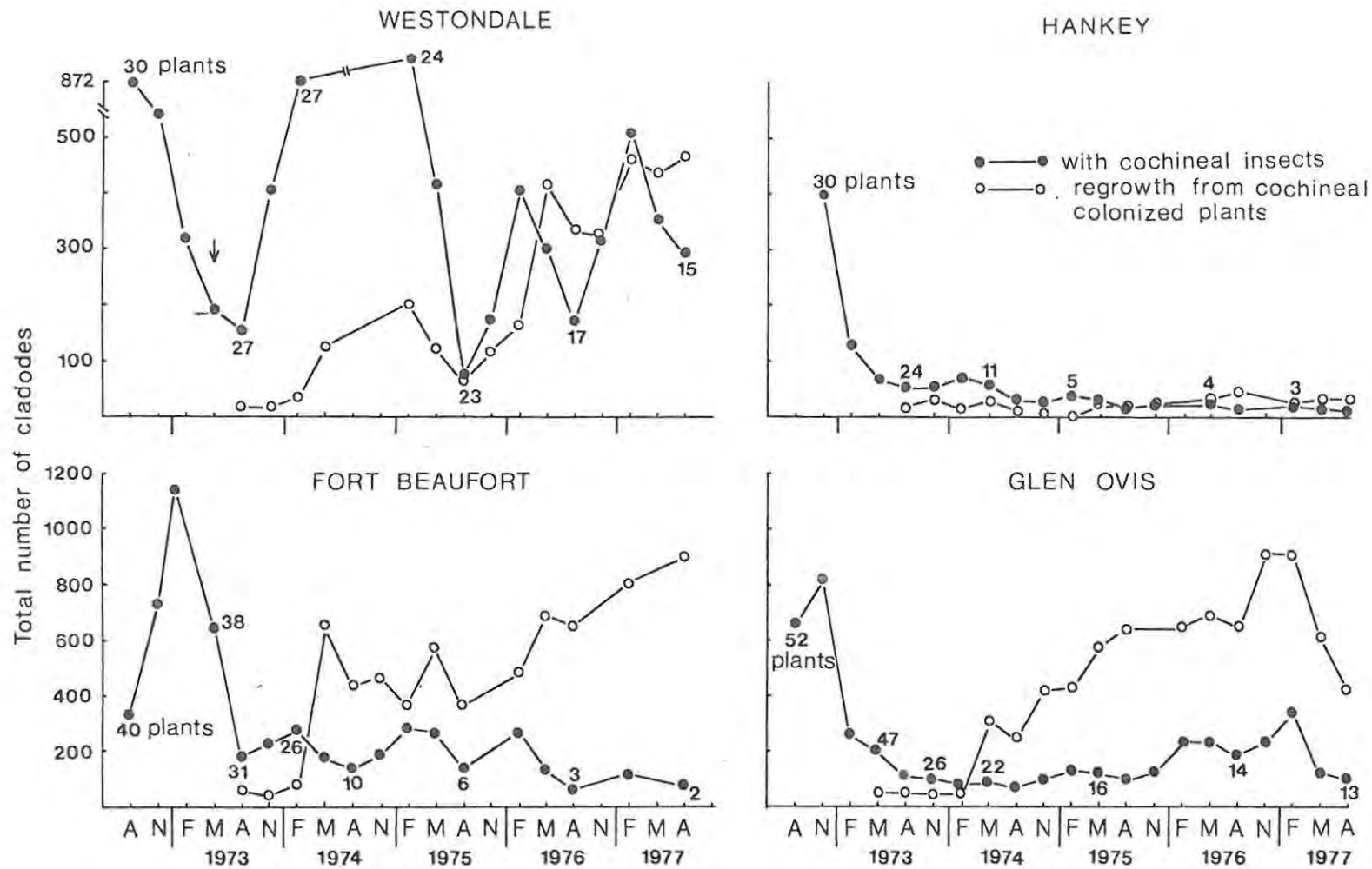
Fig. 11. Growth curves for plants inoculated with cochineal insects (solid circles) and regrowth from cladodes that have fallen (open circles), from 4 localities. The figures next to the first closed circle indicate that number of mature plants that had been colonized by cochineal insects and the subsequent figures along the line indicate the number of surviving plants. A = August; N = November; F = February; M = May.

Table 2.  Summary of the fates of jointed cactus plants five years after
they were inoculated with D. austrinus, at four localities in
the East Cape.

|  | Glen Ovis | Fort Beaufort | Westondale | Hankey |
|---|---|---|---|---|
| % Plants that died leaving no regrowth | 3,5 | 5,3 | 6,7 | 16,7 |
| % Plants that died leaving regrowth | 59,6 | 89,4 | 43,3 | 73,3 |
| % Plants that survived | 26,9 | 5,3 | 50,0 | 10,0 |

Table 3.  Total number of jointed cactus cladodes dislodged over a five
year period from 20 insect free (I/F) and 20 cochineal
inoculated (C/I) plants, and the percentage of these cladodes
that rooted to form new plants.

|  | Glen Ovis | | Fort Beaufort | | Westondale | | Hankey | |
|---|---|---|---|---|---|---|---|---|
|  | I/F | C/I | I/F | C/I | I/F | C/I | I/F | C/I |
| Number of cladodes | 9181 | 630 | 5295 | 1030 | 1884 | 1650 | 988 | 356 |
| % of cladodes that rooted | 56,9 | 8 | 76,8 | 7,3 | 52,6 | 4,9 | 65 | 2,5 |

small percentage of the plants died without leaving any trace of regrowth, while the majority of plants (except at Westondale) died but not without some of their dislodged cladodes rooting and growing again near the spot where the mother plant was standing. These abscised cladodes normally fell close to the periphery of the mother plant and very few were dispersed over longer distances. If not killed by cochineal or desiccation during hot and dry spells, the abscised cladodes rooted and grew after the first significant rains. The percentage of these cladodes that rooted is presented in Table 3 and the contrast between the figures for the insect-free and cochineal inoculated plants is clear. A high proportion of the dislodged cladodes from the insect-free plants that did not root, desiccated. This could be one of several reasons why biological control of jointed cactus using cochineal insects appears to be more efficient in arid regions (Moran & Annecke 1979; Hosking & Deighton 1981b).

In spite of the impact of cochineal insects, however, sufficient numbers of cladodes survived, rooted and multiplied and pre-inoculation populations were realized again within 5 years (see fig. 11). Jointed cactus regrowth was insignificant at Hankey and highest at Fort Beaufort. Most of this regrowth was re-colonized by cochineal insects but some escaped infestation and grew unhindered.

One main point emerged from this study namely the significant reduction of jointed cactus population levels after inoculation by D. austrinus. Although substantial regrowth of jointed cactus occurred in all but one site, the effect of cochineal was nevertheless dramatic compared to the cochineal-free plants. It is thus indisputable that the continued presence of cochineal is contributing substantially to the suppression of jointed cactus populations in the field.

Reasons for the limited success of cochineal as a biological control agent and methods that have been tried to increase the impact of this natural enemy are discussed in detail later in this thesis.

Also, these exclusion experiments provide little detailed data on population dynamics of the host plant or of its natural enemy D. austrinus. The need is to develop techniques to measure distribution, age structure and dynamics of the plant and on the insect, to determine in greater detail the effects of D. austrinus on jointed cactus plants in the field in South Africa.

## 4. JOINTED CACTUS SAMPLING AND SURVEY TECHNIQUES

Statistically acceptable sampling provides a method of estimating the absolute population parameters within certain accuracy levels. Thus, assumptions that apply to a randomly selected sample must reflect the type of variation that occurs within the entire population.

The degree of accuracy of an estimate will depend entirely on the objective of the study. For life table studies on natural populations, a high level of accuracy e.g. 10% will be necessary (= intensive sampling) but 25% error (= extensive sampling) may be sufficient in populations which exhibit ten - or even hundred-fold population changes in a season (Southwood 1978). The level of sampling accuracy also depends on available manpower. In practice, samples include elements of variance from (i) the environment, (ii) the population density, (iii) sampler and sampling errors and (iv) species behaviour reflected in population distribution characters. The latter element may be the main contributor to sample variance. More samples have to be taken if the population distribution is clustered rather than random or regular.

Materials and Methods

All experiments were done in the Eastern Cape Province of South Africa on jointed cactus infested farms which are privately owned. The location and name of the farms, and other relevant details of the experimental sites are listed in Table 4 and appendix 4.

Three dominant vegetation types (Acocks 1975), were selected in both high and low rainfall areas. Two sites, namely Westondale and Glen Ovis, were selected because of their well documented history of previous control efforts and because of the controversy that surrounds the status of D. austrinus as a biocontrol insect on these farms. The experimental sites were grazed normally by sheep and angora goats.

All jointed cactus and cochineal insect counts, were made in randomly selected permanent transects, 25 or 50 m long and 2 m wide. Each of the 50 and 100 metre squares per transect was assessed individually using a 2 x 1 m metal frame divided across the centre and moved along the transect over a calibrated tape as counting progressed (fig. 12). These counts gave the number of jointed cactus plants with or without D. austrinus for each m square.

Table 4.  Details of experimental plots.

|  | Weston-dale | Middel-burg-plaas | Glen Ovis | Maast-richt | Ganna-hoek | Cent-livres |
|---|---|---|---|---|---|---|
| Location | 25.08 E 32.56 S | 25.49 E 32.54 S | 26.09 E 33.02 S | 26.06 E 33.03 S | 26.17 E 32.54 S | 25.28 E 33.40 S |
| Veld type | Karroid Broken Veld | False Karroid Broken Veld | | | | Valley Bush Veld (cleared) |
| Mean annual rainfall mm* | 309 | 453 | 465 | 465 | 498** | 484 |
| Climate | hot/dry summers | hot summers | | | | moderate coastal climate |
|  | cold winters and mainly summer rainfall | | | | | |
| Control history | no control | inadeq-uate spraying | cleared twice mechanical-ly by state teams before 1949.  Since then spot spraying by owners. | | | continues spraying |

*   The monthly rainfall for all plots is shown in appendix 4.
**  Adelaide (= nearest rainfall data).

Four categories of O. aurantiaca plants were counted :

> (i)   individual unrooted cladodes which have been dislodged
>       from the parent plant (= category A);

> (ii)  small rooted plants each comprising five to ten cladodes
>       (= category B);

      (iii)    medium plants comprising five to ten cladodes
              (= category C) and

      (iv)    large plants with more than ten cladodes
              (= category D).

The number of cladodes on each large plant was also recorded as well as the presence or absence of cochineal colonies for each of these categories.

Control (= insect free) plots were kept free of insects by spraying all plants with Mithidathion (as already explained) whenever insects were observed during surveys. C. cactorum eggsticks were also removed from all plots during surveys.

De Lotto (pers. comm.) confirmed that the cochineal on O. aurantiaca plants were all D. austrinus. Mounted slides of young 3rd instar females from other sites were also made following De Lotto's method (in Gunn 1979) and these agreed with the description of D. austrinus (De Lotto 1974).

All counts were made by trained technical assistants and the counts were recorded on field data sheets (appendix 1).



Fig. 12.   Samplers recording jointed cactus population changes.
          Note the tape (arrow) and the 2 x 1 m$^2$ frame.  The
          transects are marked by wooden pegs.

Sample Size

Sampling was based on non-destructive in-situ counts of the plant which was
subdivided into four categories listed above.

The proportion of plants in the different categories in a jointed cactus
population varies considerably from sample date to sample date and depends
on the history of the population, e.g. the history of chemical or biological
control.  Table 5 gives the mean ratios over 2 years between the categories
for the 6 sampling localities combined.  In cochineal colonized plots, for
every one D-category plant (large plants) there were approximately 6,4
medium (C) plants, 92 small (B) plants and 89 isolated cladodes (A).  As a
general rule there were as many small plants as there were isolated cladodes.
There were also fewer large plants in the cochineal infested population than
in the insect-free plots.

Table 5.  Mean ratio for the size categories of jointed cactus for cochineal-
free and cochineal-colonized plots over two years for 6 localities
combined.  Each mean ($\bar{x}$) is based on 20 observations.  The co-
efficients of variation (CV) are also shown.

Cochineal colonized plots

| C : D | | B : D | | A : D | | B : C | | A : C | | A : B | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $\bar{x}$ | CV | $\bar{x}$ | CV | $\bar{x}$ | CV | $\bar{x}$ | CV | $\bar{x}$ | CV | $\bar{x}$ | CV |
| 6,4 | 59% | 92 | 91% | 89 | 70% | 10 | 65% | 12 | 82% | 1,0 | 60% |
| Cochineal-free plots | | | | | | | | | | | |
| 6,0 | 67% | 62 | 74% | 60 | 72% | 12 | 58% | 9 | 50% | 1,2 | 67% |
| D = large plants;  C = medium plants;  B = small plants;  A = isolated cladodes. | | | | | | | | | | | |

An assessment of optimal sample size, i.e. the number of random 1 m² quadrats
necessary to give an acceptable estimate of the population categories, was
obtained by first recording the number of categories encountered in a large
number of stratified random samples.  After the underlying population
distributions with the necessary mean and variance values were calculated,
the estimated number of samples needed to fall within the 10% and 20% margin

of error levels at the 95% level of confidence, was calculated. All such samples from various localities and dates over a large range of densities conformed to the negative binomial distribution (discussed later, Table 11 and fig. 16). If the parent distribution fits the negative binomial, the desired number of samples (N) at different accuracy levels is given by :

$$N = \frac{\frac{Z^2 \alpha}{2} \left( \frac{1}{\bar{x}} + \frac{1}{k} \right)}{D^2} \quad \text{where}$$

$\frac{Z^2 \alpha}{2}$ = confidence interval = 1,96 ($\alpha = 0,05$)

$\bar{x}$ = mean plants per sample square

k = parameter of negative binomial distribution (common k-value)

D = predetermined standard error as a decimal of the mean = 0,1 or 0,2.

This formula was derived from Rojas (1964) and Karandinos (1976). The formula given by Southwood (1971, 1978) and used by Pieters and Sterling (1974) is similar but lacks the $\frac{Z^2 \alpha}{2}$ term. Inclusion of the $\frac{Z^2 \alpha}{2}$ term increases the sample size for any desired accuracy level by a factor of 3,8. The formula by Rojas (1964) and Karandinos (1976) is correct (Van Ark, pers. comm.).

The number of m² samples necessary was calculated for each plant category separately over a realistic range of densities using a common k-value for each category. Because of the low number of D plants involved, they were combined with C category plants to increase the number of counts.

The common value of k (kc) was calculated according to the method described by Bliss and Owen (1958) and Bliss (1958) using the statistics

$$x^1 = \bar{x}^2 - \left( \frac{S^2}{N} \right) \quad \text{and}$$
$$y^1 = S^2 - \bar{x} \quad \text{where}$$

$\bar{x}$ = mean, $S^2$ = variance and N = number of individual counts on which $\bar{x}$ is based. When $y^1$ is plotted against $x^1$ the regression line of $y^1$ on $x^1$ passes

through the origins and has the slope $\frac{1}{k}$. An approximate of kc is then given by

$$\frac{1}{kc} = \frac{y^1}{x^1}$$

If $\frac{1}{k}$ is plotted against the mean and there is no trend or clustering (i.e. low r-values) the use of a common k is justified (Southwood 1978). The $x^1$, $y^1$, $\frac{1}{k}$, kc and r-values are shown in Table 6 for different jointed cactus categories. The r-values in Table 6 were not significant ( p = >0,05) and the use of the common k is thus justified.

Fig. 13 shows the number of square metre sample units required at all density levels encountered for all plant categories at the 10% and 20% precision levels. The number of random samples required increased sharply at a density of 0,3 units per m² for A and B category plants and 0,08 for C and C + D category plants.

According to fig. 13, approximately 3 000 randomly selected m² quadrats per population would be necessary to assess accurately a light jointed cactus infestation, 1 500 for a medium infestation and less for a heavy infestation at the 20% accuracy level (based on C and D plants). For the purpose of this study only 3 000 or 1 500 m² quadrats were surveyed at three-monthly intervals. Further it was impractical to allocate all 3 000 or 1 500 m² quadrats indi-vidually over the sample areas and they were therefore pooled into 30 perman-ent transects, each transect being 50 x 2 or 25 x 2 m long. Each of the 100 m² per transect was relocated and assessed individually using the 2 x 1 m metal frame as described earlier. Hairston (1971) showed that pooling the samples into grids was superior to total random sampling.

The following points emerge from this sampling system :

(1) With 3 000 m² sample units, isolated cladodes and small plants were adequately sampled at a 10% accuracy level at all popula-tion levels encountered.

(2) Medium, and medium and large plants combined, were only adequately sampled at the 20% level and then only above a density of 0,04 plants per m² . Therefore all C and D plants, individually or combined were apparently undersampled at light infestations.

Table 6. $x^1$, $y^1$ and $\frac{1}{k}$ values necessary to calculate the common k (kc) for different jointed cactus categories sampled at various localities and dates. The r-values are also shown.

| Plant Category | Locality | $x^1$ | $y^1$ | $\frac{1}{k}$ | r | kc |
|---|---|---|---|---|---|---|
| Isolated | Middelburg- | 4,14 | 15,5420 | 3,75 | | |
| Cladodes | plaas | 1,9007 | 8,36 | 4,4 | | |
| (Category A) | Westondale | 0,3026 | 2,354 | 7,78 | | |
| | | 0,1785 | 1,9388 | 10,86 | | |
| | | 0,976 | 1,477 | 15,13 | 0,23 | 0,2177 |
| | Gannahoek | 1,5541 | 8,906 | 5,73 | | |
| | | 5,8949 | 18,0846 | 3,07 | | |
| | Glen Ovis | 3,2525 | 14,8447 | 4,56 | | |
| | | 0,7793 | 5,2268 | 6,71 | | |
| | | 0,0536 | 0,3654 | 6,82 | | |
| Small Plants | Middelburg- | 7,0904 | 21,42 | 3,02 | | |
| (Category B) | plaas | 14,6366 | 44,629 | 3,05 | | |
| | Westondale | 0,3581 | 2,4572 | 6,86 | | |
| | | 0,7274 | 5,007 | 6,88 | | |
| | Gannahoek | 3,496 | 12,137 | 3,47 | | |
| | | 2,1408 | 8,43 | 3,94 | 0,12 | 0,2743 |
| | Glen Ovis | 1,5976 | 6,669 | 4,17 | | |
| | | 2,2774 | 9,5135 | 4,18 | | |
| | | 0,2753 | 1,6543 | 6,01 | | |
| | Centlivres | 1,0252 | 4,0648 | 3,96 | | |
| | | 0,687 | 3,248 | 4,73 | | |
| Medium Sized | Middelburg- | 0,1539 | 0,7261 | 4,72 | | |
| Plants | plaas | 0,1342 | 0,7618 | 5,68 | | |
| (Category C) | Westondale | 0,0083 | 0,0411 | 4,95 | | |
| | Gannahoek | 0,0435 | 0,3198 | 7,35 | 0,06 | 0,1772 |
| | Glen Ovis | 0,0221 | 0,1019 | 4,61 | | |
| | | 0,0054 | 0,1221 | 22,61 | | |
| Medium and | Middelburg- | 0,049 | 0,5563 | 11,35 | | |
| large plants | plaas | | | | | |
| combined | Westondale | 0,0007 | 0,0119 | 17,00 | | |
| (Category C + | Gannahoek | 0,0173 | 0,01487 | 8,59 | | |
| D) | Glen Ovis | 0,0115 | 0,0644 | 5,60 | 0,05 | 0,096 |
| | | 0,0028 | 0,0712 | 25,43 | | |
| | Centlivres | 0,0223 | 0,2730 | 12,24 | | |
| | Rietmond | 0,0112 | 0,0707 | 6,31 | | |
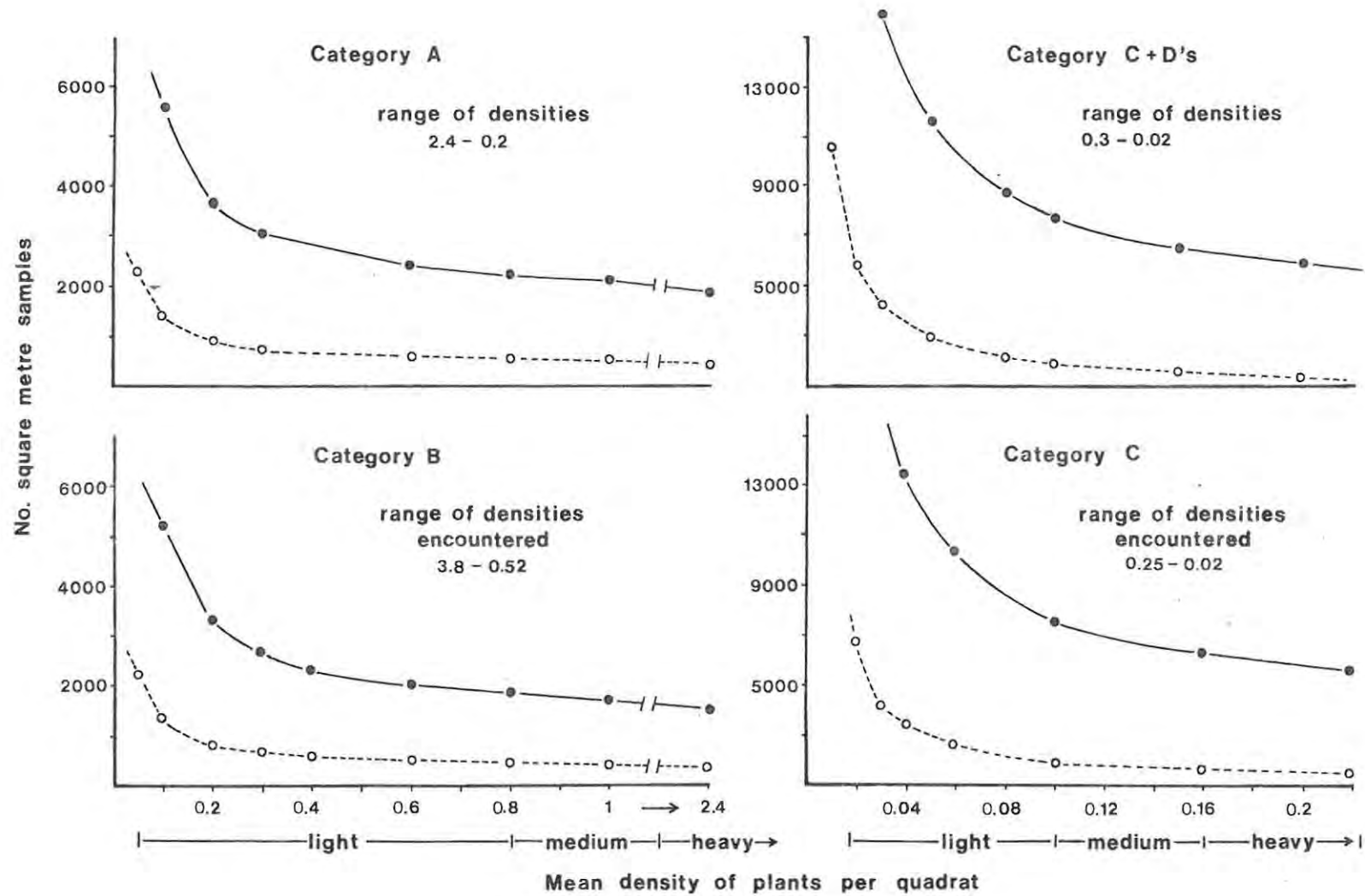
Fig. 13. Relationship between jointed cactus densities encountered and the number of sample quadrats required at 10% (solid line) and 20% (broken line) precision level, for plants in different size categories.

(3)  With 1 500 m² samples all C + D categories were undersampled at
     light and medium infestations according to this analysis.

On this basis it would seem that the sample method used in this study was
sometimes inadequate but it should be stressed that these apparent deficien-
cies are actually nullified because populations were repeatedly sampled non-
destructively along fixed permanent transects and thus random sample errors
were no longer important.

Transect Number

In the present study, the entire jointed cactus population in a study plot
was assessed by sampling 3 000 or 1 500 m² quadrats divided into a specific
number of 50 or 25 m long transects.  An assessment of the optimal number of
transects was gained by plotting the mean and confidence limits from each of
5, 10, 15 etc. randomly selected transects against the mean number of plants
recorded per transect.  For categories A, B and C the 95% confidence intervals
about the mean became minimal at about 30 transects (fig. 14).

The stratification of 100 or 50 m² quadrat samples into each of 30 transects
may sacrifice total randomness but it nevertheless retains enough randomness
and reliability to validate assumptions made on population changes at pre-
determined accuracy levels.  Pooling quadrats was not only a practical and
more accurate method to accommodate a large number of individual quadrats
(Hairston et al. 1971) but, because a series of contiguous quadrats was
counted, it also enabled determination of population distribution patterns
and clump sizes.



Fig. 14.  Mean and ± 95% confidence limits for numbers of jointed cactus
          plants per transect for categories A, B and C, for 5, 10, 15 ....
          40 randomly selected transects at Westondale.

Quadrat Size

Bormann (1953), Brown (1954), Morris (1955), Cochran (1963), Kershaw (1973),
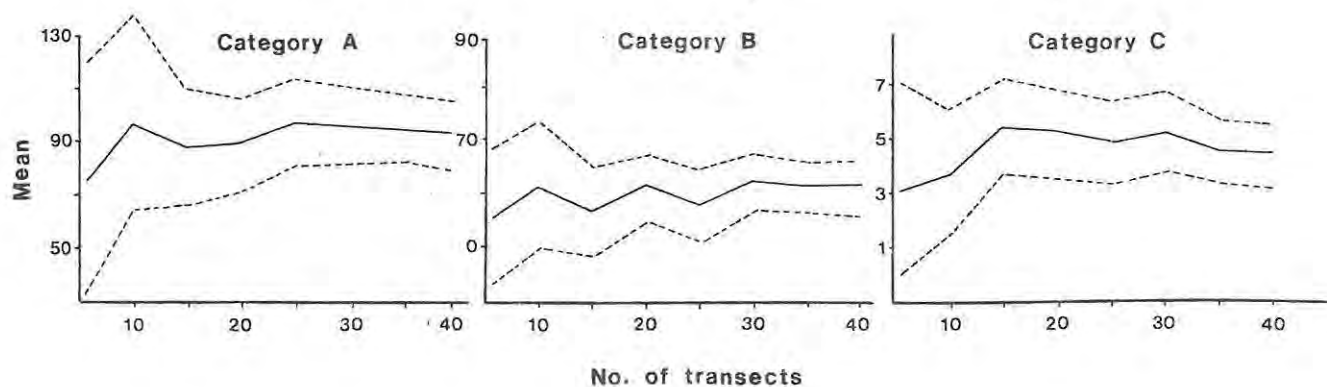Pielow (1977) and Southwood (1978) have discussed the effects of varying
quadrat shapes and sizes in population sampling. As a rule, the standard
error of a mean obtained from a sample of fixed total area tends to increase
as the size of the unit increases (Finney 1972). The most economical sample
unit will be a compromise between sampling costs, (which increase with
larger sampling units) the standard error of the mean and the sample unit
size. For a fixed sample area, division into smaller units will generally
give greater precision than division into a few large ones (Finney 1972),
but if the sample units are made too small an excess of zero counts at low
densities impedes data analysis and should therefore be avoided (Van Ark,
pers. comm.). Border effects also become increasingly important with smaller
units, especially so for jointed cactus counts, and if the sample units have
to be reallocated repeatedly or if they are far dispersed, sampling many
smaller units is more labour intensive than sampling a few large ones. If
the quadrat size becomes very small allowing only one individual to be
sampled, then the underlying distribution will incline to become random,
although it may in fact be aggregated (Taylor 1971). True random distributions
(Poisson) are not affected by quadrat size. Results obtained by varying
quadrat sizes will give valuable information on underlying distribution
patterns (Waters 1959); Lloyd 1967; Kershaw 1973; Pielou 1977).

Because jointed cactus occurs in discrete clumps it is preferable that the
quadrat size be smaller than the diameter of the clump (Greig-Smith 1964;
Iwao 1972; Kershaw 1973) and it was found in my studies that the smaller
clump diameters were less than 1 m so that the 1 m² sample unit was slightly
larger than the clump diameter.

At Uitenhage a 100 x 50 m plot, infested with jointed cactus, was selected
from a larger 2 ha plot which was completely surveyed (fig. 15) with a 1 m²
frame. Standard errors of means and mean values were calculated for
increasing sample units by pooling small units into larger ones ranging from
1 m² to 64 m². Assuming that a normal distribution of small plants occurred,
the number of sample units (N) required at a predetermined precision level
of 10% was calculated using the formula

$$N = \frac{s \times t^2}{D \times \bar{x}}$$     where t = 1,96;  D = 0,1; s = standard deviation and

$\bar{x}$ = mean (Southwood 1978). The results are listed in Table 7. Although
the number of samples required decreased with increasing quadrat size, the

**Metres**
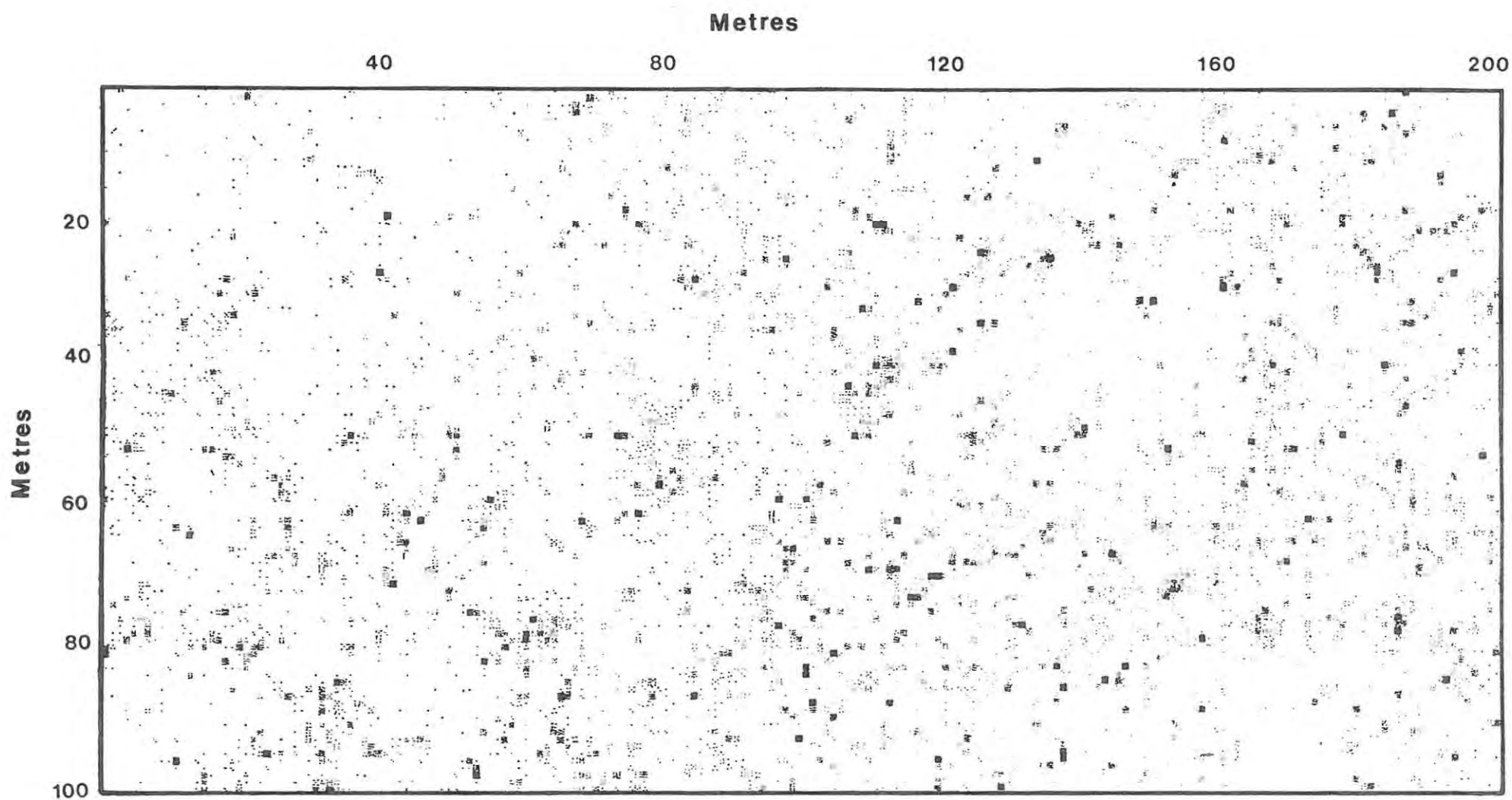


Fig. 15. Scatter diagram of a typical jointed cactus infestation, showing small plants only, on a 2 ha plot near Centlivres. Each dot represents one small plant.

actual area that needs to be surveyed increased, leaving the 1 m² as the most reliable and economical unit. Overall, the 1 m² quadrat was the most convenient size to handle although a 2 m² rectangular quadrat of 1 x 2 m would be more advantageous at low densities because of less zero counts.

Table 7. Comparison of jointed cactus sampling statistics, number of samples required and area to be sampled for different quadrat sizes.

| Quadrat size (m) | Mean | Standard error of mean | Number of samples required | Area to be sampled (m²) |
|---|---|---|---|---|
| 1 x 1 | 0,83 | 0,035 | 3402 | 3402 |
| 2 x 1 | 1,65 | 0,074 | 1931 | 3862 |
| 1 x 2 | 1,64 | 0,074 | 2030 | 4060 |
| 2 x 2 | 3,29 | 0,173 | 1218 | 4872 |
| 2 x 4 | 6,61 | 0,37 | 793 | 6344 |
| 4 x 2 | 6,61 | 0,34 | 630 | 5040 |
| 4 x 4 | 13,2 | 0,78 | 419 | 6704 |
| 4 x 8 | 26,4 | 1,73 | 261 | 8352 |
| 8 x 4 | 26,4 | 1,7 | 247 | 7904 |
| 8 x 8 | 52,7 | 3,92 | 164 | 10,494 |

Human Error

Errors in population estimates can be attributed to random sampling errors and errors of measurement or accuracy errors. Random sampling error is the deviation from the real population mean. This has been dealt with. Human error relates to the bias of the samplers in counting the plants and also arises from errors of measurement. This type of error is particularly important where the same areas are repeatedly sampled as was done in this study. Any change detected in the jointed cactus population should be attributable to changes in the population and not because of incorrect measurements by samplers.

The errors of measurement in this study are the results of :

(1)  the inability of the samplers to find small plants and subsequent incorrect counting;

(2)    misidentification between categories of plants;

(3)    errors due to border effects i.e. counting a plant
       when in fact it lies outside the quadrat and vice versa.

To test the accuracy of the samplers, 8 transects were surveyed at
Westdondale by two teams of 4 samplers each.  This information gave survey
errors between the members of the two teams which was compared by means of
t-tests for paired data at the 5% accuracy level (Table 8 a + b).

It is inevitable that some cladodes will be dislodged or small plants
uprooted while surveying, particularly when an area is subjected to several
consecutive surveys.  The destructive effect that successive surveys have
on a jointed cactus population is evaluated by means of comparing the first
survey against all the subsequent ones (Table 9).  The following points
emerge from Tables 8 and 9 :

(1)    Only 3 out of 40 surveys of categories A and B plants
       differed significantly when the counts of team mates
       were compared with each other as well as with the overall
       mean.  The samplers are therefore accurate (variation <5%)
       in their estimates and it is safe to attribute any
       significant changes in successive counts to natural changes
       in the population, which is what this sampling method
       was designed to detect.

(2)    Some samplers (e.g. man number 4) were consistently
       conservative in their counts i.e. they were inclined to
       overlook some plants, while others (e.g. man number 7)
       were liberal in their counts which is indicated by positive
       and negative t-values respectively in Table 8.  This error
       was mostly overcome by ensuring that each sampler repeatedly
       sampled the same set of transects during the successive
       surveys.

(3)    Significant differences in the number of isolated cladodes
       (category A, Table 9) indicated between the first and
       subsequent surveys, demonstrated that a number of cladodes
       are dislodged during the first survey.  No significant dif-
       ferences, however, were found between the results of

subsequent surveys. This demonstrates the importance of minimizing disturbances while the survey is in progress, especially during winter and during dry spells when cladodes are easily dislodged.

This chapter has indicated that the sampling of jointed cactus is reliable. In the next section this sampling method is used to describe population characteristics.

Table 8. A comparison between the counts of each of 8 individual men sampling A and B category jointed cactus plants along 8 transects. The values for paired t-tests comparing the performances of individual men and comparing their performances to the overall mean, are given.  * = significantly different at the 5% level.

| a. | PLANT CATEGORY | OVERALL MEAN | TEAM 1 | | |
|---|---|---|---|---|---|
| MAN 1 | A | 0,76 | | | |
|  | B | -0,26 | MAN 1 | | |
| MAN 2 | A | 0,27 | 0,19 | | |
|  | B | 0,36 | -0,42 | MAN 2 | |
| MAN 3 | A | 0,14 | 0,22 | 0,07 | |
|  | B | -0,77 | 0,52 | 0,63 | MAN 3 |
| MAN 4 | A | -0,71 | 0,95 | 0,58 | 0,5 |
|  | B | 0,53 | -0,45 | -0,76 | -0,45 |

Table 8b. on following page.

Table 8 (continued)

| b. | PLANT CATEGORY | OVERALL MEAN | TEAM 2 | | |
|---|---|---|---|---|---|
| MAN 5 | A | -0,61 | | | |
| | B | 2,08 | MAN 5 | | |
| MAN 6 | A | 2,46* | -1,76 | | |
| | B | 2,12 | -0,19 | MAN 6 | |
| MAN 7 | A | 0,01 | -0,04 | 1,93 | |
| | B | -2,1 | 2,67* | 6,70* | MAN 7 |
| MAN 8 | A | -1,11 | 0,09 | 2,3 | 0,19 |
| | B | -1,4 | 1,88 | 1,7 | 0,46 |

Table 9. Paired t-values for 8 transects combined comparing the first and subsequent surveys (i.e. surveys 2, 3 and 4) of A and B category jointed cactus plants. * = indicates significance at the 5% level.

| | TEAM 1 | | | | | |
|---|---|---|---|---|---|---|
| Plant Category | 1 vs. 2 | 1 vs. 3 | 1 vs. 4 | 2 vs. 3 | 2 vs. 4 | 3 vs. 4 |
| A | 3,47* | 3,73* | 3,53* | 0,95 | 0,82 | 0,92 |
| B | 1,50 | 2,26 | 0,07 | 0,30 | 2,12 | 0,89 |
| | TEAM 2 | | | | | |
| A | 3,88* | 3,85* | 4,25* | 1,09 | 2,01 | 0,82 |
| B | 0,88 | 3,54* | 2,24 | 1,56 | 2,32 | 0,13 |

## 5.  JOINTED CACTUS POPULATION STATISTICS

### Variance Mean Relationships

Frequency distributions, showing the number of quadrats containing 0, 1, 2, etc. plant categories per $m^2$ unit at all sites were skewed because of a large number of empty quadrats (fig. 16). This implies that the distribution was probably not normal.

Variance mean relationships for all categories of plants and from all localities were typically of aggregation distributions where the variance exceeded the mean (fig. 17). All counts departed noticeably from the line of Poisson (random) expectation described by a $S^2 = m$ relationship and followed a $S^2 = am^b$ relationship where the variance ($S^2$) is proportional to a fractional power of the mean (m) and where b = the slope and a the intercept on a log variance against the log mean plot (Taylor 1961; 1971) : b may be used as an index of aggregation.

The departure of the line $S^2 = am^b$ from the Poisson expectation was the greatest for isolated cladodes and small plants (fig. 17) suggesting a higher degree of aggregation in these categories.

The values in fig. 16 can also be fitted to a line of negative binomial expectation, as illustrated by Harcourt (1963), described by $S^2 = \dfrac{m + m^2}{k}$ .

### Negative Binomial Distribution

Frequency distributions of counts were fitted to several discrete frequency distributions using the Fortran computer program of Gates and Ethridge (1972) which they based on Fisher's maximum likelihood estimate. The chi-square  test for goodness of fit between observed and expected values at the 5% level of significance were also calculated and are listed in Table 10.

Except for a few cases with large frequencies (usually with high counts at the end of the tail) all distributions approximated the negative binomial most closely (Table 10). The close fit between observed and expected counts on the basis of the negative binomial distribution is illustrated in fig. 16. The Neyman type A and logarithm with zeros distributions gave the second best fit. The former was particularly common in populations with

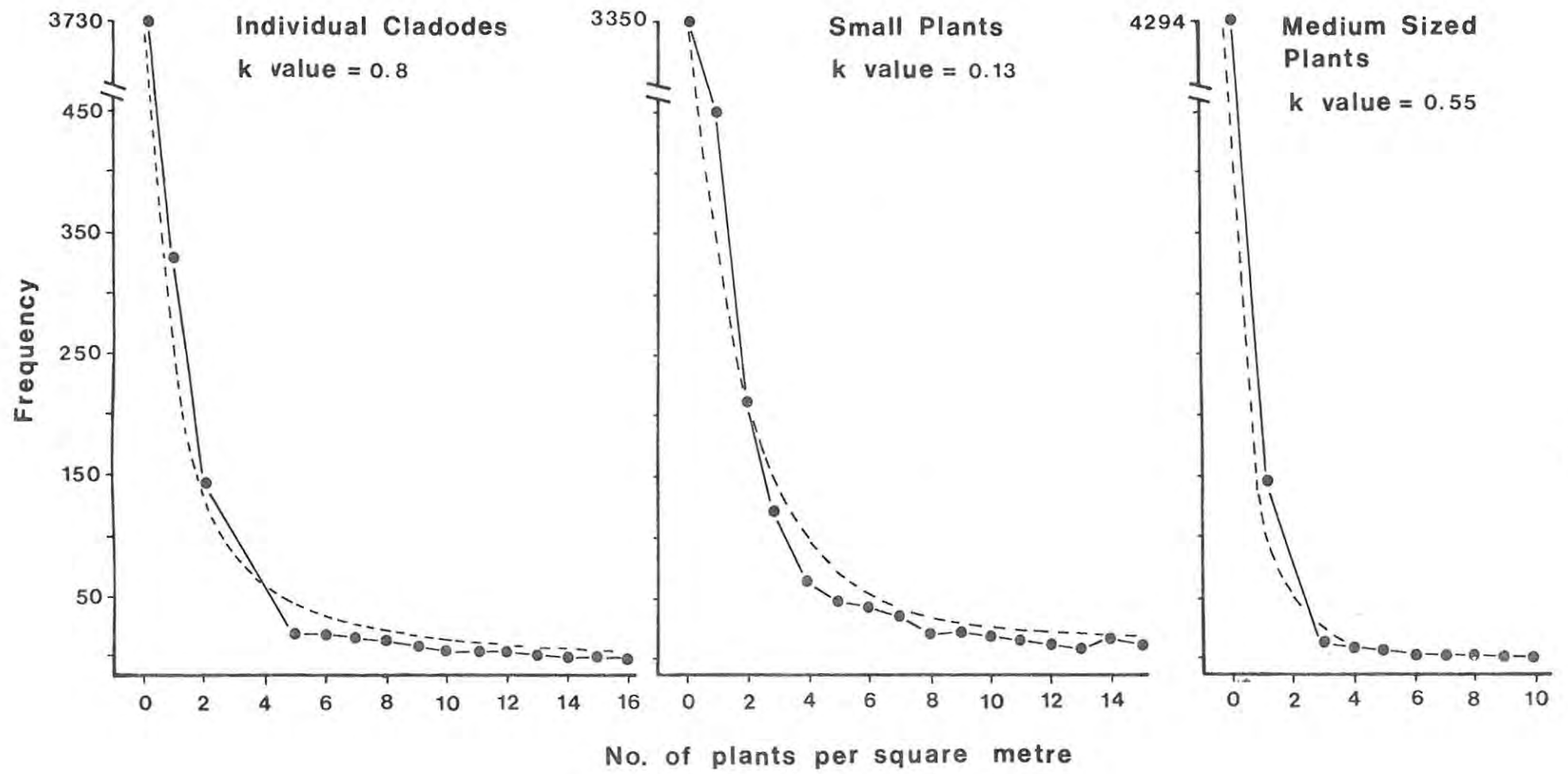Fig. 16. Observed distribution of O. aurantiaca in the field at Maastricht (solid line) and the theoretical curve for the negative binomial distribution (broken line).
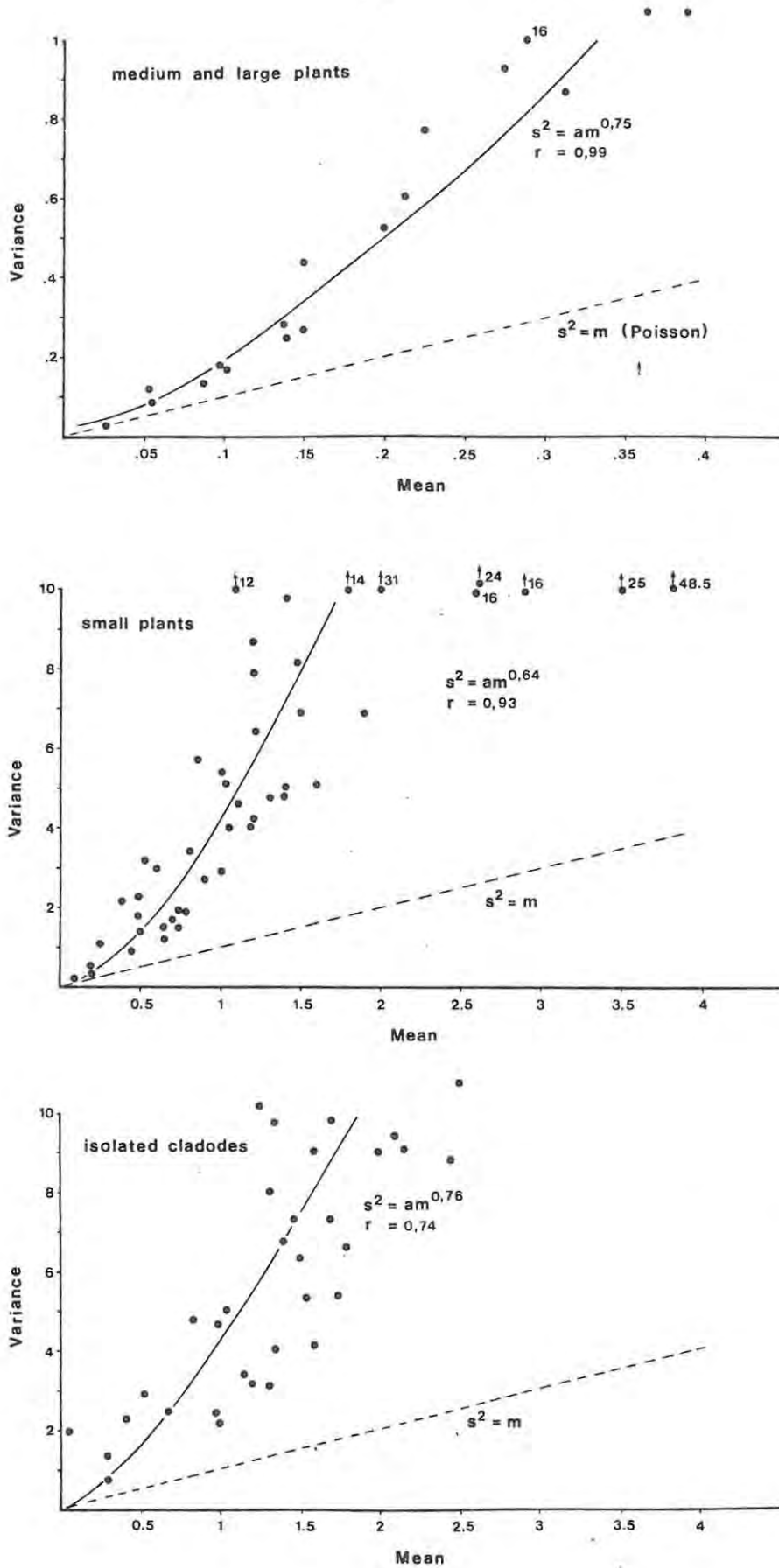
Fig. 17. Variance mean relationships for isolated cladodes, small plants and medium and large plants. Each dot is based on a sample of 100 - 4 000 m² quadrats. The broken straight line is the expected relationship for a Poisson series.

long bimodial frequency distributions. This is because of inflation by excessive zero frequencies (Itô 1967). The Poisson and positive binomial distributions resulted in a poor fit and are not shown.

Table 10. Fitting $\underline{O}$. aurantiaca population frequency distributions to various discrete known distributions indicated by means of Chi-square values. (NS) indicates non-significant differences between observed and calculated figures at the 5% level. All data were based on 1 $m^2$ samples.

| Locality and Category | Total Frequency | CHI-SQUARE VALUES | | | |
|---|---|---|---|---|---|
| | | Negative Binomial | Neyman's A Distr. | Log with Zeros | Poisson with Zeros |
| Ganna- A | 100 | 5,44 NS | 14,54 | 7,99 | 35,17 |
| hoek A | 100 | 4,21 NS | 3,85 | 5,85 NS | 6,73 NS |
| A | 100 | 9,57 NS | 16,12 | 12,71 NS | 34,99 |
| A | 800 | 21,66 | 185,63 | 23,05 | 544,70 |
| A | 100 | 2,96 NS | 4,40 NS | 6,82 NS | 138 |
| A | 100 | 9,08 | 6,17 NS | 16,60 | 138 |
| B | 100 | 6,62 NS | 11,97 | 8,38 NS | – |
| B | 100 | 7,72 NS | 5,53 NS | 10,99 | – |
| B | 100 | 6,92 NS | 8,72 NS | 13,02 NS | – |
| Weston- B | 100 | 6,03 NS | 2,62 NS | 6,34 NS | 2,74 NS |
| dale B | 100 | 3,59 NS | 4,81 NS | 4,88 NS | 5,95 NS |
| B | 100 | 6,26 NS | 27,20 | – | 47,85 |
| B | 100 | 6,47 NS | 7,53 NS | 6,81 NS | 12,53 |
| B | 2000 | 28,28 | 677 | 23,80 | 1119 |
| A | 4000 | 42,74 | 1324 | 24,20 | 3607 |
| C | 4000 | 10,82 NS | 18,90 | 10,44 | 20,16 |
| D | 4000 | 0,17 NS | 0,13 NS | 0,18 NS | 0,15 NS |
| Glen B | 4000 | 40,77 | 2169 | – | – |
| Ovis C | 4000 | 11,87 | 58,96 | 8,62 NS | – |
| Weston- A | 2000 | 27,40 | 713 | 21,60 NS | – |
| dale B | 1500 | 16,01 NS | 121 | 13,30 NS | – |
| C | 2000 | 1,94 NS | 5,12 NS | 1,96 NS | – |

All O. aurantiaca population distributions are thus adequately expressed by
the negative binomial distribution which is suitable to describe contagion.
The nature of this contagion is well illustrated by a scatter-diagram (see
fig. 15) of a heavy jointed cactus infestation, showing all the small plants
as dots in a 2 ha plot.  Dots were evenly spaced in each square when pre-
paring the map although the plants were probably more densely aggregated in
the true situation.  Nevertheless, there is a significant tendency for the
cactus to occur in clumps which is understandable in a plant that relies on
vegetative propagation from cladodes that fall close to the parent plant.

The application of the negative binomial distribution to biological data
and its theory has been outlined by many authors e.g. Fisher (1941), Anscombe
(1950), Bliss and Owen (1958), Rojas (1964), Harcourt (1963, 1965),
Andersen (1965).  It is described by two parameters namely the mean (m) and
the dispersion parameter k.  The most common method for calculating k is
described by Katti and Gurland (1962) using the formula $S^2 = m + m^2/k$.
The value of k as a parameter for aggregation is discussed by Waters (1959),
Andersen (1965), Iwao and Kuno (1971), Mukerji (1973), Cadahia (1977) and
Taylor et al. (1979).  This point will be taken up again in a subsequent
chapter.

Because jointed cactus frequency distributions approximated the negative
binomial distribution, the data are unsuitable for parametric statistical
tests.  It was found empirically (appendix 3) that transformations using
log (x + 1) (where x = observed count) was suitable but in this study such
transformations were not used because the data were obtained from repeated
sampling of the same cohort (= transects), because of the limited use that
was made of ANOVA and because transformations can lead to serious problems
in the interpretation of results and the construction of life-budgets
(Lyons 1964; Southwood 1978).

## 6. SAMPLING D. AUSTRINUS POPULATIONS ON O. AURANTIACA

Sample Method

After the female crawlers of D. austrinus have settled at the final feeding site they remain sessile for the rest of their lives. The females secrete a woolly wax around the periphery of the body which eventually covers the entire insect (Moran & Cobby 1979).  These white covers on the females are conspicuous in jointed cactus infested veld (fig. 4).

Concurrent with the host plant surveys, the presence or absence of cochineal insects on each individual plant was recorded but it was impossible to estimate in situ the number of females on the plant or their developmental stage.  To supplement the information obtained from the plant surveys therefore    additional random samples of 40 plants colonized by D. austrinus and consisting of 20 B category (small) plants and 20 C + D category (large) plants were taken from the periphery of each sample plot.  These random samples were obtained by throwing a wire pointer as far as possible and the nearest infested plant to the pointer was uprooted, marked, placed into a paper bag and kept in a cool bag or in the vegetable compartment of a 'fridge until it was analyzed, one to four days after the sample was taken. The following information was obtained from each sample : (1) the weight of the plant as well as the weight and length of each individual cladode; (ii) the number of cladodes colonized by D. austrinus and (iii) the females and crawlers from each cladode were carefully brushed off with 70% alcohol, counted and stored.

To obtain further information on the population distribution of the insects in the sample plots, the data from the transect surveys and the 40 supplement cochineal samples (20 B category plants and 20 C + D category plants) were pooled.  The number of plants with 0, 1, 2 etc cochineal females per plant was obtained from these pooled data using the formula :

$$\frac{20}{x} \times \frac{y}{1} - 20 = Z \qquad \text{where}$$

x = number of colonized jointed cactus plants in all transects

y = number of uncolonized jointed cactus plants in all transects, and

z = number of uncolonized plants in a sample population of which 20 plants were colonized by D. austrinus.  For example : if x = 100 and y = 1 000 then for that particular sample date and area 180 plants will be uncolonized for each of the 20 colonized plants sampled.

From frequency tables (Table 11) the mean number of cochineal females per plant, standard deviations and population distribution parameters could be obtained for small (B) and large (C + D) plant categories.

## Cochineal Population Distributions

Several discrete frequency distributions were fitted to these frequency tables using the Fortran computer programme of Gates and Ethridge (1972). Table 11 also lists the chi-square values when expected values for cochineal distributions were compared with observed data from several localities and at various cochineal insect densities.

The best overall fit for all distributions tested was obtained with the negative binomial distribution. Some frequency tables could not be fitted to this distribution because low k-values caused iteration problems (H. van Ark, pers. comm.).

The mean density of cochineal insects per plant (Table 11) varied considerably because of seasonal fluctuations. Variances in relation to the means are high resulting in Co-efficients of Variation (CV) of 125% - 1 671%, which also expresses the non-even distribution of cochineal insects on their host plants. A few plants bear many cochineal insects but most are cochineal-free.

## Sample Size

The approximate number (N) of jointed cactus plants that have to be sampled at random to obtain a representative estimate of cochineal insect densities within 10% or 20% accuracy levels, was obtained using the formula by Karandinos (1976) :

$$N = \frac{\frac{Z^2\alpha}{2} \left(\frac{1}{\bar{x}} + \frac{1}{k}\right)}{D^2} \qquad \text{where}$$

$\dfrac{Z^2\alpha}{2}$ = confidence interval = 1,96

$\bar{x}$ = mean number of cochineal insects per plant (densities)

$k$ = parameter of the negative binomial distribution

$D$ = predetermined standard error as a decimal of the mean = 0,1 or 0,2.

Table 11.  Fitting D. austrinus population frequency distributions to various discrete known distributions indicated by chi-square values. (NS) indicates non-significant differences between observed and calculated figures at the 5% level. The means, variances, co-efficients of variation (CV) and k-values are also shown.

| Locality Date Plant size | Total Freq-uency = Z* | k Value | Mean Females per plant | Vari-ance | CV | Neg. Bino-mial | Ney-mans Type A | Log. with zeros | Pois-son |
|---|---|---|---|---|---|---|---|---|---|
| MIDDEL-BURGPLAAS | | | | | | Chi-square values | | | |
| Small plants | | | | | | | | | |
| Jan 1976 | 925 | 0,01 | 0,07 | 0,39 | 892 | 10,6[NS] | 17,3 | 10,9[NS] | 92 |
| Febr. 1977 | 679 | 0,02 | 0,09 | 0,51 | 788 | 12,7[NS] | 9,6 | 12,9[NS] | 106 |
| Nov. 1977 | 319 | 0,05 | 0,14 | 0,48 | 504 | 3,7[NS] | 0,6[NS] | 3,9[NS] | 48,5 |
| Aug. 1978 | 103 | 0,12 | 0,62 | 2,47 | 253 | 8,9[NS] | 5,4[NS] | 10,3[NS] | 70,2 |
| Aug. 1979 | 63 | 0,16 | 1,84 | 14,36 | 206 | 16,6[NS] | 12,5[NS] | – | 158 |
| Large plants | | | | | | | | | |
| Febr. 1977 | 292 | 0,03 | 0,26 | 1.88 | 527 | 8,4[NS] | 21,9 | – | 55 |
| Nov. 1977 | 323 | 0,03 | 0,17 | 0,83 | 534 | 8,4[NS] | 4,2[NS] | 8,7[NS] | 61,6 |
| Aug. 1978 | 108 | 0,17 | 1,22 | 10,53 | 265 | 35,1 | 28,7 | – | 168 |
| Aug. 1979 | 50 | 0,21 | 2,30 | 17,19 | 180 | 12,1[NS] | 23,3 | – | 176 |
| WESTONDALE | | | | | | | | | |
| Small plants | | | | | | | | | |
| Febr. 1977 | 263 | 0,12 | 0,42 | 3,49 | 447 | 23,9 | 47,4 | – | 150 |
| Aug. 1977 | 293 | 0,09 | 0,38 | 2,98 | 363 | 14,1[NS] | 21,6 | – | 192 |
| Nov. 1977 | 165 | 0,05 | 0,64 | 4,85 | 340 | 34,2 | 37,8 | – | 110 |
| Aug. 1978 | 251 | – | 0,41 | 2,99 | 421 | – | 10,2[NS] | – | 175 |
| Large plants | | | | | | | | | |
| Febr. 1977 | 130 | 0,52 | 1,32 | 17,35 | 314 | 39,8 | 83,2 | – | 333 |
| Aug. 1977 | 176 | 0,05 | 0,63 | 4,80 | 348 | 42,4 | 13,6[NS] | – | 139 |
| Nov. 1977 | 114 | 0,17 | 1,02 | 9,63 | 303 | 30,3 | 52,0 | – | 168 |
| Aug. 1978 | 292 | 0,03 | 0,28 | 1,68 | 463 | 11,5[NS] | 2,6[NS] | – | 73,9 |
| GLEN OVIS | | | | | | | | | |
| Small plants | | | | | | | | | |
| Aug. 1977 | 160 | 0,09 | 0,37 | 1,61 | 344 | 7,7[NS] | 5,6[NS] | 8,4[NS] | 101 |
| Nov. 1977 | 88 | 0,10 | 1,35 | 9,31 | 226 | 21,3[NS] | 8,2[NS] | – | 270 |
| Febr. 1978 | 80 | 0,14 | 0,92 | 6,12 | 267 | 10,2[NS] | 18,2 | – | 59,9 |
| Aug. 1978 | 67 | 0,15 | 1,41 | 10,31 | 227 | 13,6[NS] | 22,3 | – | 152 |
| Large plants | | | | | | | | | |
| Aug. 1977 | 68 | 0,17 | 1,26 | 7,13 | 212 | 7,6[NS] | 8,6[NS] | – | 91,5 |
| Nov. 1977 | 62 | 0,17 | 1,73 | 12,14 | 201 | 9,4[NS] | 9,4[NS] | – | 142 |
| Febr. 1978 | 60 | 0,34 | 0,83 | 2,27 | 181 | 4,8[NS] | 1,8[NS] | 6,6[NS] | 24[NS] |
| Aug. 1978 | 35 | 0,43 | 3,37 | 17,95 | 126 | 11,7[NS] | 9,3[NS] | – | 190 |
| GANNAHOEK | | | | | | | | | |
| Small plants | | | | | | | | | |
| Aug. 1976 | 3589 | 0,18 | 0,02 | 0,15 | 1671 | 5,2[NS] | 10,3[NS] | – | 308 |

* i.e. Z + 20 (calculated as shown in text).
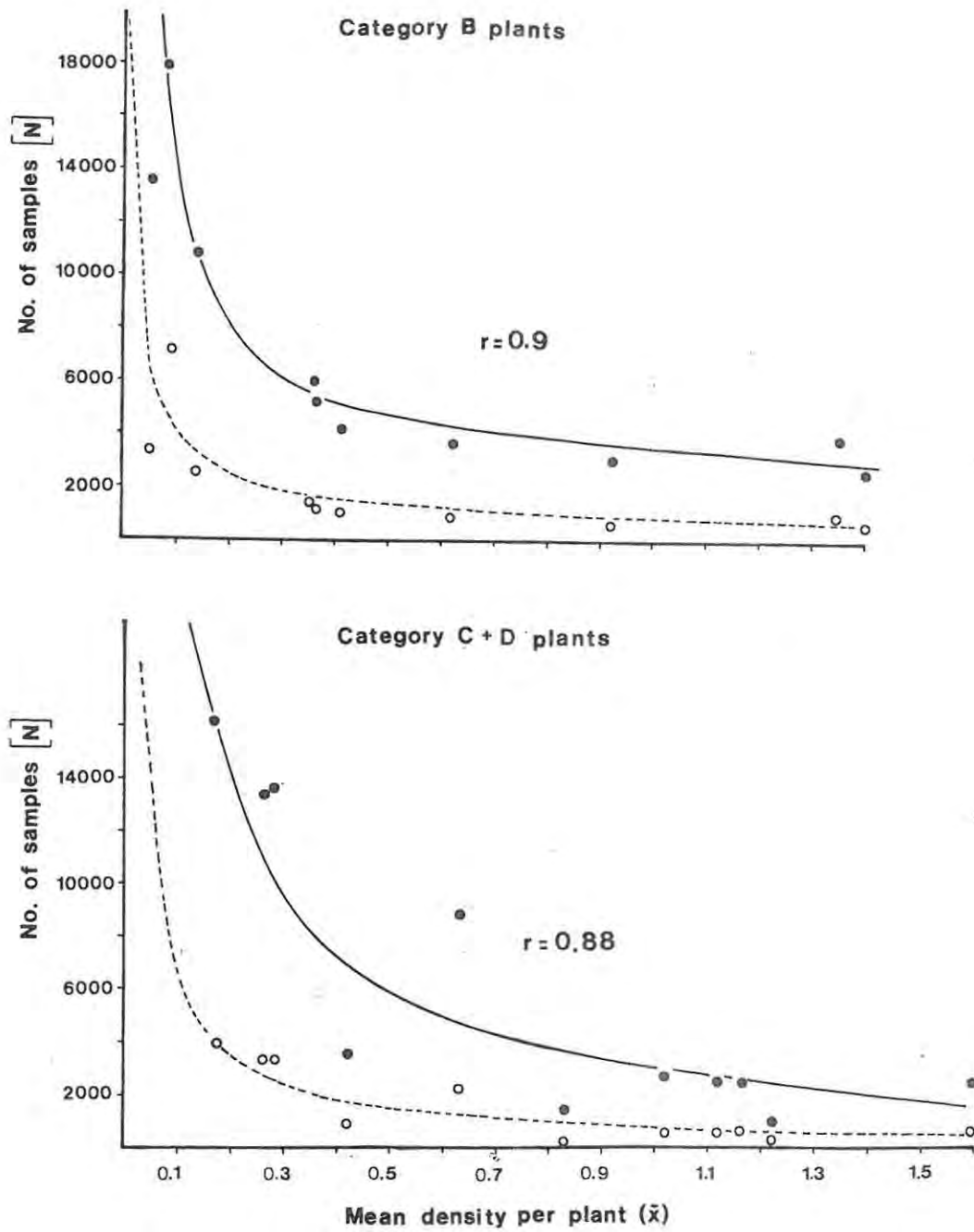
Fig. 18. Relationship between the mean densities of cochineal females per plant ($\bar{x}$) and the number of plant samples required for 10% (solid line) and 20% (broken line) precision levels.

The number of plant samples (N) corresponding to each mean and k-value (from Table 11) was plotted against cochineal density ($\bar{x}$). The resulting curves are described by a power regression for 10% and 20% accuracy levels and are graphically represented in fig. 18 for B category and C + D category jointed plants.

Fig. 18 shows that a sample of 1 000 to 2 000 plants at the 20% accuracy level would be adequate to cover the range of cochineal densities most likely to be encountered in the eastern Cape if categories B and C + D are sampled separately.

The sample curves shown in fig. 18 can however, be combined. This will then provide information on the number of plants (i.e. B, C and D categories combined) that need to be sampled to achieve accuracy at the 20% level (fig. 19).
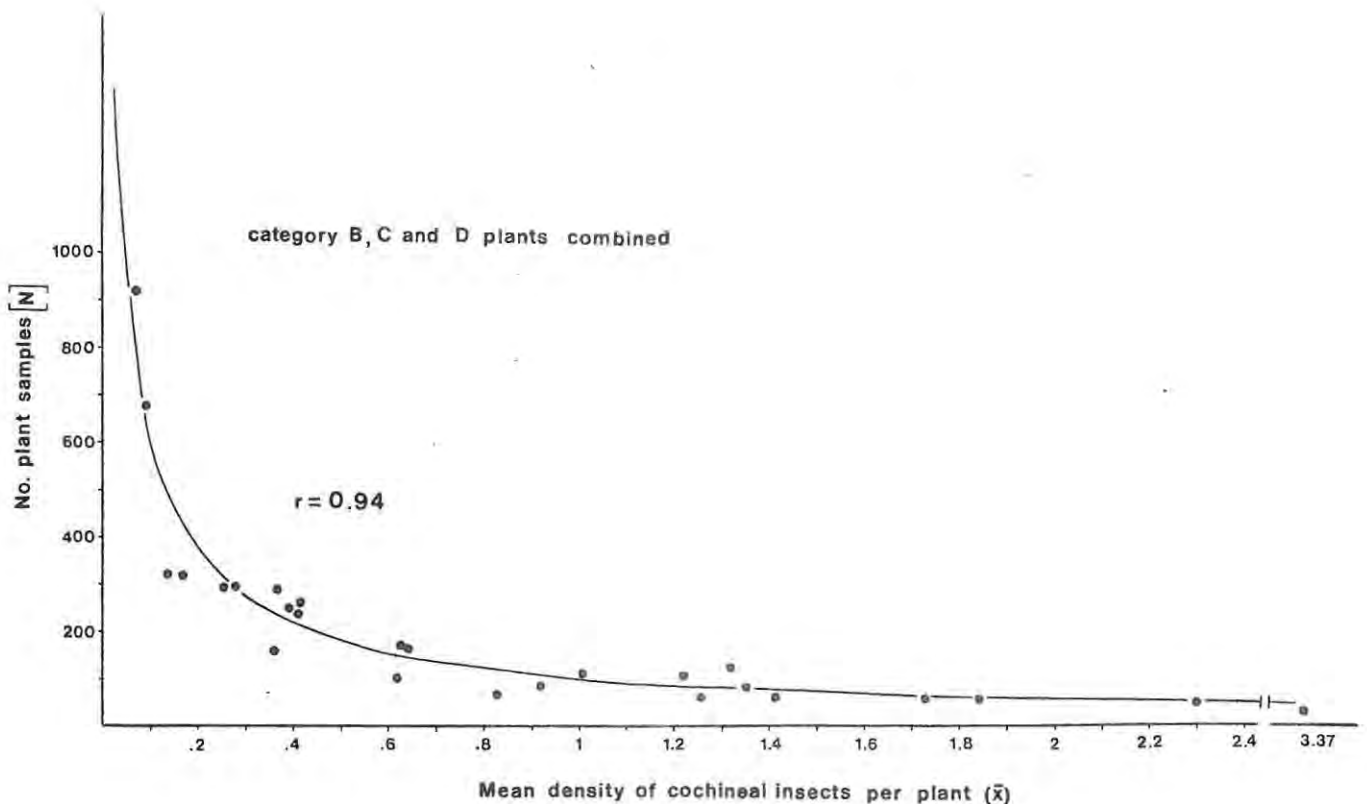


Fig. 19. Relationship between density of cochineal females per plant and the number of jointed cactus plants that should be sampled (all categories combined) for a required precision of 20%.

A typical density of D. austrinus in the field is 0,3 cochineal females per plant. Fig. 19 shows that about 300 plant samples (N) are required at this cochineal density to achieve a 20% accuracy and fewer at higher cochineal densities. Usually about 600 plants (i.e. if B, C and D plant categories are combined) were sampled which is adequate even at low cochineal population densities. There are thus cogent reasons for combining B, C and D category plants when estimating population densities of D. austrinus in the field.

There is no doubt from the results reported in this section that jointed cactus populations are highly aggregated and this fact is of fundamental importance in sampling the host plant and its natural enemies.

# 7. AGGREGATION INDICES AND THE DETECTION OF SPATIAL PATTERNS IN $\underline{O}$. $\underline{AURANTIACA}$

An aggregation index measures the degree of clustering of individuals, or it may be a measure of a populations' spatial pattern. There are several techniques and ways of measuring aggregation and they do not necessarily all measure the same thing (Pielou 1977). The detection of spatial patterns or cluster sizes on the other hand gives approximate measurements of the actual size or diameter of the clusters in an aggregated population and is discussed later.

Information on the spatial patterns and aggregation indices of jointed cactus infestations is important in understanding the ecology of the plant and has far reaching consequences in chemical or biological application methods (Zimmermann 1979). For example the degree of aggregation of an infestation will give information (a) on the history of a population; (b) on the efficiency that can be expected from chemical control and (c) on density dependence and the efficiency of $\underline{D}$. $\underline{austrinus}$. Although the aggregation of a jointed cactus infestation may be apparent (fig. 15) and its underlying causes obvious, it remains important to describe this aggregation in some quantitative way. Aggregation in jointed cactus may not only be caused by its mode of vegetative reproduction but may also be caused by, for example, habitat preferences.

Jointed cactus does not occur in discrete habitat units but occupies a continuum in space which necessitates the use of an artificial arbitrarily defined sample unit, in this case a quadrat. It follows that all measures of aggregation based on quadrat data will in practice give different values for different quadrat sizes although every index attempts to remain unaffected by quadrat size. For example, if a population is randomly distributed (Poisson) the distribution will remain Poisson and is not affected by quadrat size. This does not apply to the negative binomial distribution or any other distribution that describes aggregation. Much information on spatial patterns may be gained by examining the way in which the aggregation varies with quadrat size and for this purpose it is essential to use a quadrat with an area equal or smaller than the area of the clump. (Iwao 1972; Kershaw 1973). For jointed cactus it was found that a quadrat of 1 m² was adequate for most infestations (see chapter 4). Because populations

vary considerably in time it follows that at very low densities the chances
of individuals occurring in any sample unit is so low that their distribution
becomes random (Southwood 1978), or if an epidemic population becomes so
dense that every sample unit has one or more individuals in the quadrat, even
though they are aggregated, the population inclines towards the Poisson
(Waters 1959). These extremes were seldom encountered in the range of
jointed cactus infestations using a 1 m² quadrat.

Most indices described are related to each other and involve the ratio of
the mean and the variance in one or other way (Patil & Stiteler 1974). It
is the arrangement of these and other parameters which attempts to make
the index independent of mean density (Skellam 1952; Green 1966) and to a
lesser extent independent of quadrat size (Pielou 1977). The index must
always have a high correlation with clumping.


The following indices were tested for density dependence based on quadrat
counts of jointed cactus.


(a)  Variance/Mean Ratio (v/m)

This index is best known as the I-index of clumping (I = (v/m) - 1, where
v = variance and m = mean) of David and Moore (1954). It is still frequently
used by many ecologists. Its  history and merits are reviewed by Greig-
Smith (1964); Green (1966); Patil and Stiteler (1974) and Pielou (1977).


In contagious populations the value of this index however, is often influ-
enced by the density and the size (e.g. quadrat) of the sample unit
(Southwood 1978). Myers (1978) found that the v/m relationship was only
weakly related to density but it also showed a high correlation with her
dispersion co-efficient. Iwao (1970) used this dependence with density to
demonstrate mortality density dependence relationships.


The v/m index approximates unity for random (Poisson) distributions and is
always greater than unity for aggregated distributions.


(b)  Morisita Index (I $\sigma$ ) of Dispersion

Morisita (1964) proposed that the diversity of numbers of individuals per
quadrat be used as a measure of spatial pattern and is defined as

$$I\sigma = \frac{n \ \Sigma xi \ (xi - 1)}{t \ (t - 1)} \quad \text{where xi is the number}$$

of individuals in the $i^{th}$ quadrat, $t = \Sigma xi$. The value of $I\sigma$ is equal to unity in random distributions, and greater or less than unity in aggregated and regular distributions respectively. The index is discussed by Iwao (1970) and Stiteler and Patil (1971). One of the main advantages of this index is its claim of independence of the sample mean and a reasonable independence of the quadrat size. It is valid only if the quadrats used are small relative to the cluster size and if, within a cluster, the individuals are more or less randomly spaced (Poole 1974; Pielou 1977).

## (c)  k-Value of the Negative Binomial Distribution

When the number of plants per quadrat has a negative binomial distribution and provided the clumps are discrete, the parameter k may be used as a measure of aggregation (Anscombe 1950; Waters 1959; Waters & Henson 1959; Harcourt 1960, 1961, 1963; Bliss 1971; Hassell & May 1974 and Southwood 1978). Kuno (1968) suggested the use of the k-index regardless of the underlying distribution.

An interesting property of k is that it remains unaltered when the population is decreased randomly (Pielou 1977) assuming that the possibility of death of an individual is the same when density is high as when density is low. This suggests a density independent mortality in an aggregated population which seldom occurs (Taylor et al. 1979). It is therefore generally accepted that k is dependent of density (Myers 1978, Van Ark pers. comm.) Even if it is possible to assume that deaths occur randomly, k is determined not only by aggregation tendencies intrinsic to most species, but also by environmental heterogeneity. Separating one from the other is difficult (Poole 1974). In view of these limitations imposed to discrete clumps (which seldom occur) and the constraint of movement between clumps to validate the k-index, there are few organisms to which this can apply (Taylor et al. 1979). Beside the strong dependency of k on the mean it may also have the same value at two different densities, a serious defect in a parameter which is supposed to define aggregation (Taylor et al. 1979). The instability of k as an aggregation index was also noted by Harcourt (1963) who noticed that k frequently increased with the mean.

In general, k-values may range from 0 to infinity (= Poisson). Therefore, the smaller the k-value the greater the aggregation. In jointed cactus populations the k-values, based on 1 m² quadrats ranged from 0,061 - 0,446

and these are listed in Table 12. In these data there was no relationship between the variance and k for small plants, which contradicts Taylor's observation (Taylor 1979) that the status of k depends on the status of the variance as a measure of aggregation.

The k-values based on jointed cactus populations were however, unstable and generally did not relate to clumping. One reason for the instability may be the excessive counts of empty quadrats at very low density populations.

## (d) Lloyd's Index of Mean Crowding

Lloyd (1967) proposed an index of mean crowding, mainly for free moving animals that have a continuous habitat. He defines the index as the "mean number per individual of other individuals in the same unit" expressed by

$$m* = m + \frac{(V - 1)}{(m)}$$ where m = mean and V = variance. One advantage of

this index is that random deaths leave the index unaltered (Pielou 1977). The ratio of mean crowding to mean density can also be used as a relative measure of aggregation or "patchiness" (Lloyd 1967).

Iwao (1972) and Myers (1978) found that the m*-index of Lloyd has a strong relationship with density and therefore do not recommend it as a measure of aggregation.

## (e) Green's Coefficient of Dispersion

Green's index is described as

$$C_x = \frac{\frac{V}{m} - 1}{\Sigma x - 1}$$ and is a modification of the variance/mean ratio

which is supposed to remove several of its disadvantages (Green 1966). The $C_x$ - co-efficient varies from 0 (= randomness) to +1 (= maximum positive contagion) regardless of sample size and mean. Myers (1978) found that this index was independent of density and that it was a reliable indicator of aggregation.

## (f) Clumping Variable

A quick measure of aggregation (called the clumping variable - $I_z$) which was developed and used in this study on jointed cactus, is obtained from normal quadrat sampling by calculating the ratio of the sum of all individuals ($\Sigma x$)

in all quadrats over the total number of occupied quadrats ($\Sigma$ N). This index $I_z = \dfrac{\Sigma x}{\Sigma N}$ can vary from 1 for total randomness to large numbers for highly aggregated populations. The advantage of this method lies firstly in its simplicity and ease of calculation. This index is however, strongly dependent on quadrat size and it is essential to select a quadrat size which will give not less than approximately 20% empty quadrats. For the range of jointed cactus densities the 1 m² quadrat was acceptable for all population sizes encountered during the course of this study.

Table 12. Mean, variance and k-values calculated from jointed cactus 1 m² quadrat samples from 3 different localities and on different dates. A = isolated cladodes, B = small plants and C + D = medium and large plants.

| Locality and Plant Category | | Number quadrats sampled | Mean | Variance | K Value |
|---|---|---|---|---|---|
| GANNAHOEK | A | 3 000 | 1,24 | 10,15 | 0,206 |
| | A | 3 000 | 2,43 | 20,51 | 0,446 |
| | B | 3 000 | 1,87 | 14,00 | 0,154 |
| | B | 3 000 | 1,46 | 9,89 | 0,313 |
| | C + D | 3 000 | 0,21 | 0,53 | 0,167 |
| | C + D | 3 000 | 0,13 | 0,28 | 0,128 |
| MIDDELBURGPLAAS | A | 1 500 | 2,04 | 17,58 | 0,259 |
| | A | 1 500 | 1,38 | 9,94 | 0,196 |
| | B | 1 500 | 2,66 | 24,09 | 0,320 |
| | B | 1 500 | 3,83 | 48,46 | 0,310 |
| | C + D | 1 500 | 0,39 | 1,12 | 0,281 |
| | C + D | 3 000 | 0,22 | 0,78 | 0,142 |
| GLEN OVIS | A | 3 000 | 1,80 | 16,65 | 0,243 |
| | A | 635 | 0,88 | 6,12 | 0,127 |
| | B | 3 000 | 1,26 | 7,93 | 0,239 |
| | B | 641 | 1,51 | 11,03 | 0,189 |
| | C + D | 3 000 | 0,15 | 0,25 | 0,244 |
| | C + D | 3 000 | 0,12 | 0,17 | 0,199 |
| WESTONDALE | A | 3 000 | 0,55 | 2,90 | 0,146 |
| | A | 3 000 | 0,42 | 2,36 | 0,137 |
| | B | 3 000 | 0,60 | 3,06 | 0,146 |
| | B | 3 000 | 0,85 | 5,86 | 0,154 |
| | C + D | 3 000 | 0,09 | 0,13 | 0,203 |
| | C + D | 3 000 | 0,03 | 0,04 | 0,061 |

Insect and plant ecologists (Hairston et al. 1971; Kuno 1972; Iwao 1972, Myers 1978) have all used simulated programmes to evaluate and select suitable aggregation indices. One prerequisite for a reliable aggregation index is its true independence of density (Myers 1978) and not as a statistical artefact. In many plant and insect populations, however, aggregation tends to be larger in high densities as a result of vegetative reproduction in plants (e.g. jointed cactus) or parthenogenesis in insects (Forsythe and Gyrisco 1963).

Pre- and post-spray surveys on jointed cactus populations have shown that aggregation is marked at high (pre-spray) infestation levels and low in post-spray populations. In selecting a suitable aggregation index for jointed cactus we would therefore expect a positive correlation with density in pre-spray populations and a low correlation in post-spray (more random) populations. Therefore high index values at pre-spray and low values at post-spray infestations would best reflect the true situation for jointed cactus populations.

A Fortran computer programme (DISIND) was used to calculate the Morisita index of dispersion, variance/mean ratio and Green's co-efficient. The k-values and Lloyd's index were obtained from another Fortran computer programme (DISFRED). The clumping variable ($I_z$) was obtained from field data.

All indices were correlated with pre- and post-spray population densities based on small plants for three localities (figs 20 - 22). Table 13 represents a summary evaluation of the aggregation indices for jointed cactus populations. Numerical values were allocated as shown in Table 14 to the degree of correlation for each of the indices. The index with the highest positive score is the most suitable index for jointed cactus populations.

Results

The variance/mean ratio behaved uniformly well at all localities showing a high correlation with density for pre-spray populations and a low correlation for post-spray populations. This index also decreased according to expectation from high values in the pre-spray populations to low values in the post-spray populations. Myers (1978) found that the variance/mean index best described aggregation, although it was only weakly correlated to

GLEN OVIS     Category B
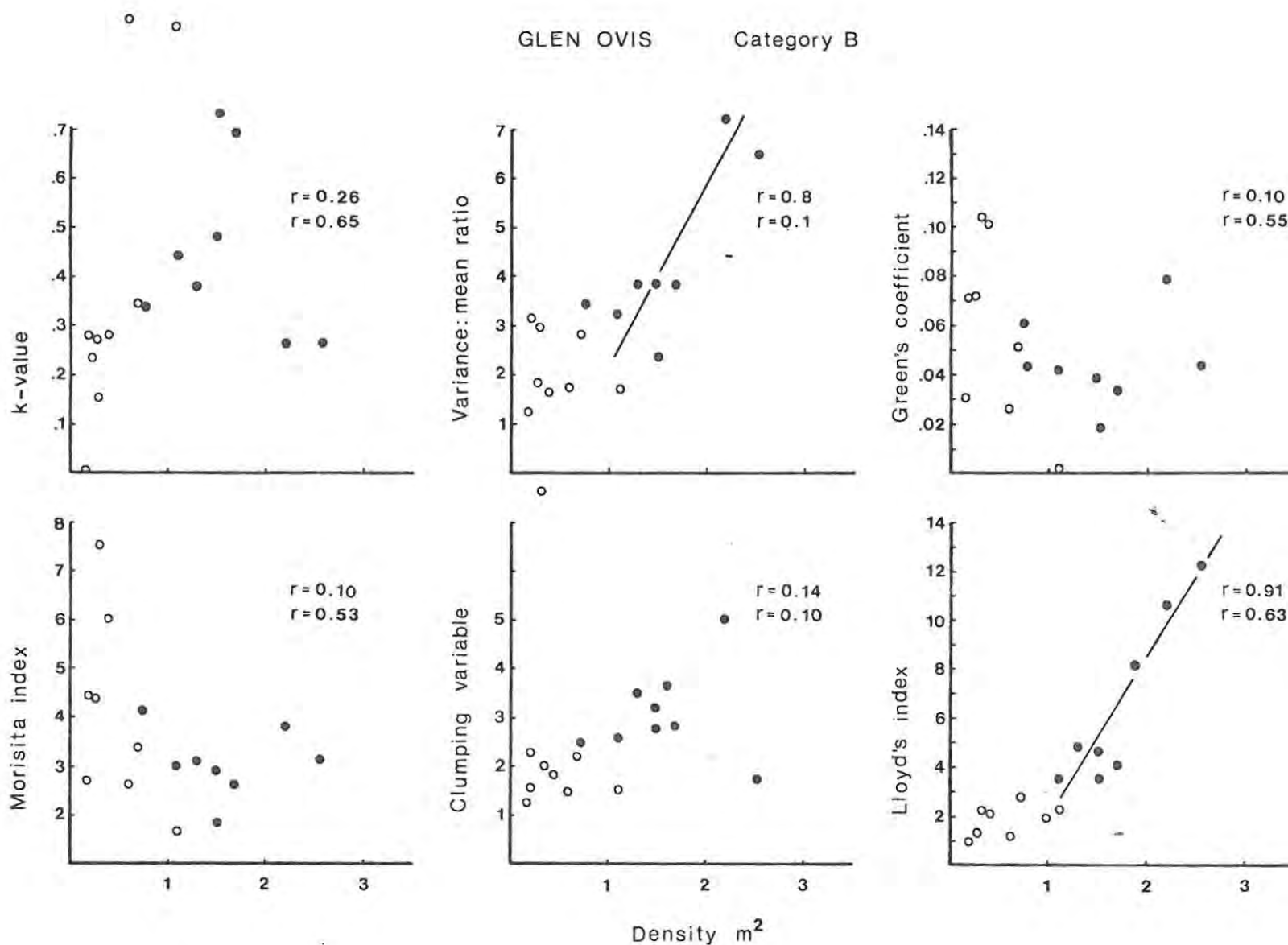
Fig. 20.  Relationship between six aggregation indices and densities of small jointed cactus plants for aggregated pre-spray (closed circles) and less aggregated post-spray (open circles) populations at Glen Ovis.  Significant correlations are shown (P < 0.05) by a solid line (pre-spray) or by a broken line (post-spray).  r-Values for pre-(upper figure) and post-spray (lower figure) are given.  Each data point is based on 100 samples.
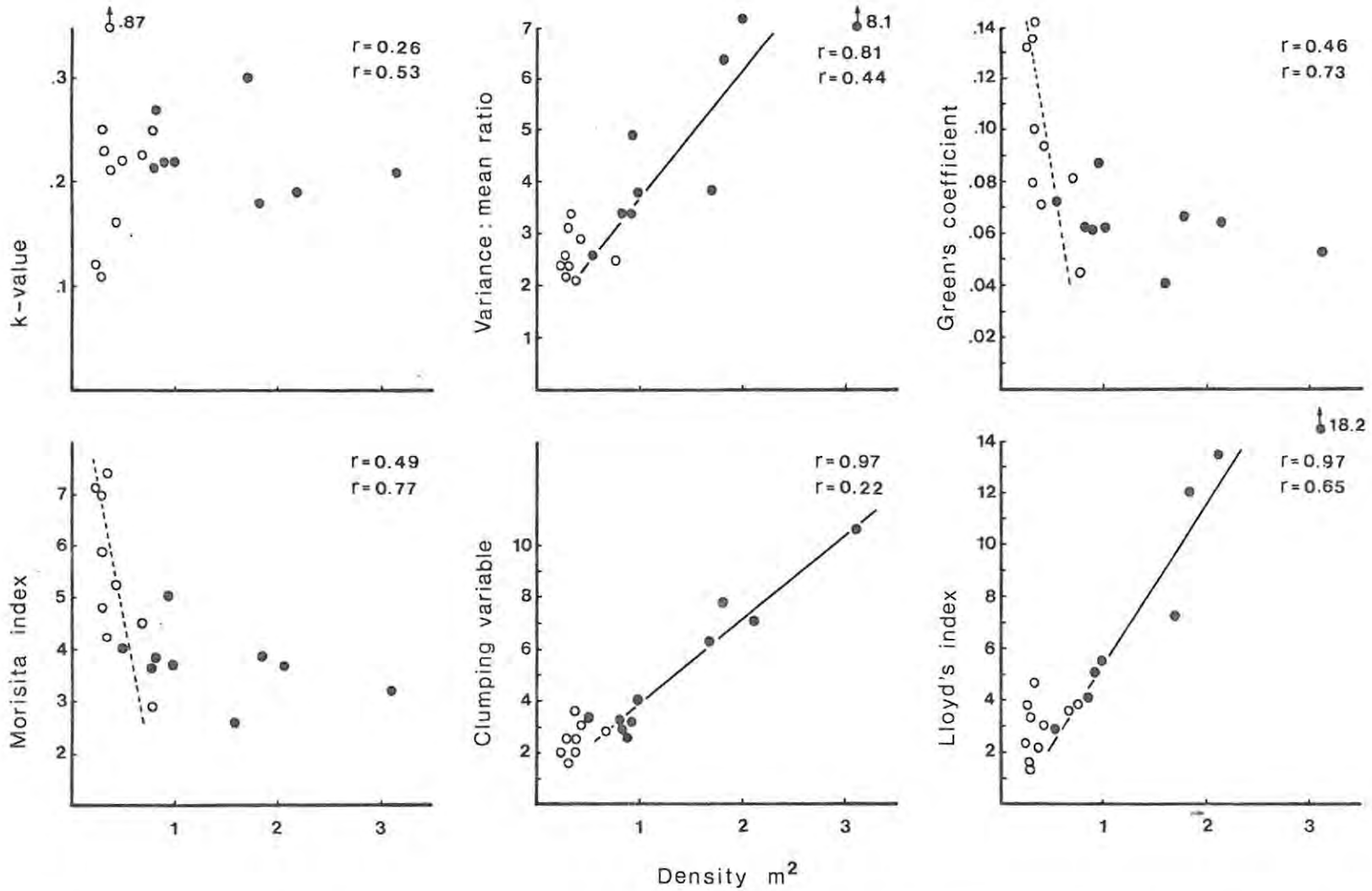
Fig. 21.  Relationship between six aggregation indices and densities of small jointed cactus plants for aggregated pre-spray (closed circles) and less aggregated post-spray (open circles) populations at Maastricht.  Significant correlations are shown (P = < 0,05) by a solid line (pre-spray) or by a broken line (post-spray).  r-Values for pre- (upper figure) and post-spray (lower figure) are given.  Each data point is based on 100 samples.
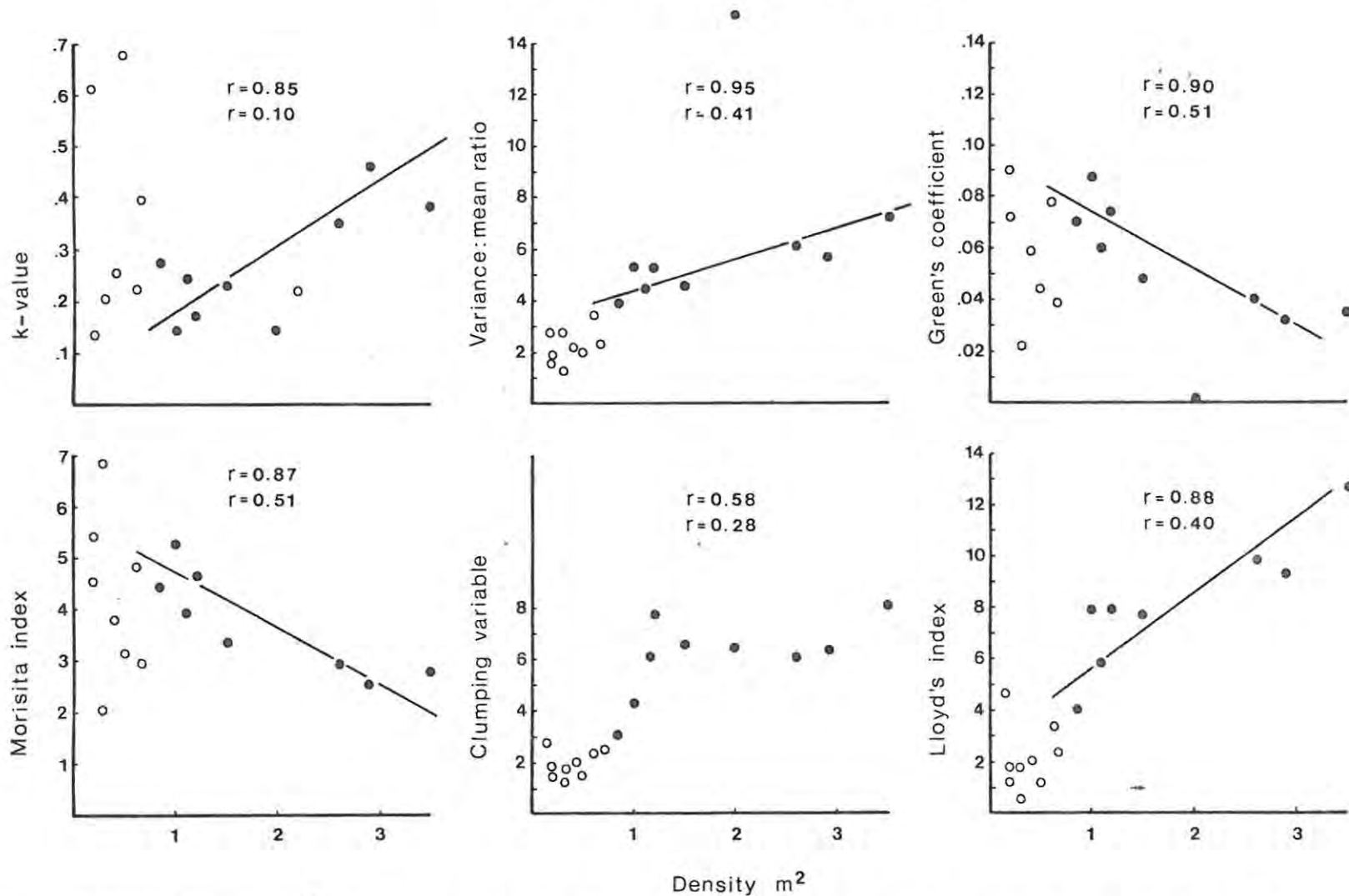
Fig. 22. Relationship between six aggregation indices and densities of small jointed cactus plants for aggregated pre-spray (closed circles) and less aggregated post-spray (open circles) populations at Middelburgplaas. Significant correlations are shown ( P = < 0,05) by a solid line (pre-spray) or by a broken line (post-spray). r-Values for pre- (upper figure) and post-spray (lower figure) are given. Each data point is based on 100 samples.

Table 13. Summary of results to select a suitable aggregation index for jointed cactus population
(see text and Table 14). Index values and their correlation with density is expected
to be high at pre-spray populations and low at post-spray populations.

| Indices | Correlation with density (score from Table 14) | | | | | | Evaluation at pre-spray populations | | | Total score |
| | Pre-spray | | | Post-spray | | | | | | |
| | Glen Ovis | Middel-burg-plaas | Maas-tricht | Glen Ovis | Middel-burg-plaas | Maas-tricht | Glen Ovis | Middel-burg-plaas | Maas-tricht | |
|---|---|---|---|---|---|---|---|---|---|---|
| Variance : mean ratio. | 8 | 8 | 9 | 8 | 5 | 5 | * | * | * | 43 |
| Lloyd's index | 9 | 8 | 9 | 3 | 5 | 2 | * | * | * | 36 |
| Clumping variable | 1 | 5 | 9 | 8 | 7 | 7 | * | * | * | 37 |
| Morisita index | 1 | 8 | 4 | 4 | 4 | 2 | X | ? | X | 23 |
| Green's coefficient | 1 | 9 | 4 | 4 | 4 | 2 | X | ? | X | 24 |
| k-value of n.b.d. | 2 | 8 | 2 | 3 | 8 | 4 | X | ? | X | 27 |

* = agrees with expectancy
X = disagrees with expectancy

density in her simulated data. Lloyd's index and the clumping variable also fulfilled the requirements for jointed cactus data while Green's co-efficient and the Morisita index were inconsistent and confusing. The values of r for these indices are inclined to decrease with density and often give higher values for the post-spray populations whereas the opposite should be the case. The k-indices are difficult to interpret and leave no clear picture, and this agrees with similar observations by Taylor et al. (1979) and Harcourt (1967).

For detailed quantification of aggregation of jointed cactus data using the 1 m² sampling frame, the variance/mean ratio index was adopted. It has the advantage that it is easy to compute and readily understandable.

Although the clumping variable has limited use because of certain prerequisites it is nevertheless useful because it provides a quick and simple field measure of aggregation which has practical advantages.

Table 14. Score for different r-values at pre- and post-spray populations of jointed cactus for score allocation in Table 13.

| r-Values of correlation coefficient | Score | |
|---|---|---|
| | Pre-spray | Post-spray |
| 0 - 0,09 | 0 | 9 |
| 0,1 - 0,19 | 1 | 8 |
| 0,2 - 0,29 | 2 | 7 |
| 0,3 - 0,39 | 3 | 6 |
| 0,4 - 0,49 | 4 | 5 |
| 0,5 - 0,59 | 5 | 4 |
| 0,6 - 0,69 | 6 | 3 |
| 0,7 - 0,79 | 7 | 2 |
| 0,8 - 0,89 | 8 | 1 |
| 0,0 - 0,99 | 9 | 0 |

Detection of Spatial Patterns in Jointed Cactus Infestations

Early attempts were made by Cooper (1961) and Greig-Smith (1964) followed by Anderson et al. (1969) and Kershaw (1973) to detect the approximate area

occupied by a clump, using the mean square of the sampling units vs. the quadrat size in a continuous grid of quadrats. Pielou (1977) however, lists seven drawbacks to this method. She questions the validity of the variance calculations and the doubling of blocksizes to different shapes. Goodall (1974) and Zahl (1974) proposed alterations to this method which supposedly overcome some of these shortcomings.

Iwao (1968) developed a method for analyzing the aggregation patterns in biological populations by using the relationship between mean crowding (m*) and density (m) which he found fitted a linear regression described by $m* = \alpha + \beta m$. The parameter $\alpha$ indicates the tendency to crowding or repulsion and $\beta$ is related to the pattern of habitat utilization (Southwood 1978). A further development of the m* - m method was its relationship to successive quadrat sizes which gave information on the area occupied by a clump and also information on the distribution patterns of clumps (Iwao 1972). Iwao and Kuno (1971) showed that the random removal or adding of individuals in a population changed m* and m at the same rate and they concluded that should quadrat sizes change, the same principle should apply. But if there is some clumping in the population the m* - m relationship obtained by successive changes in quadrat sizes would show a turning point around the quadrat size approximately equal to the clump area (Iwao 1972). He also used the $\rho$-index plotting it against quadrat sizes where

$$\rho = \frac{m*_i - m*_{i-1}}{m_i - m_{i-1}}$$

and i = 1, 2, 3 etc. is the order of quadrat sizes. For the smallest quadrat size $\rho = \frac{m*_1}{m_1}$. The index indicates the ratio of the increment of m* against m while the quadrat size increases from the $(i-1)^{th}$ to the $i^{th}$ size.

Pre- and post-spray data for jointed cactus on a 0,5 ha sample plot at Gannahoek and Middelburgplaas were used in this study. Twenty-five transects were combined to give 10 transects of 64 m lengths sampled with 1 m² frames. These m² samples were then successively enlarged to give 2, 4, 8, etc. m² block sizes. The m* and m values were then calculated for each block size. Plotting m* on m and changes of the $\rho$-index for the successive quadrat sizes both indicate clump size diameters.

Fig. 23 (a) is a schematic diagram showing the expected m* - m relation-
ship with successive increases of jointed cactus quadrat sample sizes.
The line (H)$\overset{*}{*}$ described by m* = $\alpha$ + $\beta$m for increasing quadrat sizes (see
fig. 23 (a)) is typical of aggregated population distributions consisting
of scattered clumps (fig. 15) and deviates from the Poisson line (A).
The deviation (B) from the Poisson line and the non-linear (convex) nature
of the m* on m line for increasing quadrat sizes are further indications
of the degree of aggregation in a population.  The m* on m regression
lines of pre-spray jointed cactus population surveys (figs  24 and 25)
also deviate from the Poisson line and thus fit the above description of
a highly aggregated population.  This deviation is, however, considerably
less for post-spray jointed cactus populations and shows that chemical
spraying of jointed cactus has eliminated most of the clumps leaving
behind a more random jointed cactus population.
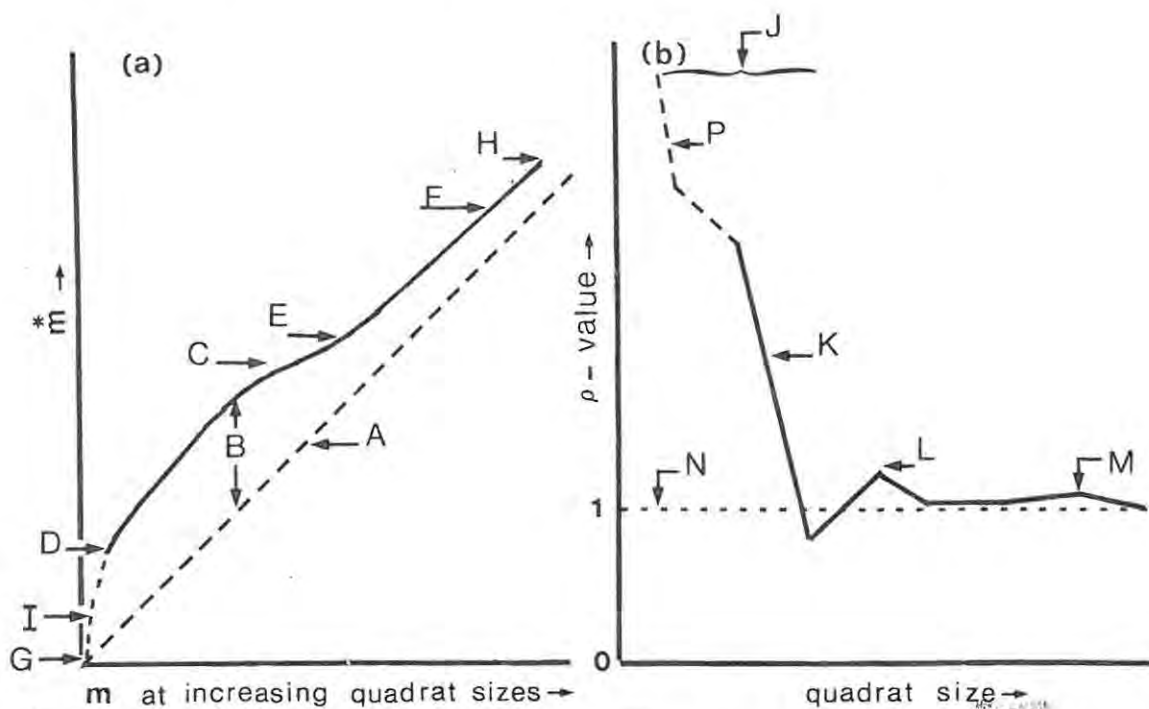


Fig. 23.  Schematic diagram of m* on m (left) and $\rho$-index (right)
          relationships with successive increases in jointed cactus
          quadrat samples.  For explanation of symbols see text.
          The broken lines (P) and (I) show the expected courses of
          the lines at quadrat sizes of less than 1 m$^2$.

The $\alpha$-value (intercept (G) of the regression lines) will increase with
increasing quadrat sizes until a turning point is reached (D) where the
quadrat size exceeds the clump area.  Such turning points are not clearly

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$\overset{*}{*}$ Symbols in text refer to the feature illustrated in fig. 23.

# GANNAHOEK

## pre-spray
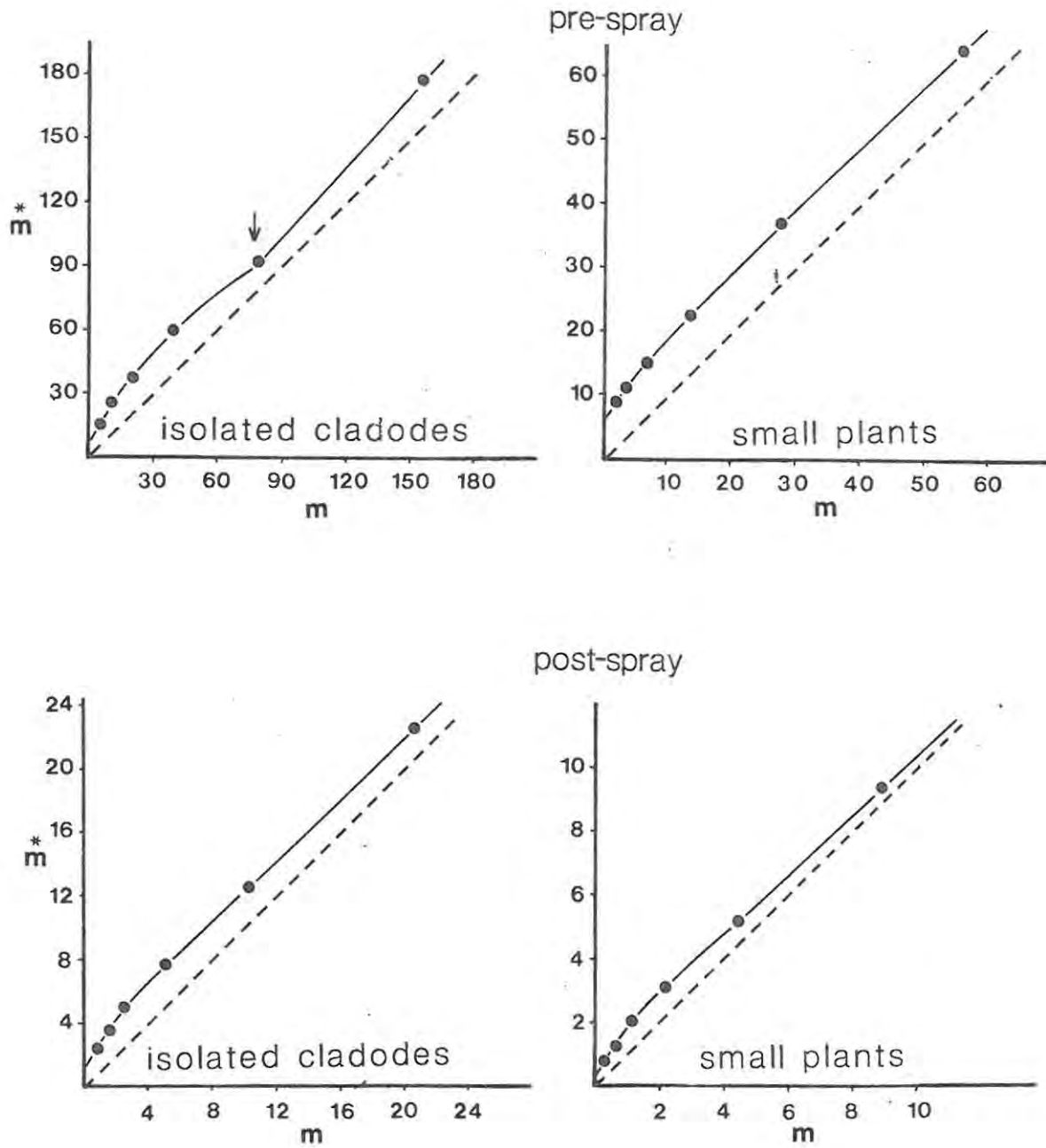


## post-spray



Fig. 24. The x* on x relationship for pre- and post-spray populations for small plant categories at Gannahoek. The broken line shows the relationship for a random (=Poisson) distribution (see text).
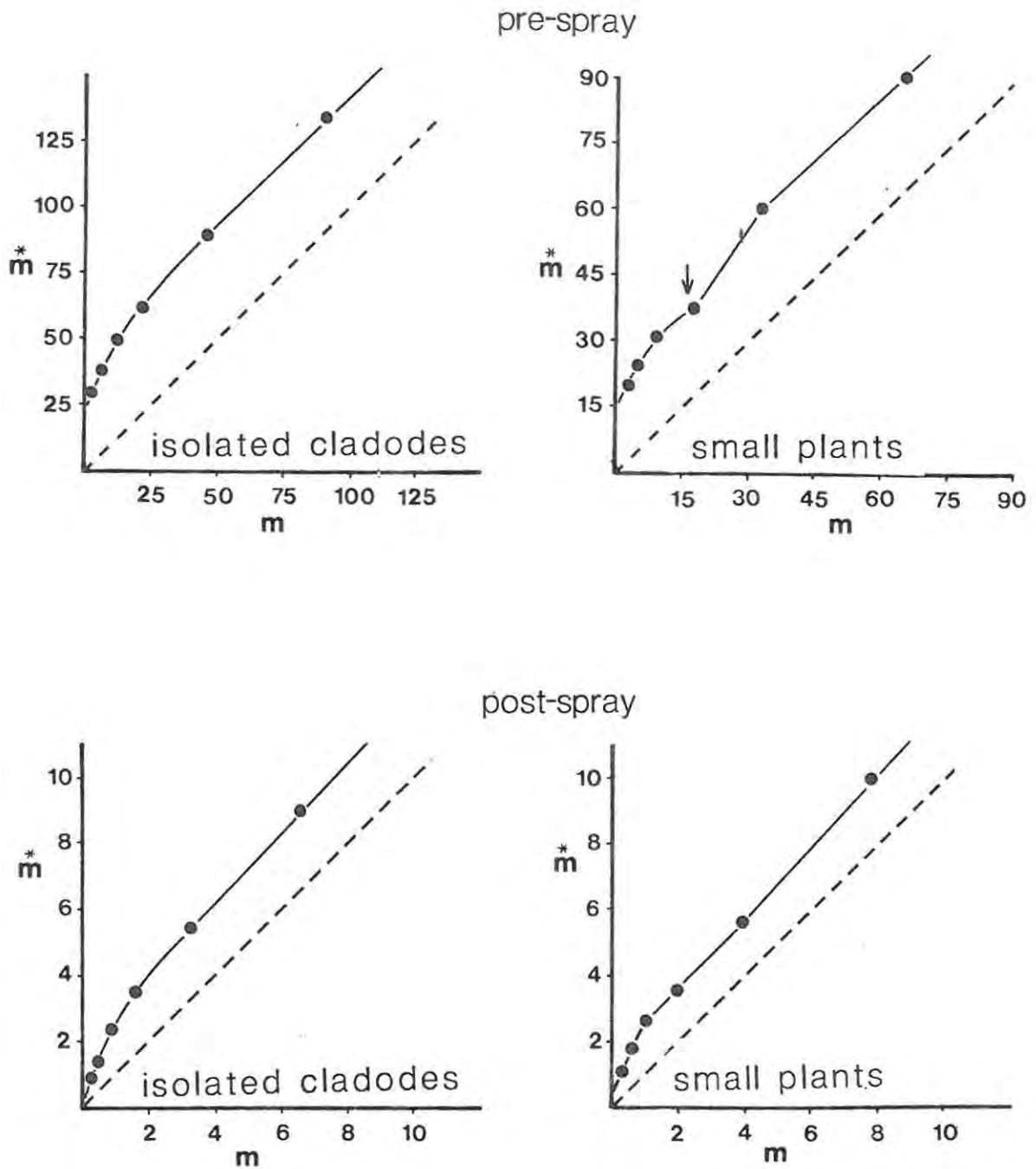
Fig. 25.   The x* on x relationship for pre- and post-spray popula-
           tions for small plant categories at Middelburgplaas.
           The broken line shows the relationship for a random
           (= Poisson) distribution (see text).

recognizable from figs 24 and 25 which suggests that clump sizes at the
smallest quadrat sizes must vary (Iwao 1972). As the quadrat sizes
increase, the regression line however, becomes linear (F) and parallel to
the Poisson (A) i.e. when the variances begin to stabilize.

The $\alpha$-values at the first quadrat size (D) are relatively high in figs
24 and 25 for pre-spray populations. This suggests further that the
smallest quadrat size used in this study was too large to detect clumps
of less than 1 m diameter. When continually decreasing the quadrat size
samples in an aggregated population, the intercept value of the regression
must eventually approach zero (Iwao 1972). The convex (C) nature of the
regression line and the prominent trough (E) at Middelburgplaas (fig. 25)
indicate the existence of compound clumps.

For clump area determinations Iwao (1972) suggested the $\rho$-index which is
also plotted against increasing quadrat size. Fig. 23 (b) is a schematic
diagram of such a relationship which can be expected for jointed cactus
population surveys at different quadrat sizes. Observed relationships
between the $\rho$-indices and quadrat sizes for Middelburgplaas and Gannahoek
are shown in fig. 26.

All $\rho$-values decreased rapidly (K in fig. 23 b) after the first quadrat
size indicating that it just exceeded a clump diameter of 1 m. Field
observations on jointed cactus populations, however, showed that clumps
of smaller and larger diameters than 1 m also occur but because 1 $m^2$ was
the smallest quadrat size used, smaller clumps could not be detected by
the $\rho$-index method. In fig. 23 (b) however, it is speculated that the
decreases in the $\rho$-indices as observed in fig. 26 are continuations from
similar decreases at smaller quadrat sizes (P) and that clumps of various
sizes (J) actually occur.

According to fig. 26 (Middelburgplaas, pre-spray population) compound
clumps of 8 m̃ also occurred (see arrow). Peaks (L) at the larger quad-
rat sizes indicate the presence of larger clumps and by visual inspection
of the scatter diagram of a jointed cactus infestation (fig. 15) such
larger clumps are recognizable.

The decrease of the $\rho$-indices in the post-spray jointed cactus populations
(fig. 26) was less drastic but clump sizes of 1 m or less were still
present. The $\rho$-values in the post-spray jointed cactus populations,
however, stabilized (M) rapidly around unity (N) when the same number of
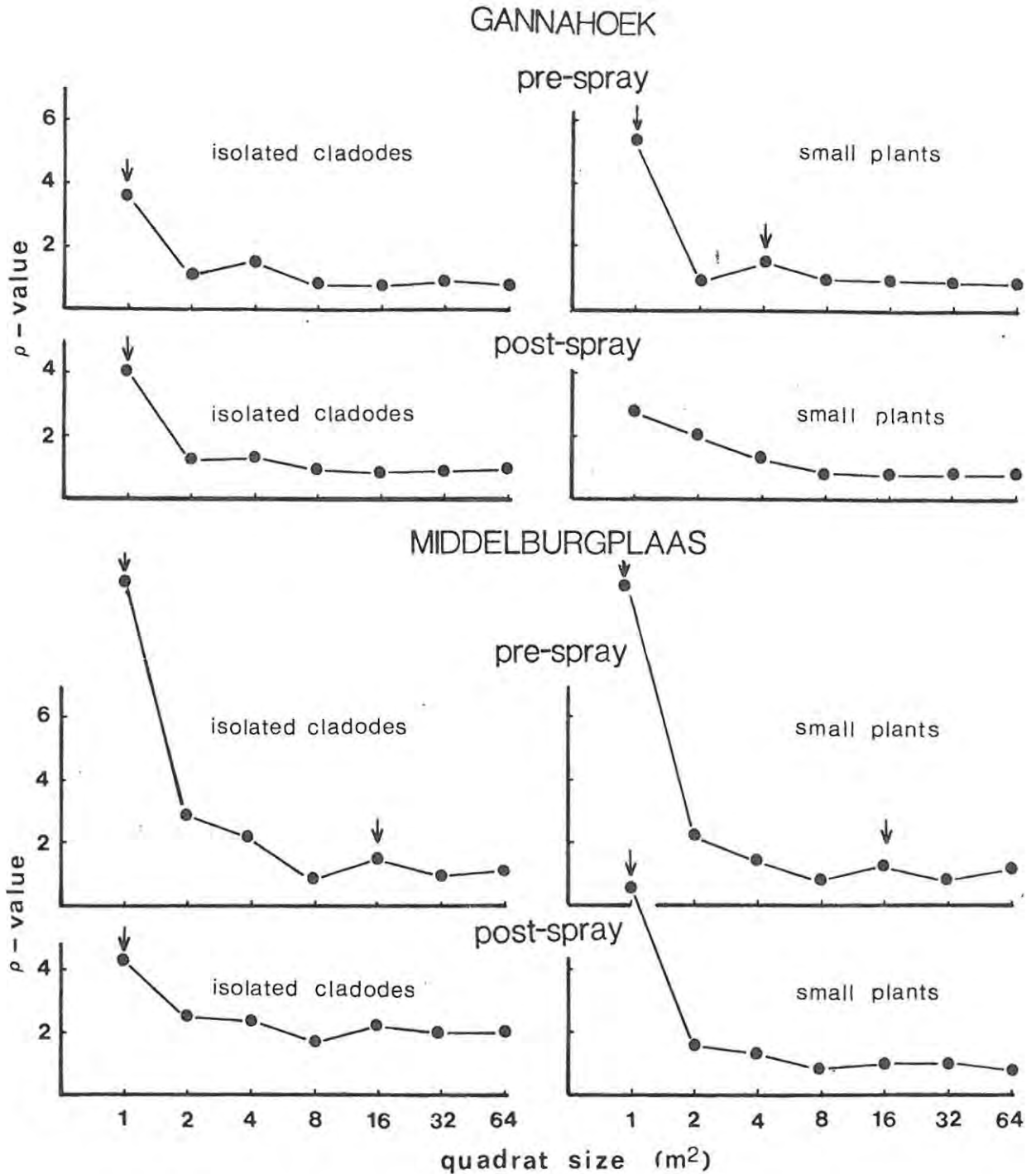
Fig. 26. The $\rho$-values plotted against quadrat sizes for pre- and
post-spray jointed cactus populations to detect clump
diameters for small plant size categories at Gannahoek
and Middelburgplaas. The arrows indicate clump sizes at
the corresponding quadrat size or smaller (see text).

clumps are found in each successive quadrat which is an indication of randomness.

Clumps play a key role in the efficient dispersal of D. austrinus crawlers and Gunn (1979) suggests that the efficiency of D. austrinus as a biological control agent of O. aurantiaca depends entirely on the presence of clumps and large plants in a jointed cactus population. The importance of aggregation in a jointed cactus population in relation to the efficiency of chemical control is fully discussed in appendix 5, and the interrelationship between aggregation, biological and chemical control is discussed in the next chapter.

## 8. HERBICIDAL CONTROL IN RELATION TO THE DISTRIBUTION OF JOINTED CACTUS AND EFFECTS ON COCHINEAL POPULATIONS

One of the main aims of this study was to assess quantitatively the efficiency of spray operators in detecting and treating jointed cactus in relation to the size and distribution of the target plant and also to investigate the effects of this herbicidal treatment on cochineal populations (Zimmermann 1979).

These experiments were done near Grahamstown on the farm Maastricht (see Table 4). A total area of 6 ha was selected for spot-spray application (fig. 27) of the iso-octyl ester of Picloram (Tordon M 3142 at 0,19% of 480 g.a.e./ $\ell$) diluted with illuminating paraffin (kerosene). This herbicide mixture was used for jointed cactus control in South Africa until August 1981. Because the herbicide usually takes several weeks to produce visible symptoms on jointed cactus, Waxolene oil solvent dye (1 g$\ell$ ) was added to the spray solution. By comparing numbers of dyed and undyed plants, a few days after spraying, efficiency of the spray teams could be assessed.

Jointed cactus and cochineal counts were made before and after spraying in ninety randomly selected permanent transects. All results were expressed as density of cactus plants per $m^2$ (= aggregation) or as the number of plants in the total 4 500 metre squares sampled.



Fig. 27. Chemical control is by spot spraying of scattered jointed cactus plants.

All four plant categories (A – D) were counted and the presence or absence of cochineal colonies was recorded for each plant category.

The spray team comprised permanently employed spray operators. They did not know that their performance was being assessed and they were not aware of the significance of the small pegs denoting the transect lines.

Efficiency of Herbicidal Control

Overall efficiency of the spray team was found to be low. Table 15 shows that about 21% of the single cladodes, 32% of small plants and about 12% of the medium-sized plants were overlooked during herbicide applications. The spray operators were always 100% efficient in locating and treating large plants. The smaller plants are often hidden under grass and low bushes which must in part explain the low searching efficiency of the spray team. If this were the only or overriding cause, however, a high correlation would be expected between the amount of ground cover and searching efficiency. Percentage ground cover (fig. 28) was assessed visually for each of the 4 500 metre squares. Using pre- and post-spray treatment data for isolated plants only (to eliminate any influence of aggregation) no significant correlation was established between searching efficiency and ground cover (fig. 28). Clearly some other factor is of major importance.

Table 15. Efficiency of spray teams in treating O. aurantiaca plants with herbicide.

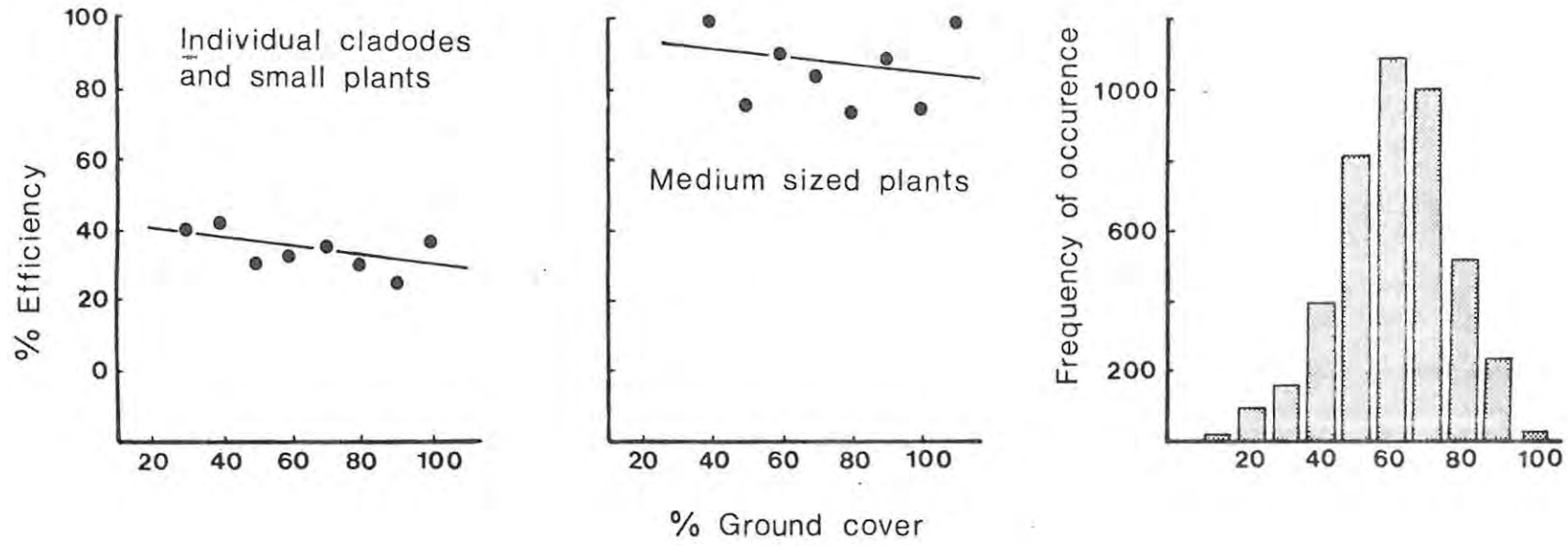|  | Single cladodes | Small plants | Medium plants | Large plants |
|---|---|---|---|---|
| No. of plants in 4500 metre squares prior to treatment | 3777 | 5381 | 346 | 31 |
| No. of plants remaining untreated | 805 | 1694 | 41 | 0 |
| Percentage untreated plants | 21.3 | 31.5 | 11.9 | 0 |

Fig. 28. Percentage efficiency of the spray team in locating and treating isolated individuals of
O. aurantiaca as a function of the percentage ground cover together with a histogram of the
frequency distribution of ground cover.

The distribution of O. aurantiaca in the field is highly aggregated. It is clear that if aggregation were total, i.e. if all individual plants were found in clumps, searching efficiency of spray teams would increase greatly because no isolated plants would be missed and clumps would be easily located. Conversely, if individual plants were isolated and randomly distributed, searching would be extremely difficult and treatment efficiency would fall markedly, especially in the case of smaller plants. The importance of clumping as a determinant of searching efficiency is illustrated in fig. 29. The correlation between searching efficiency and clump size was highly significant (P < 0,001) for individual cladodes and smaller plants, and significant (P < 0,05) for medium-sized plants.

Treatment efficiency was also greater than 80% for the medium-sized plants (which are easily visible), and where these were aggregated in clumps of more than five individuals, efficiency was 100% (fig. 29).

## Herbicidal Treatments and Host Plant Distribution in Relation to Cochineal Populations

All large plants were eliminated by herbicidal treatment (Table 15) so that all cochineal insects died on these plants. Pre- and post-treatment counts of the smaller plants show a marked reduction in the percentage of cochineal-bearing plants after spraying (Table 16).

If cochineal insects were randomly distributed on their host plants (irrespective of plant size or the degree of aggregation), then a reduction in host numbers following herbicidal treatment would result in a proportionate reduction in host numbers of plants bearing cochineal. The percentage of cactus plants bearing D. austrinus would be expected to remain unchanged. However, a significant positive correlation was found between the presence of cochineal and the degree of aggregation of the host-plants (fig. 30). For individual cladodes and small plants the correlation was significant at P < 0,001 and at P < 0,05 for medium-sized plants. Bearing in mind that the efficiency of herbicide treatment is also correlated positively with aggregation of the cactus (fig. 29), the marked reduction in the percentage of cochineal insects present after herbicidal treatment (Table 16), is explained.
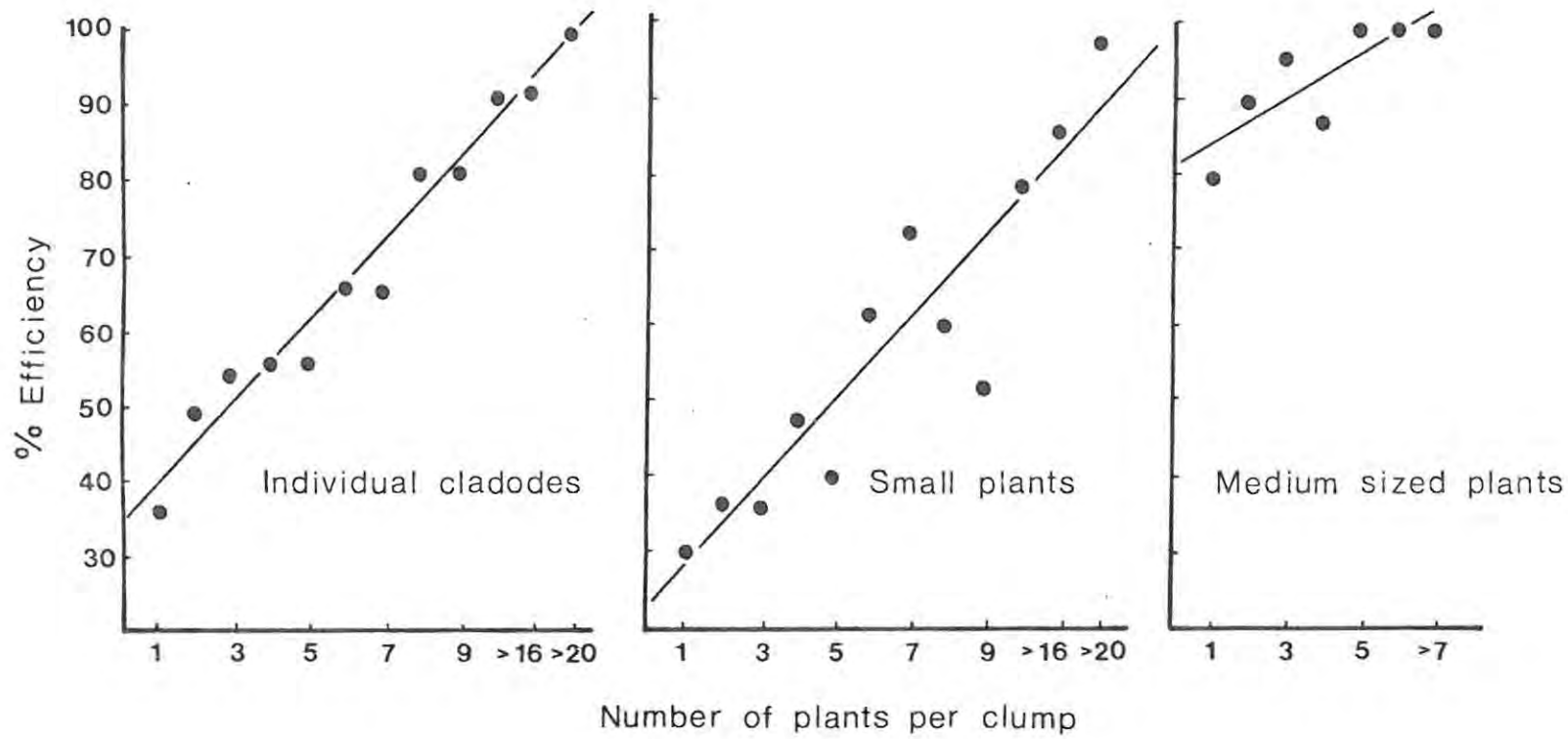
Fig. 29.  Percentage searching efficiency of the spray team as a function of aggregation (clump size) of O. aurantiaca.
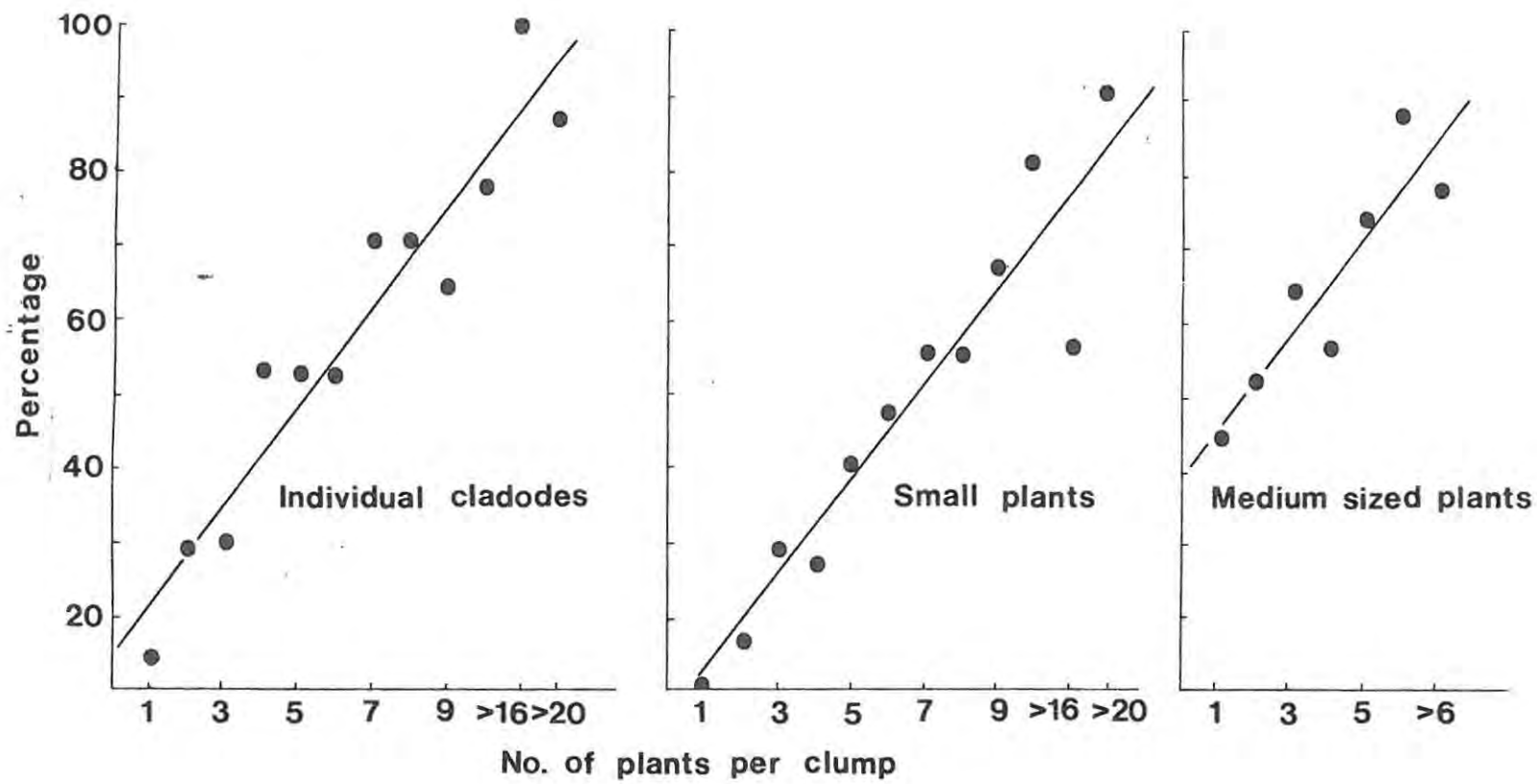
Fig. 30.  The percentage of O. aurantiaca plants bearing populations of the cochineal, D. austrinus as a function of plant aggregation.

Table 16. Number and percentage of O. aurantiaca plants bearing
populations of the cochineal, D. austrinus, before and
after herbicidal treatment.

| | Individual cladodes | | | Small plants | | | Medium plants | | |
|---|---|---|---|---|---|---|---|---|---|
| | Total | With cochineal | (%) | Total | With cochineal | (%) | Total | With cochineal | (%) |
| Before treatment | 3777 | 1267 | 33,5 | 5381 | 1631 | 30,3 | 346 | 181 | 52,3 |
| After treatment | 805 | 114 | 14,1 | 1694 | 206 | 12,2 | 41 | 9 | 21,9 |

The continued selective spraying of cochineal colonized plants since 1957
must have contributed to the diminution of cochineal populations over
the years. This also explains in part the increasing distrust in the
capabilities of cochineal to contribute to the control of the weed.

These findings have clear implications for rationalizing the herbicidal
and biological control programmes against jointed cactus in South Africa.
It is now opportune to define those areas that are suitable for biological
control. Spraying in heavy infestation areas with high cochineal popu-
lations (mainly comprising of open veld) should cease because the large
plants and clumps that are most effectively controlled chemically,
comprise the main reservoir for cochineal populations. Spraying in these
areas could be limited to selected areas only e.g. in riverine bush where
cochineal is less effective than in open vegetation. The decision to
use either chemical or biological control procedures in any area should
be based on frequent assessments of jointed cactus and natural enemy
populations. In biological control areas the effect of D. austrinus
could e.g. be improved by enhancing dispersal of the insect (Gunn 1979).

These studies have further shown that the efficiency of chemical control
is low and that spray teams should be instructed to direct their atten-
tion mainly towards large plants and clumps of the weed. Efficiency of
control would then increase in relation to time and money spent.
Savings of 35 - 47% in total costs were obtained by modifying the spray
techniques accordingly (Zimmermann & Malan 1980). Details on the modified
technique are outlined in appendix 5.

It was also clear from this study that a premium should be placed on research aimed at replacement of the paraffin carrier in the herbicide with substitutes that are cheaper and do not have an insecticidal effect on the natural enemies of jointed cactus.  Recent studies by Zimmermann et al. (1981) have shown that a water based herbicide, namely MSMA (Monosodium methanearsonate), is a highly satisfactory substitute.

## 9. COCHINEAL INSECT ABUNDANCE IN RELATION TO AGGREGATION AND DENSITY OF THE HOST PLANT

It was shown above that the presence of cochineal insects is positively associated with aggregation of the host plant and that this relationship is affected by herbicidal control practices. A continuation of this study was made to investigate these relationships at different levels of cochineal incidence and at different host plant densities. This understanding is important because stabilization of jointed cactus populations will depend mainly on the reproduction rate of jointed cactus and on the density and increase of D. austrinus. Factors that limit the density and increase of cochineal insects should therefore be identified.

Data from five experimental plots that were sampled at three·monthly inter-vals for four years by means of 30 randomly scattered but permanent trans-ects were used for this study. (Full details on the sampling plots and sampling methods have been described).

From the four year's sampling data, the combined surveys with low, medium and high levels of jointed cactus infestations were selected and analyzed for density dependence. Only small plants were investigated in this study because this was the most abundant category and they were present at all aggregation levels. Only the combined medium and large plants at Middelburgplaas were included in this study.

The changes in plant density over the four year period are illustrated in figs 39 - 41. Aggregation during the same time did not change much and was always high. Aggregation was defined as the number of plants in a $m^2$ (= clump). One plant per $m^2$ was taken to be random (= non-clumped) and >20 plants per $m^2$ was rated as highly clumped. In this study all transects in each plot were divided into equal groups, one above and the other below average (= transect average) jointed cactus infestation levels. The number of transects was doubled by dividing each of the 50 m long transects in half, because long transects often included high and low density patches and the object of this study was to analyze them separately. The cochineal colonization for each clump size and for each of the two density levels was then calculated.

Endemic, Median and Epidemic Levels of Cochineal Abundance

The relationships between high and low density transects at different levels
of cochineal abundance and aggregation are illustrated in fig. 31 and dia-
grammatically presented in fig. 32.

Low Cochineal Abundance (= Endemic Level)

Cochineal abundance for all aggregation levels at endemic cochineal popula-
tions were low and exceeded 20% of plants colonized only at the >20 plants
per m² aggregation level (fig. 31). The difference between high and low
density transects is insignificantly small. Indications of a slight but
consistent increase of cochineal bearing plants occurred with increasing
aggregation (fig. 31).

Median Cochineal Abundance Level (= Median Level)

The percentage of plants bearing cochineal was higher than in the preceeding
level but seldom exceeded 40% of plants colonized. The linear relationship
between cochineal abundance and aggregation is, however, obvious with clear
differences between high and low density transects (fig. 31). Low density
transects showed less cochineal colonization than the high density tran-
sects. This relationship was also recorded for Maastricht for isolated
cladodes, small plants and medium and large plants (fig. 30).

High Cochineal Abundance (= Epidemic Level)

The percentage of plants bearing cochineal insects was highest in dense
transects but the linear relationship between cochineal bearing plants and
aggregation has become less prominent and is inclined to follow a horizontal
line (fig. 31). There are no differences between high and low density
transects.

The numerical response i.e. the relationship between the abundance of cochi-
neal insects and host plant densities and aggregation is illustrated in a
diagram (fig. 32). The numerical response follows a sigmoid pattern which
is typical of many animal predator-prey systems (Hassell 1978). The lack of
density dependence in the endemic level which corresponds to the "extinction
valley" of Southwood and Comins'(1976) synoptic model, occurs at low
cochineal insect and host plant abundance. The prominent density dependent
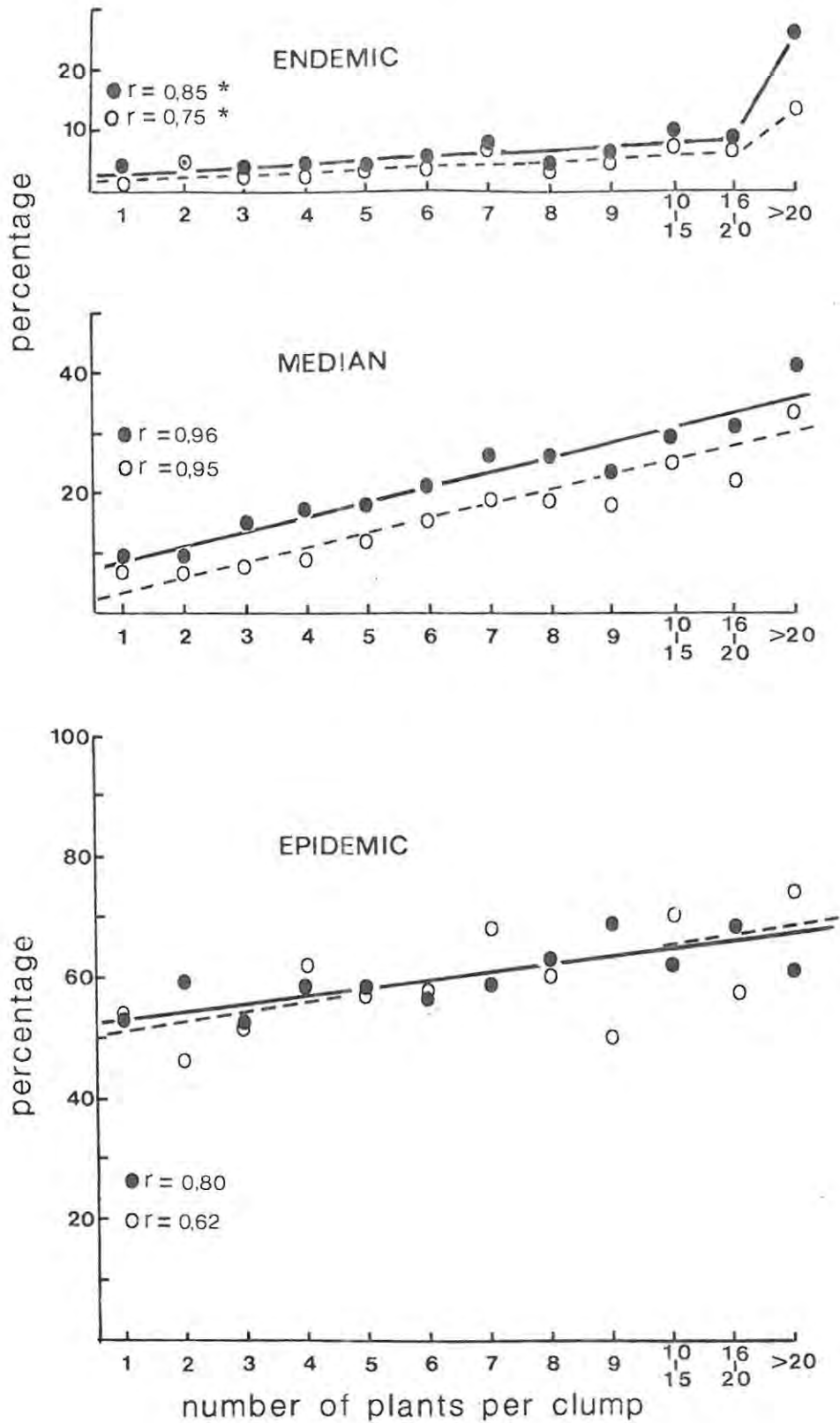
Fig. 31. The percentage cochineal abundance in high (closed circles) and low (open circles) density transects of jointed cactus as a function of plant aggregation. Three abundance levels are identified namely endemic, median and epidemic (see text). *Regressions are calculated up to a density of 16 - 20 plants per clump for the endemic levels.
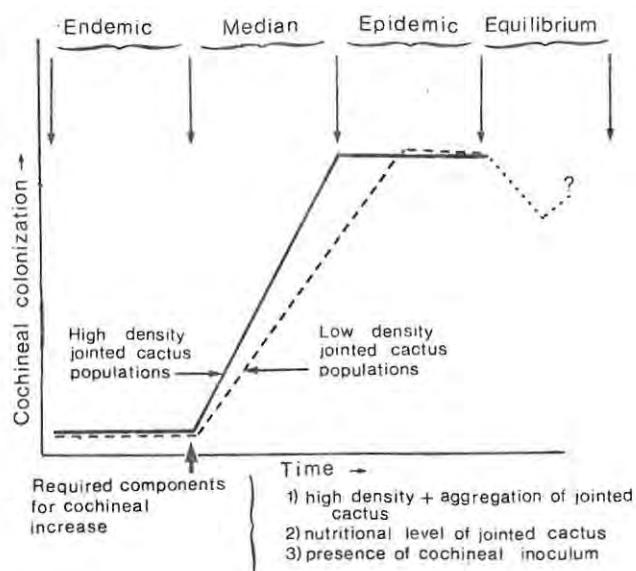
Fig. 32a. A diagrammatic representation of the three levels of cochineal insect abundance in a jointed cactus infestation illustrated as a numerical response curve. Three interacting components are required before the cochineal insects can increase to median and epidemic levels and these are listed in the figure. The broken line indicates a delayed density dependent response in the median level as observed for jointed cactus density transects.
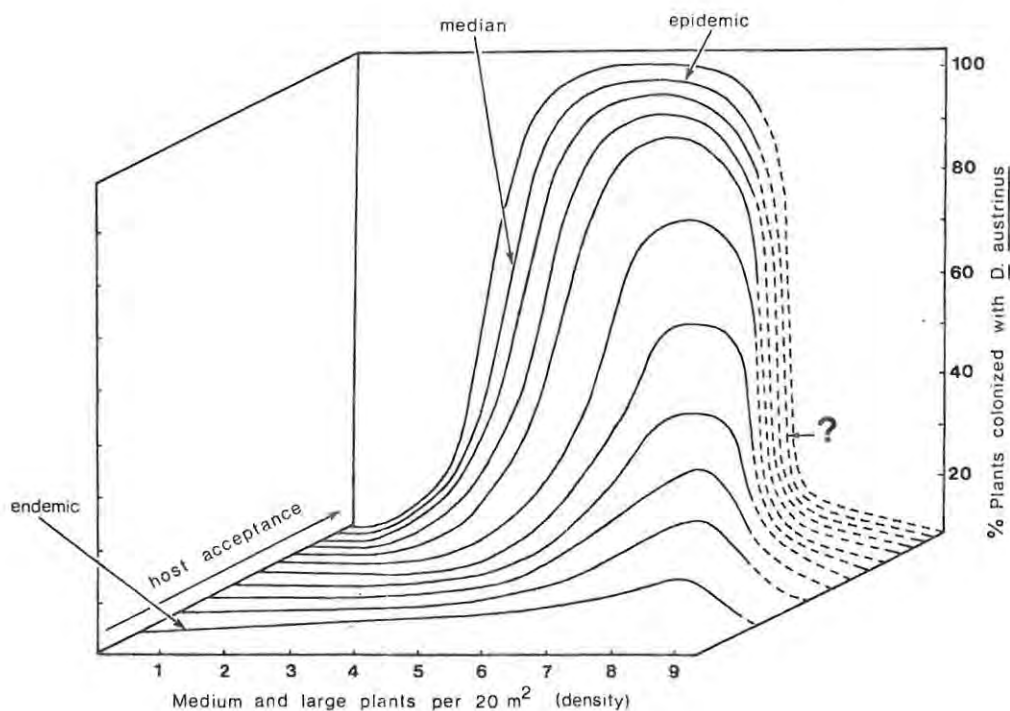


Fig. 32b. A sepeculative synoptic model of a jointed cactus infestation affected by D. austrinus as a function of weed density and host plant acceptance by dispersing cochineal crawlers. It is assumed that an adequate cochineal inoculum is present (After Southwood & Comins 1976).

increase of the median level (fig. 32a) towards the "epidemic ridge"
(fig. 32b) hinges upon at least three parameters namely (i) a minimum
density and aggregation level of the jointed cactus infestations ($>1$
medium and large plants per 10 $m^2$); (ii) host plant acceptance of dispersing
cochineal crawlers which presumably depend on the nutritional value of the
host plants (see discussion) and (iii) the presence of an adequate cochineal
inoculum.

The epidemic ridge of the sigmoid curve is reached at the upper equilibrium
point where density dependence ceases and where the rate of cochineal
colonization varies between 40 and 80%. This level is normally of short
duration and the curve soon falls again towards the endemic level (= "crash
valley") or starts to oscillate around the equilibrium level after about
12 months (fig. 43).

Because of the continuous chemical spraying of jointed cactus populations
and the consequent selective elimination of cochineal insects, median and
epidemic population levels seldom occur because parameters (1) and (3)
(see fig. 32a) become rare. Most jointed cactus infestations therefore are
at the endemic level. The cochineal inoculum in an endemic population
level is found mainly in the few large plants and clumps (see endemic level
in fig. 31), and these will again be eliminated after a follow-up chemical
treatment. This continuous process of selective cochineal elimination may
eventually carry the cochineal population to extinction.

The slow increase in cochineal populations in infestations of jointed cactus
after herbicidal treatment, as described in chapter 10 (see fig. 33), is a
feature of great concern. The apparent inability of cochineal to spread
efficiently at low densities is mainly an artefact brought about by the
chemical spray campaign because chemical spraying not only destroys the main
reservoirs of D. austrinus as shown in this study, but also eliminates all
points of dispersal and reduces interplant distances and that in turn pre-
vents dispersal.

## 10. RECOVERY OF JOINTED CACTUS INFESTATIONS
## AFTER HERBICIDAL TREATMENT

Weed inspectors recommend that follow-up operations on jointed cactus
infestations after herbicidal treatment (= residue populations) should not
be delayed for more than 6 - 8 months (ANON 1972), but few farmers heed
this recommendation.

The aim of the investigation reported in this chapter was to evaluate this
recommendation by means of projections based on growth curves of jointed
cactus after herbicidal treatment and at the same time to follow the fate
of the residue cochineal insect population.  It has already been shown that
cochineal insect populations are selectively eliminated as a result of
normal spray operations and that the residue jointed cactus population is
virtually free of cochineal.  This explains the low incidence of cochineal
in areas where heavy spraying is practiced and where cochineal insects are
traditionally known to exert considerable pressure on infestations.

One heavy and one medium jointed cactus infestation was sprayed by the same
team at 'Rietmond' (26° 32' E : 33° 54' S) on 24-05-1976 and on Maastricht
on 24-05-1977 (see Table 4 for details on Maastricht).  Thirty (at Rietmond)
and 60 (at Maastricht) 50m² permanent transects were surveyed shortly
before and shortly after herbicidal treatment.  The same permanent transects
were re-surveyed at 2 and then 6 monthly intervals after treatment for 33
months and the increase in the number of plants expressed as the total
number of cladodes over all categories gave some indication of the recovery
rate of the two infestations.  The total number of cladodes over all
categories was calculated from the assumption that each small plant (B
category) and each medium plant (C category) has a mean of 3 and 8 cladodes
respectively per plant.  The number of cladodes on large plants (D category)
was counted and added to the total.  The presence or absence of cochineal
insects on all plants was also recorded.

The recovery of the residue populations over 33 months is illustrated in
fig. 33.  (The efficiency of the herbicidal treatment can be calculated
from the differences between the first and second columns of each locality).
The population increase was approximately linear for both localities with
r = 0,61 for Rietmond and r = 0,97 for Maastricht (fig. 33).  If these
lines are projected to the pre-treatment level it would have taken 74 and
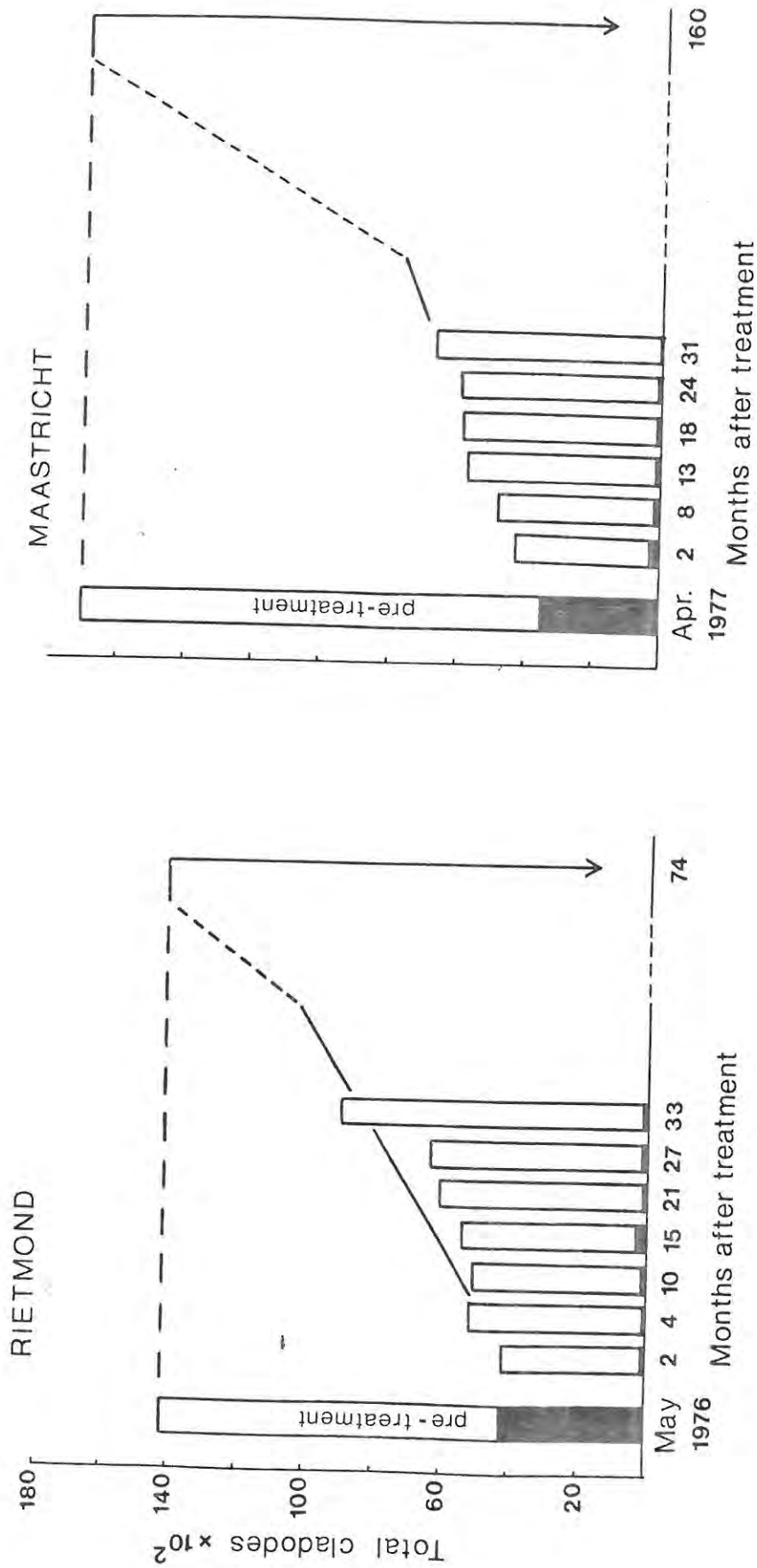160 months respectively for the residue infestations at the recorded rate

Fig. 33. Regrowth of post-spray jointed cactus infestations and linear projections to show the approximate time necessary to reach the pre-spray levels. Population sizes are expressed as total number of cladodes. The shaded areas indicate the number of cladodes bearing cochineal insects.

of increase, to reach the pre-treatment infestation level. However, predictions based on extrapolations that lie outside the data points and also based on regressions that are derived from time dependent data, should be read with caution (Van Ark 1981). The slope of the extension line may well be different from the one that is presented. Indications are that the slopes will become steeper and the figures of 74 and 160 months are probably over-estimates. Indeed, the data for growth of insect free jointed cactus populations from Glen Ovis, a site near Maastricht, (fig. 42), indicate a more realistic rate of jointed cactus population growth. This suggests a rise in population density to pre-treatment levels within 97 months after treatment. The linear extrapolation to 160 months in fig. 33 is therefore certainly an overestimate.

It was shown that post-spray infestations of jointed cactus consist mainly of isolated cladodes and small plants and that these are often subjected to severe desiccation, (see chapter 11), a mortality factor which seldom operates on the larger C and D category plants. Therefore a slow increase in populations in the first 12 - 24 months after spraying can be expected before the shift from small to larger categories gains momentum. Large plants produce and abscise large numbers of cladodes annually which contribute substantially to the spread and increase of the infestation and also to the formation of clumps. The overestimation for the recovery time of the post-treated jointed cactus infestation from fig. 33 is thus explained.

Two important points emerge from this study :

(i) Recommendations for follow-up herbicidal treatments at intervals of 6 - 8 months are clearly unrealistic because jointed cactus populations have changed very little during this time. Most plants in the regrowth population are small and follow-up treatment will be inefficient. The criterion should be that follow-up treatments are recommended once the jointed cactus population comprises mostly medium to large (C + D category) plants. At this stage

   i.e. approximately 2-3 years after treatment, jointed cactus populations would increase rapidly and start to interfere with livestock. As discussed previously these large category plants are most efficiently controlled herbicidally.

(ii) Spraying operations reduced cochineal population densities drastically at all sites (fig. 33). The surviving cochineal insects did not increase linearly in step with host plant population growth but remained at approxi-

mately the same level for 33 months (shaded areas in fig. 33). The contribution of this small cochineal population in suppressing the recovery of jointed cactus infestations must be negligible and the regrowth can therefore be compared to the growth of an insect-free population. This regrowth of jointed cactus populations after herbicidal treatment outstrips the growth of cochineal insect populations because the interplant distances are large and the target plants small which prevents adequate dispersal of cochineal crawlers. Follow-up herbicidal treatment at this point will further reduce the cochineal reservoir present on the larger plants and the problem is exacerbated. This reinforces the conclusions drawn from chapter 8 that chemical spraying of jointed cactus is antagonistic in a variety of ways to biological control and that cochineal insects cannot be expected to contribute to suppression of the weed under these circumstances.

## 11. GROWTH AND MORTALITY OF O. AURANTIACA POPULATIONS WITH AND WITHOUT D. AUSTRINUS

It has been shown (chapter 3) that D. austrinus is able to destroy
O. aurantiaca plants if the plants are manually inoculated with cochineal
insects. The efficiency of these insects, however, varied considerably at
the various localities.

The insect exclusion trials described in chapter 3 cannot be related to
normal field populations of jointed cactus in South Africa because : (i) all
individually selected plants in the treated plots were manually inoculated
with D. austrinus : under normal conditions a near 100% infestation rate
could only occur in exceptional cases at epidemic cochineal population
levels; (ii) a small area underneath each plant was cleared of other vegeta-
tion : this decreased interplant competition in favour of O. aurantiaca,
and provided an ideal "nursery" for dislodged cladodes; (iii) the continued
removal of rooted cladodes from underneath the insect-free plants also
decreased intraspecific competition; (iv) the exclusion of all stock from
the experimental plots allowed the plants to attain sizes which they would
seldom reach under normal conditions and (v) the evaluation of D. austrinus
on small category plants (A + B) was ignored, although they comprise the
bulk of the jointed cactus populations.

In this chapter D. austrinus will be evaluated further under "normal" field
conditions and the major mortality factors that operated on O. aurantiaca in
five different areas will also be evaluated.

Few attempts have been made to study life tables and survivorship curves of
plants (Huffaker & Kennett 1959; Van der Meijden 1971; Sharitz & McCormick
1972; Mack 1976; Walloff & Richards 1977; Dempster & Lakhani 1979;
Zimmermann & Malan 1981). Most biological control studies on weeds aim at
evaluation by comparing plant growth with and without the presence of the
natural enemy, often using some before and after deocumentation e.g. photo-
graphs (De Bach et al. 1976; Goeden 1981). Many of these evaluations,
however, are non-quantitative.

Some reasons why the population dynamics of higher plants have failed to
develop to the same extent as those on animals are given by Harper (1977)
Most of the problems are of a practical nature (Wapshere 1970; Forno &
Harley 1976).

Jointed cactus and other Opuntia weeds, however, are special cases amenable to the construction of partial life tables because :

(i)    the plant is simple and well defined by cladodes which can be easily counted;

(ii)    all rooted plants reproduce asexually by means of dislodged cladodes and there are no seeds to complicate life tables;

(iii)    only two natural enemies, namely C.cactorum and D. austrinus, feed on jointed cactus in South Africa, thus simplifying any life table study.

The five experimental plots used to determine jointed cactus life tables varied from 2 to 4 ha, and are described in Table 4.  On two of these sites, namely Centlivres and Middelburgplaas, populations of the natural enemy D. austrinus were introduced prior to the determination of life tables by releasing cochineal crawlers from "towers" as described later in the chapter.  The permanent transect method (see chapter 4) was adopted to monitor jointed cactus populations at three-monthly intervals.  A smaller plot of 1 to 2 ha adjacent to each of these plots was regularly sprayed with methidathion to remove all D. austrinus from the jointed cactus plants. This insect-free jointed cactus population was then monitored in the same way as the normal jointed cactus population.

A separate destructive random sample comprising 20 small and 20 large plants infested with D. austrinus were taken from the periphery of each plot (except at Centlivres) at six-weekly intervals (see chapter 6).

Introduction of a Cochineal Inoculum

All plants at Centlivres were free of cochineal insects when the surveys started and a chochineal inoculum was introduced at the Centlivres site by crawler (= first instar nymphs) releases from "elevated towers" (Gunn 1979). A basket, 1 m square and 30 cm deep, was filled with cochineal infested cladodes which was then placed on top of a 4 m high metal pole which was held upright by four guy-ropes (see fig. 34).  The top of the basket was covered with double nylon gauze to protect the cochineal and cladodes from rain and sun and to prevent the contents of the basket from falling out during handling.

The density of crawlers that "rained" from the "towers" was monitored using sticky impact traps developed by Gunn (1979). Instead of glass sheets which are heavy and prone to breakage, a 29 x 21 cm (the size of A4 paper) masonite board was fixed onto a 40cm long peg which was hammered into the ground to a depth of 10 cm. White A4 size duplicating paper was painted with a thin film of Formex, diluted in paraffin to provide the permanent sticky surface. The paper was fixed onto a second board that was tied onto the first board. After 7 days the paper sheets were replaced and the number of crawlers that were trapped was recorded.

The traps were arranged in a 10 m grid pattern. The total number of crawlers recorded per $1m^2$ surface trap area in relation to the position of the "release towers" is given in fig. 35. Figures 36 and 37 are contour maps of these crawler densities on the experimental plots. The maps were provided by SYMAP computer programmes and are based on a n-th order polynomial (Dougenik & Sheehan 1975).

The same methods were used to release crawlers at Middelburgplaas between 3-11-1977 and 25-11-1977 to enhance the endemic levels of cochineal insects.



Fig. 34. Inoculation of a jointed cactus infestation by means of crawler releases from "elevated towers". Note the sticky traps in the background.

## CENTLIVRES

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1 | 3 | 2 | 1 | 1 | 1 | 0 | 1 | 0 |
| 2 | 0 | 0 | 3 | 2 | 0 | 4 | 0 | 2 |
| 3 | 0 | 1 | 2 | 2 | 0 | 3 | 2 | 0 |
| 1 | 0 | 1 | 2 | 2 | 2 | 5 ★ | 2 | 0 |
| 1 | 0 | 2 | 3 | 1 | 4 | 2 | 1 | 0 |
| 0 | 0 | 2 | 3 | 2 | 7 | 8 | 1 | 1 |
| 0 | 1 | 5 | 7 | 4 | 2 | 2 | 1 | 1 |
| 11 | 5 | 4 | 18 | 13 | 11 | 3 | 4 | 6 |
| 1 | 5 | 3 | 12 | 6 | 4 | 2 ★ | 1 | 4 |
| 2 | 3 | 2 | 2 | 5 | 5 | 3 | 0 | 5 |
| 3 | 3 | 5 | 4 | 5 | 9 | 6 | 3 | 2 |

## MIDDELBURGPLAAS

| | | | | | | |
|---|---|---|---|---|---|---|
| 4 | 3 | 1 | 6 | 2 | 2 | 2 |
| 2 | 4 | 3 | 3 | 0 | 2 | 1 |
| 5 | 7 | 5 | 6 | 2 | 3 | 1 |
| 9 | 10 | 10 | 7 | 5 | 5 | 2 |
| 7 | 22 | 20 | 19 | 10 | 6 | 0 |
| 27 | 25 | 48 | 22 | 12 | 9 | 1 |
| 44 | 37 | 93 | ★ | 42 | 14 | 4 |
| 15 | 32 | 50 | 71 | 53 | 12 | 4 |
| 13 | 22 | 22 | 17 | 19 | 9 | 6 |
| 7 | 16 | 11 | 6 | 5 | 4 | 3 |

├──20m──┤

Fig. 35. Total number (per m² ) of D. austrinus crawlers caught on impact
traps after release from "elevated towers", between 3 - 25
November 1977 (Middelburgplaas) and 13 - 26 October 1977
(Centlivres). ★ = release towers.
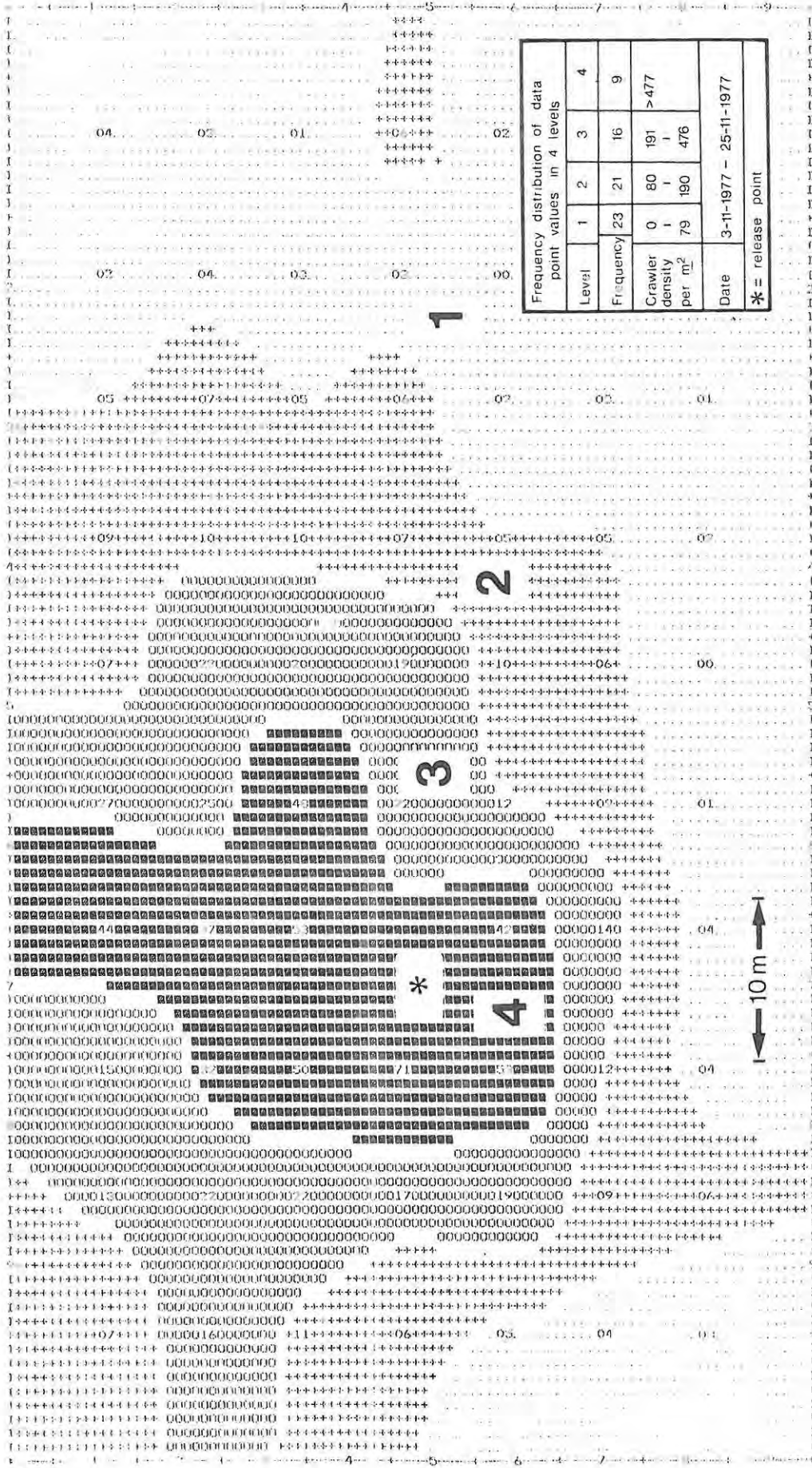
Fig. 36. Contour map of crawler densities introduced from one "release tower" at Middelburgplaas.
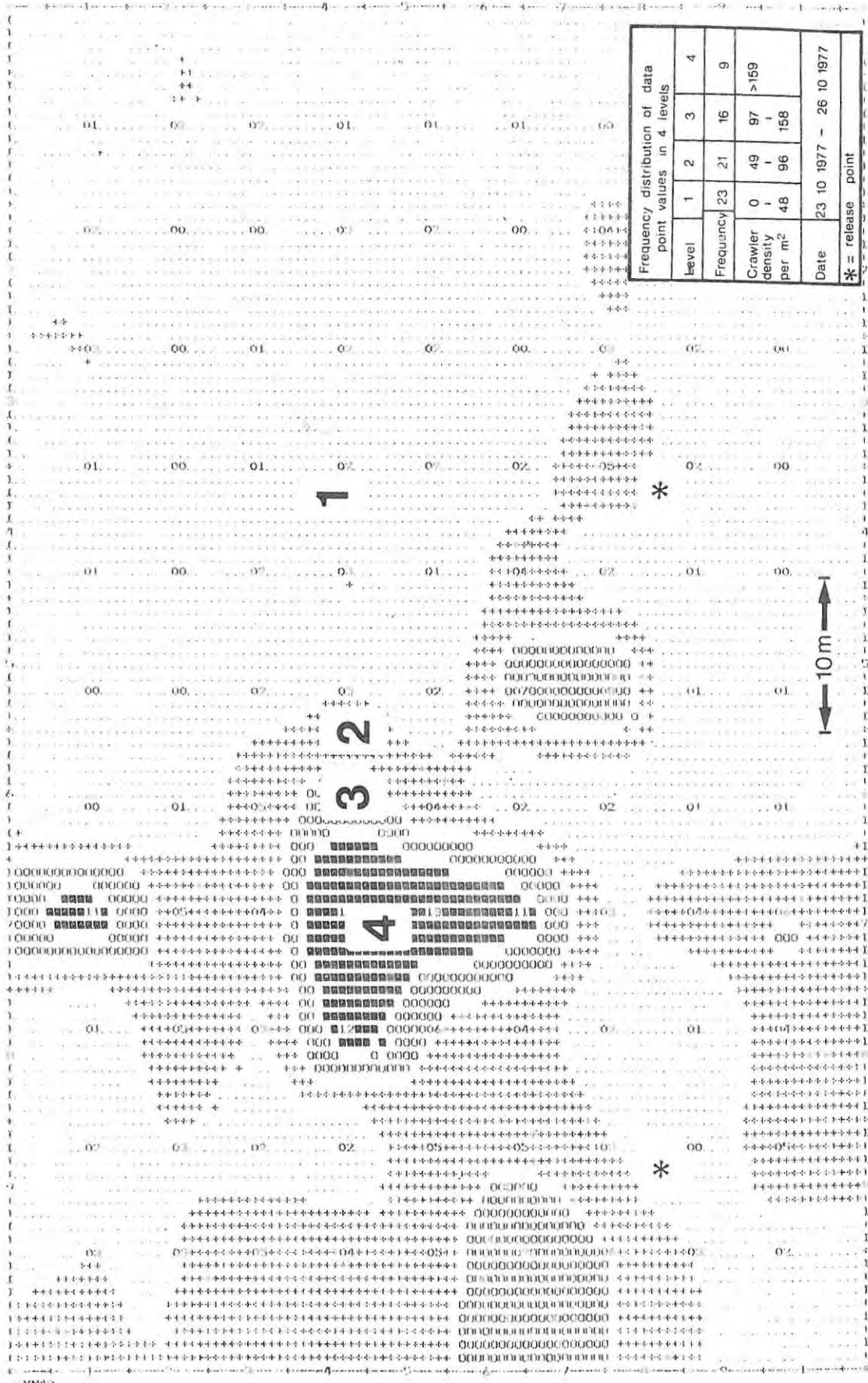
Fig. 37. Contour map of crawler densities introduced from two "release towers" at Centlivres.

| Frequency distribution of data point values in 4 levels | | | | |
|---|---|---|---|---|
| Level | 1 | 2 | 3 | 4 |
| Frequency | 23 | 21 | 16 | 9 |
| Crawler density per m² | 0 – 48 | 49 – 96 | 97 – 158 | >159 |
| Date | 23 10 1977 – 26 10 1977 | | | |

* = release point

Methods for Obtaining Jointed Cactus Mortality Curves

Figure 38 illustrates the factors that affect jointed cactus mortality with
and without the presence of D. austrinus. Propagation and dispersal is by
means of isolated cladodes (category A) that have become dislodged from
rooted plants and they can themselves root and grow to form small (category
B) plants, then medium (C category) and later large (D category) plants.
More of the insect-free plants successfully progress through this series than
do plants that are colonized by cochineal insects (fig. 38). Also the insect-
free plants produce greater numbers of cladodes which eventually abscise
and become rooted themselves (i.e. revert to category A plants). During
winter or times of stress, joints may be abscised so that there is a decrease
in the number of large category C and D plants as is indicated in the
diagram in fig. 38, and this regression is more noticeable for plants that
are attacked by cochineal insects.

It should be stressed that C and D category plants are attacked by cochineal
insects which cause the abscission of individual cladodes or the eventual
mortality of the plant, but that the entire plant is killed only after most
of the cladodes have been killed or shed and the plant has regressed to a
B-category plant. Cochineal insects, therefore, only cause the mortality
of A and B category jointed cactus plants. The regression of D-category
plants colonized with D. austrinus to B-category plants takes considerably
longer than 3 months and is thus readily detected by the sampling method.

The sampling data from 30 transects gave seasonal and long term fluctuations
in normal jointed cactus populations which were then compared with insect-
free populations. Mortalities and "births" were obtained by comparing the
counts between successive surveys as recorded on budget data sheets
(appendices 1 and 2).

Seasonal Fluctuations in Jointed Cactus Populations

Figures 39 - 41 show the fluctuations in numbers of jointed cactus plants
for insect-free and normal jointed cactus populations over four years for
five localities, and they illustrate a number of features which are listed
below by number and marked accordingly on the graphs :

   (i)   Insect-free populations of jointed cactus increased dramatically
         over the four year period especially at Gannahoek and Centlivres
         but less so at the other sites.
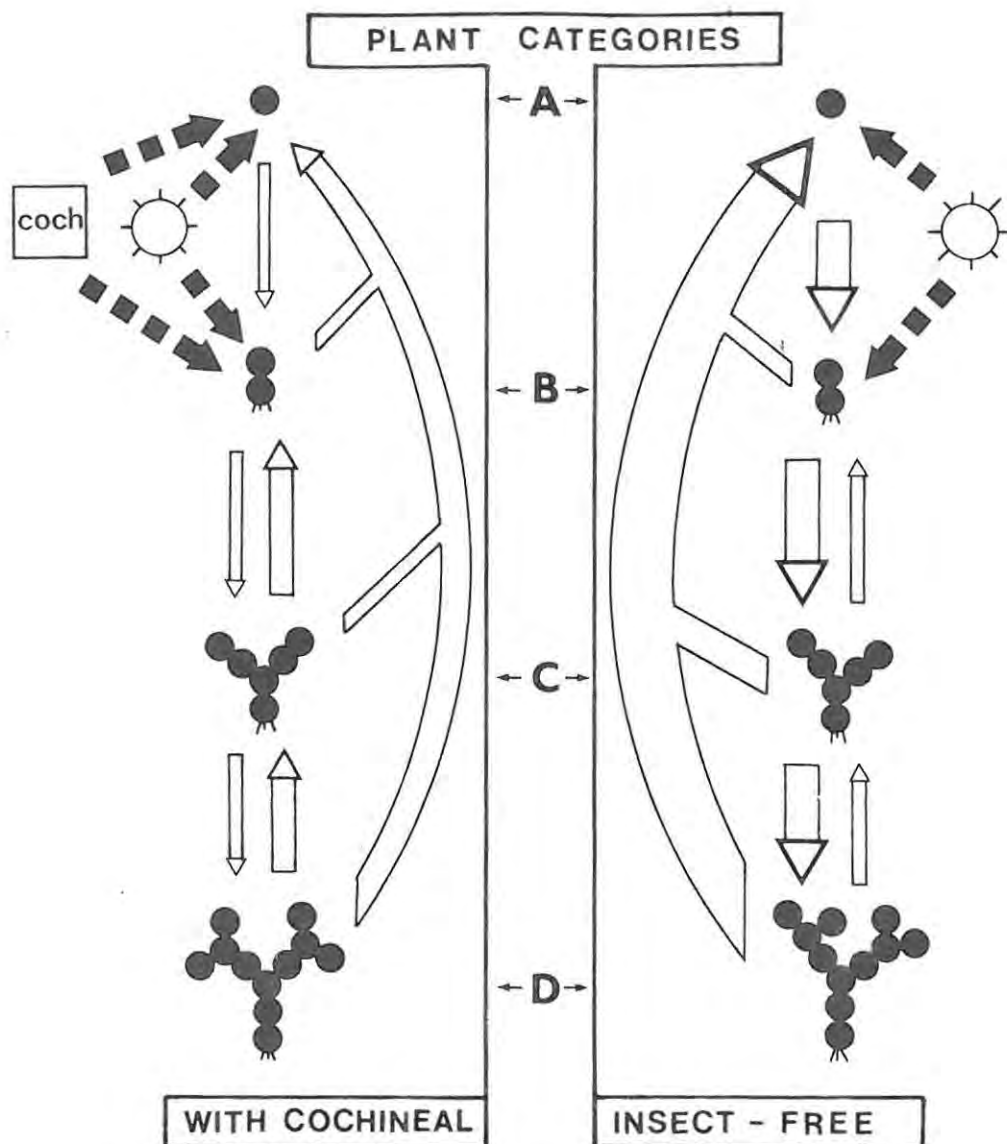
Fig. 38.  Diagrammatic representation of a jointed cactus life model
with and without the presence of the cochineal insect,
D. austrinus.  The thicker arrows on the right hand side of
the diagram indicate a greater recruitment of plants into
each category and a greater production of isolated cladodes from
each of the insect-free categories.  The major mortality factors
(broken arrows) operating on A and B category plants are ☼ =
abiotic, mainly desiccation and cochineal insects = coch .

(ii)  For C and D category plants at all sites with and without
      cochineal insects, there were always clear seasonal fluctua-
      tions with the number of plants decreasing during winter and
      increasing during summer (see Glen Ovis as an example, fig. 39).

(iii) The opposite effect is evident for isolated cladodes at all
      sites with numbers increasing during winter and decreasing
      during summer (see Glen Ovis, fig. 39, as an example).  During
      summer, established jointed cactus plants are producing large
      numbers of cladodes which are abscised during winter as discus-
      sed in chapter 3 which deals with the phenology of the plant
      and which explains the events reported here.

(iv)  Small plants in category B do not show seasonal increases or
      decreases in number because in summer B-category plants are
      growing rapidly and progress to C-category plants and the drop
      in numbers is offset by recruitment from A-category plants
      (see Glen Ovis for example).  These seasonal events (ii) - (iv)
      above are generally consistent for all jointed cactus populations
      with and without cochineal populations.

(v)   The percentage of plants bearing D. austrinus on the other hand,
      did not show any clear seasonal patterns (see Gannahoek fig. 39
      for an example).

(vi)  Generally the differences in jointed cactus populations with
      and without cochineal insects are not very marked and the
      suppressing effect of the cochineal insects is often overridden
      by more spectacular seasonal fluctuations in jointed cactus
      numbers (see Gannahoek for an example).

(vii) But at Centlivres "tower releases" of cochineal crawlers in early
      summer (see arrow in fig. 41) resulted, after some months'
      delay, in a large build-up of cochineal populations and conse-
      quently significant decreases in jointed cactus numbers.

(viii) At Middelburgplaas the effect of cochineal releases was less
       dramatic and the latent period before the build-up of cochineal
       numbers was much longer but eventually caused a considerable
       decrease of C and D category plants (see fig. 40).

Fig. 39  Fluctuations in the number of $\underline{O}$. $\underline{aurantiaca}$ plants in cochineal-free and normal populations for four years at Gannahoek and Glen Ovis. The proportion of categories colonized with $\underline{D}$. $\underline{austrinus}$ is also shown. The numbers (i) – (x) indicate features that are discussed in the text.
F = February; M = May; A = August; N = November.
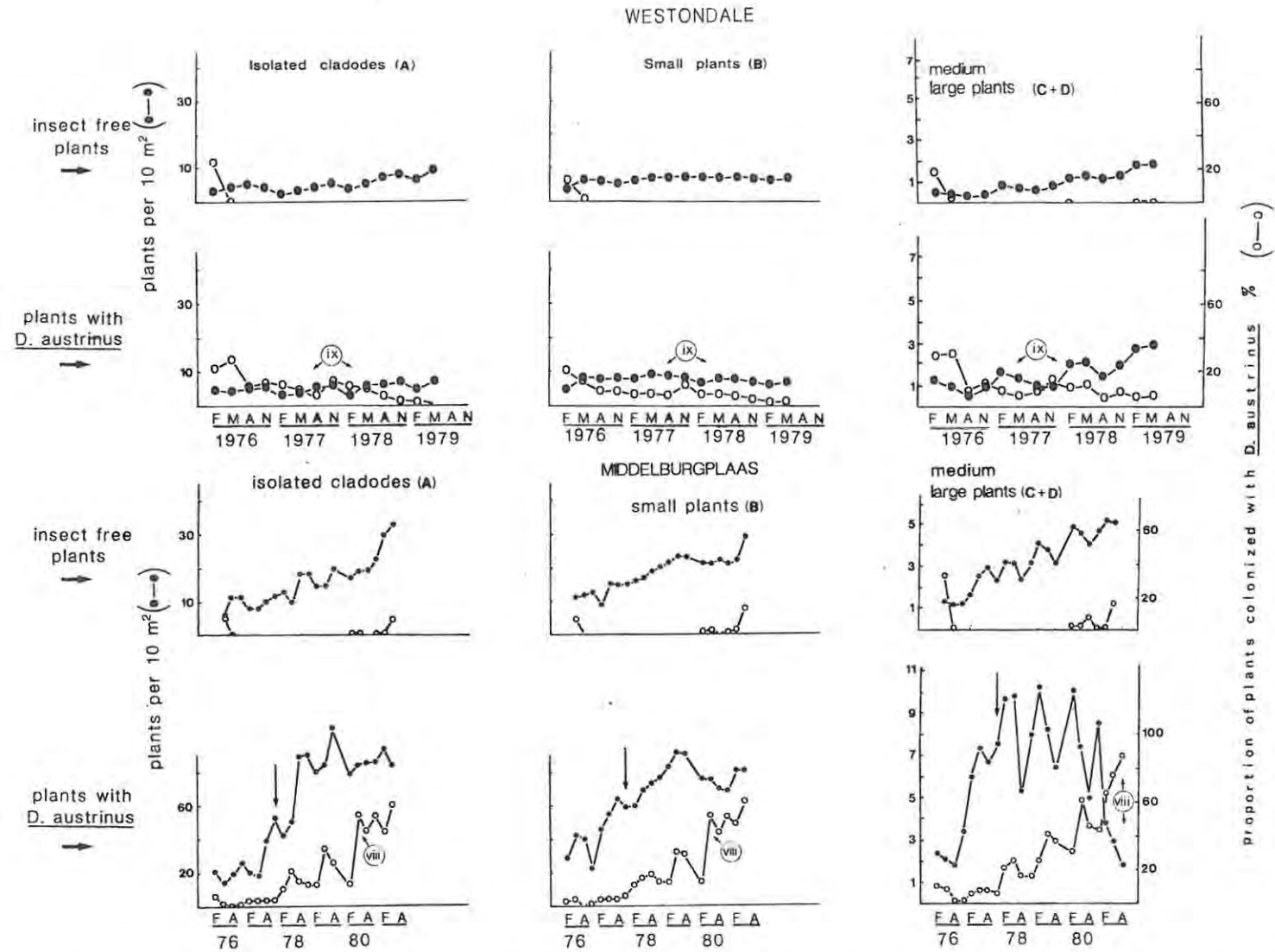
WESTONDALE



Fig. 40. Fluctuations in the number of O. aurantiaca plants in cochineal-free and normal populations for four years at Westondale and Middelburgplaas. The proportion of categories colonized with D. austrinus is also shown. The numbers (i) − (x) indicate features that are discussed in the text. F = February; M = May; A = August; N = November. Arrows indicate the times of "tower releases" of D. austrinus.
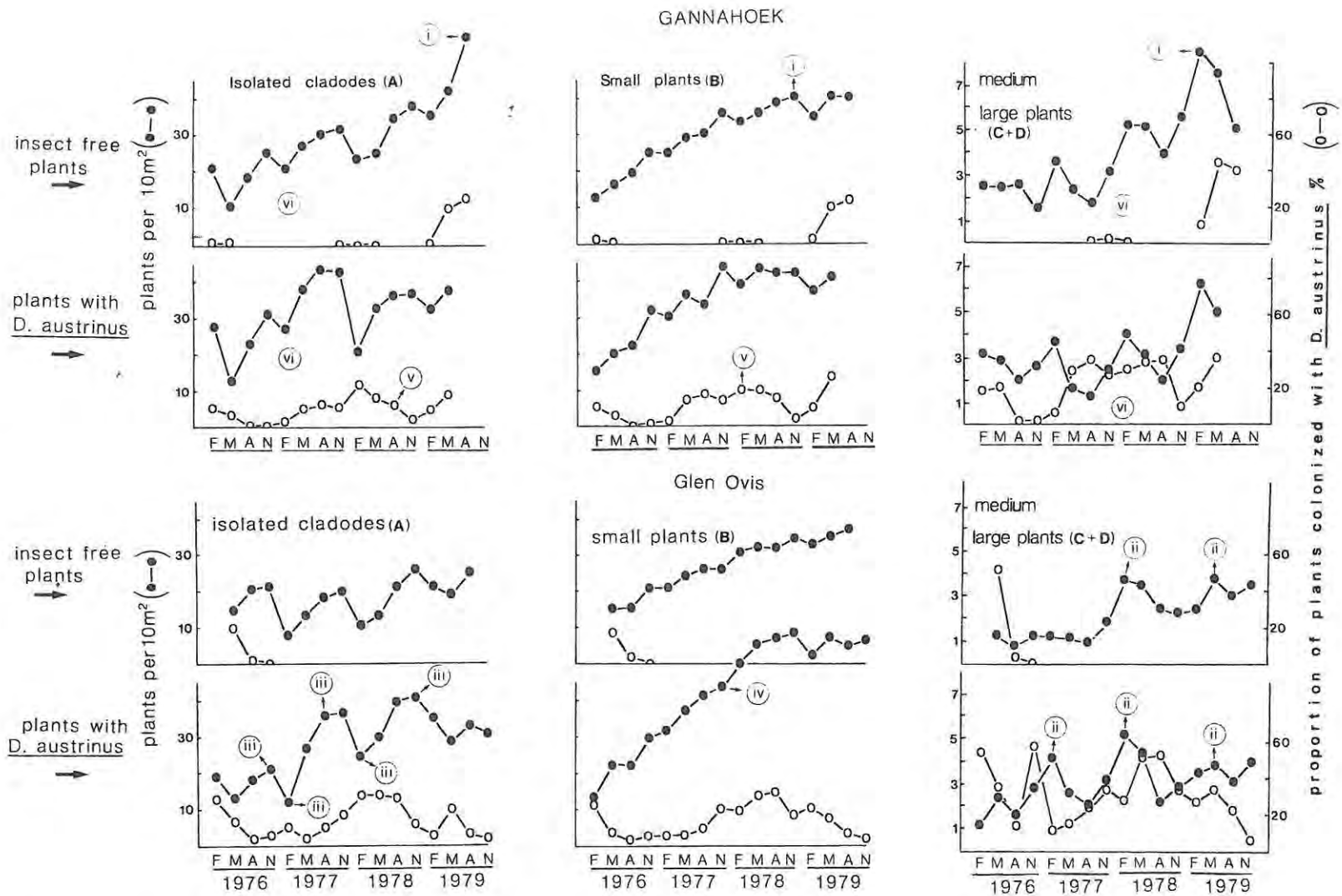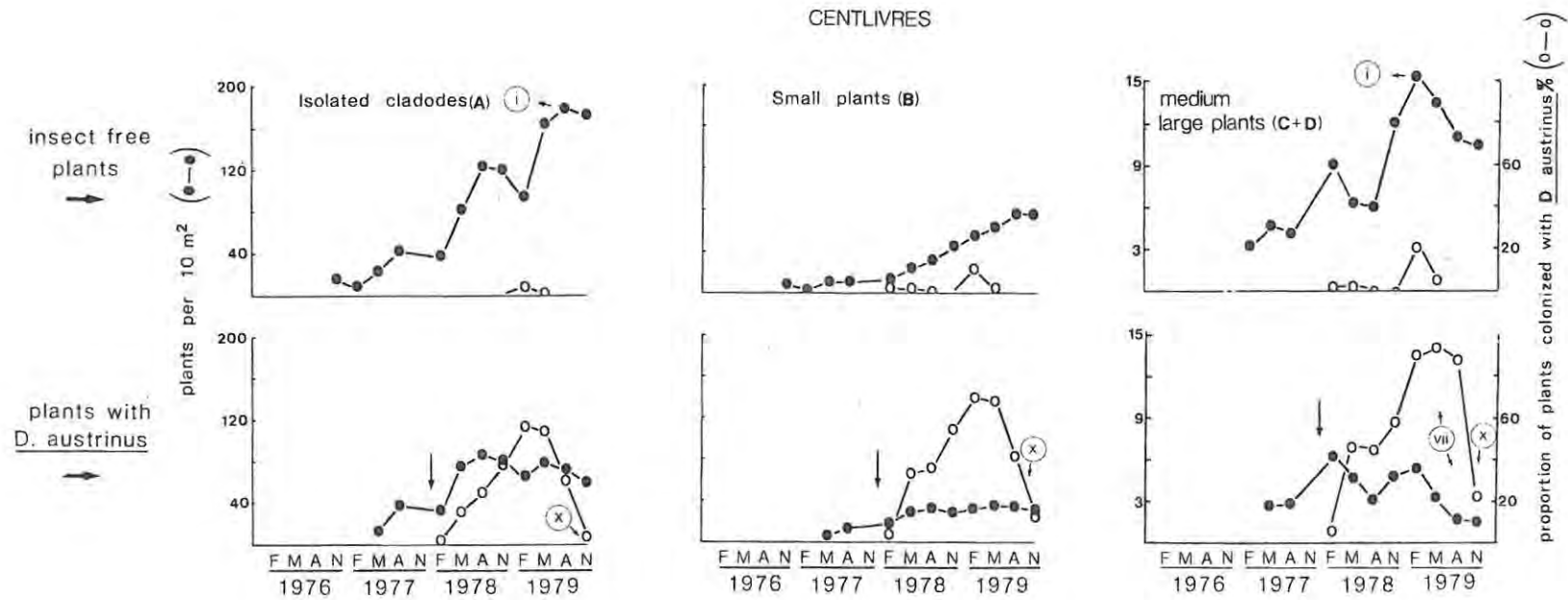
Fig. 41. Fluctuations in the number of O. aurantiaca plants in cochineal-free and normal populations for four years at Centlivres. The proportion of categories colonized with D. austrinus is also shown. The numbers (i) - (x) indicate features that are discussed in the text. F = February; M = May; A = August; N = November. Arrows indicate the times of "tower releases" of D austrinus.

(ix)  With regard to all the features mentioned above, Westondale was
      exceptional : populations of jointed cactus and cochineal insects
      were consistently low (see fig. 40).

(x)   The sharp decrease in the cochineal population at Centlivres
      recorded for August and November 1979 (fig. 41) was the direct
      result of 368 mm rain that fell during July and August 1979
      (appendix 4).  This feature confirms earlier reports by Pettey
      (1948) that heavy rain has a detrimental effect on cochineal
      populations.

Growth of Jointed Cactus Populations With and Without Cochineal Insects

These events and the contrast between plants with and without cochineal
insects may also be considered from a different viewpoint to emphasise the
differences in growth between the sites (figs 42 and 43).  For these
comparisons the jointed cactus population may be expressed as the total
number of cladodes in the population, rather than as the number of plants
in each of 4 categories.



Fig. 42.  Growth of five insect-free O. aurantiaca populations based on
          total cladodes in 1 500 m² samples.  F = Februrary; M = May;
          A = August; N = November.

The fit of the data points to the linear regressions for insect-free jointed cactus populations at 5 sites over a 4 – 6 year period are all highly significant (fig. 42). Because the data are on a time scale making consecutive data points dependant on each other, the statistical comparisons of such lines using ANOVA is non-valid. The points along the line are therefore for visual comparison only. Table 17 gives the percentage increase after 3 years' growth.

Clearly the insect-free jointed cactus population at Centlivres has increased rapidly over the period, that at Westondale was lowest and the other sites were intermediate in this regard.

Centlivres is a coastal site and very suitable for jointed cactus increase. In comparison the high rate of desiccation of cladodes and plants, together with the low growth rate at Westondale, which is a hot and dry inland site, accounts for the poor performance of jointed cactus at that site. The other three sites namely Gannahoek, Glen Ovis and Middelburgplaas have approximately the same growth rate and are located in the same veld type (see Table 4).

Table 17. The percentage increase in the insect-free jointed cactus populations after three year growth based on total cladodes at five sites.

| Site | Cladodes (x $10^2$) on May 1976 | Cladodes (x $10^2$) on May 1979 | % increase |
|---|---|---|---|
| Centlivres (from Febr. 1977) | 115 | 867 | 654 |
| Gannahoek | 125 | 365 | 192 |
| Glen Ovis | 115 | 245 | 113 |
| Middelburgplaas | 77 | 185 | 140 |
| Westondale | 43 | 80 | 86 |

Turning now to the effects of cochineal insects on jointed cactus at the five sites (fig. 43), it is evident that the differences between sites were maintained. However, during the first few years of observations (1976 – 1977) when cochineal populations were low, jointed cactus growth

was little affected and remained linear. From 1978 onward, with a build-up
of cochineal population numbers (figs 39-41), the growth of jointed cactus
populations decreased. At Middelburgplaas and Centlivres, population growth
of jointed cactus actually declined approximately 18 months after mass
release of cochineal crawlers (see arrows fig. 43). At these two sites
nearly 80% of all plants were eventually colonized by cochineal insects
(figs 39-41). At Middelburgplaas, however, the jointed cactus infestation
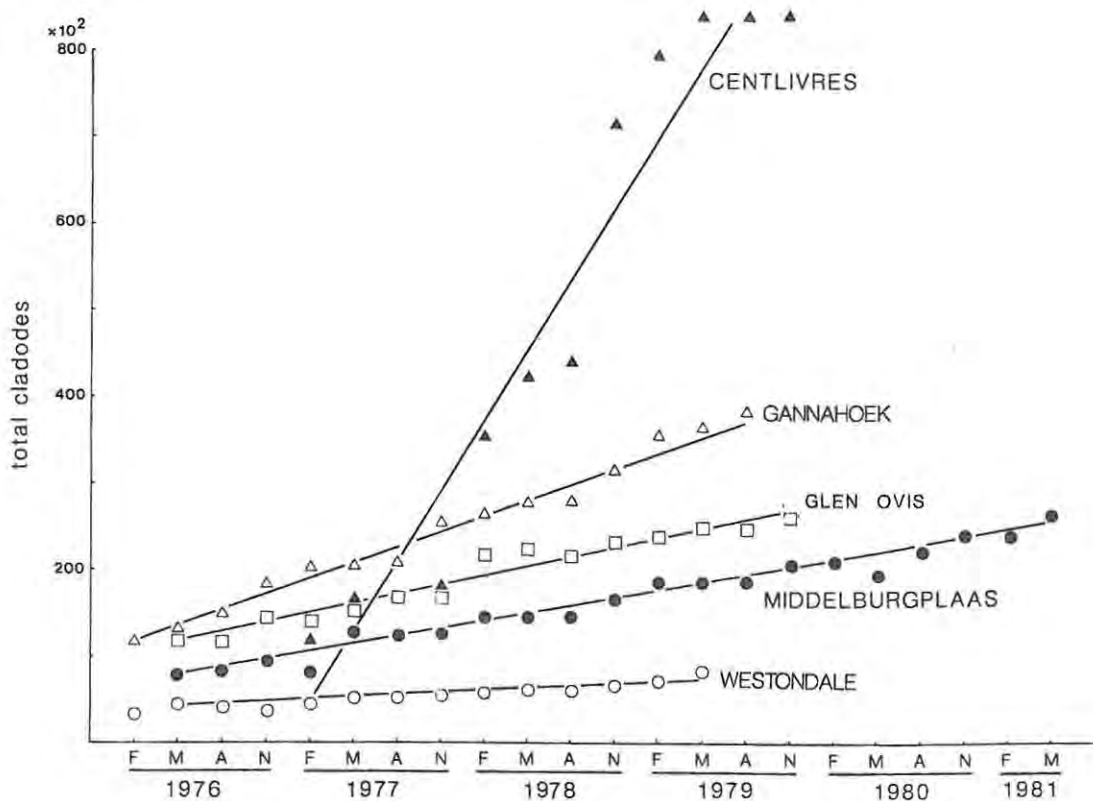showed signs of recovery after November 1980 (fig. 43).
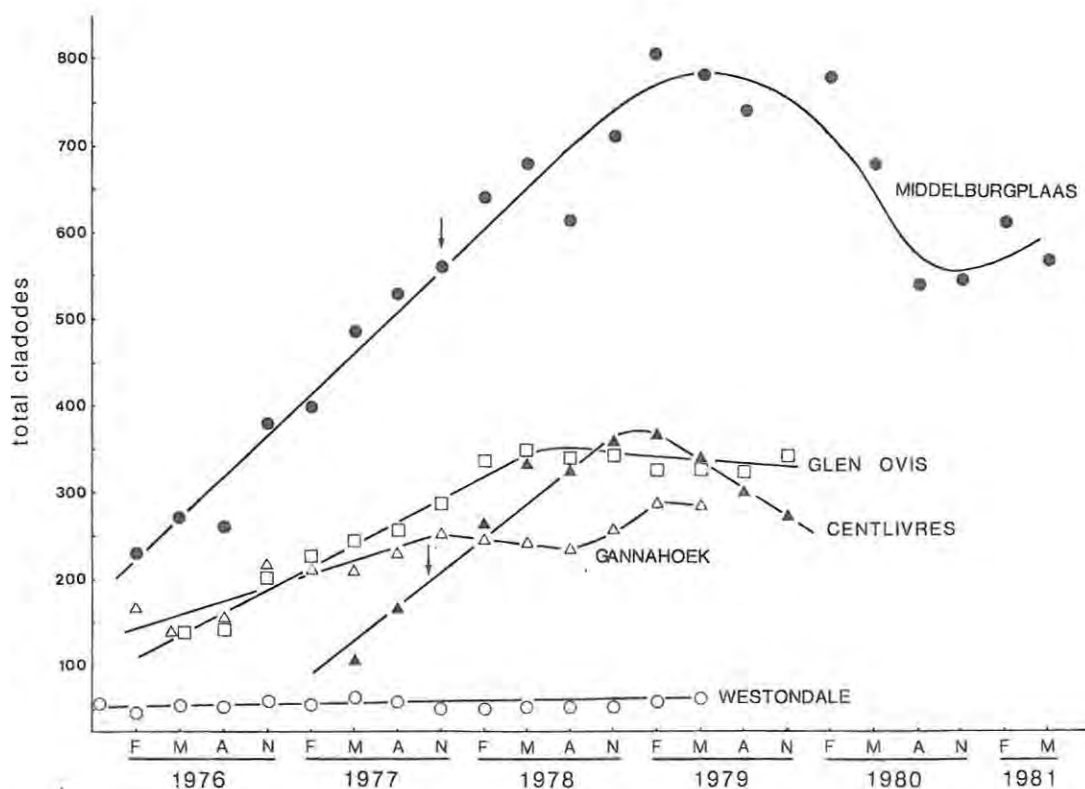


Fig. 43. Growth of five natural    O. aurantiaca populations based on
total cladodes in 1 500 m² samples. F = Februrary; M = May;
A = August; N = November.

Arrows indicate "tower releases" of cochineal crawlers at
Centlivres and Middelburgplaas.

Lastly, the differences in population levels between the insect-free and
natural jointed cactus populations at Middelburgplaas (figs 42 and 43)
require explanation. Although the plots chosen for monitoring of jointed
cactus populations with and without cochineal insects were adjacent to each

other, the former by chance, had a far higher number of total cladodes
and this makes direct comparisons of growth difficult.

'Birth' and Death rates of jointed Cactus Populations

The observed growth rates for jointed cactus populations recorded (figs
42 and 43) may be detailed further by considering the birth and death
rates of cladodes in the populations.

The nett birth rate per 1 000 cladodes in four jointed cactus populations
is shown in figs  44 - 47.  The mortality rates for isolated cladodes and
small plants are also illustrated separately for normal and insect-free
jointed cactus populations.  Methods for obtaining birth and mortality data
have been discussed above.

Abiotic mortality is caused primarily by desiccation of isolated cladodes
and small plants.  Insignificant numbers of isolated cladodes, however,
disappear and may be carried out of a transect by animals or may be washed
away by rainwater.  These losses were not separated from desiccation which
was the major cause of mortality of isolated cladodes.

Figs  44 - 47 illustrate the following features which are listed below by
number and marked accordingly on the graphs :

  (i)    A seasonal 'birth' pattern showing peaks in winter was typical
         for all sites (for example see fig. 44).  This is to be expected
         because plants abscise terminal cladodes in late summer and winter
         (see also phenology data in fig. 9).  The birth rates were approxi-
         mately the same for the natural and insect-free jointed cactus
         populations.

  (ii)   The birth rate at Centlivres (fig. 46) was the highest and this
         was a significant contribution to the high growth rate of jointed
         cactus at this site as illustrated in fig. 42.

  (iii)  The sharp decrease in the birth rate in the natural jointed cactus
         population at Centlivres after November 1978 (fig. 46) was caused
         by the high mortality of plants that died as a consequence of
         cochineal insect attack.

(iv)   Desiccation of isolated cladodes and small plants was the key-
       mortality factor operating on all jointed cactus populations
       (see fig. 44 for example).

(v)    Peak mortalities for isolated cladodes caused by desiccation
       were always recorded during mid-summer (see fig. 45 for example).

(vi)   Mortality of small plants through desiccation,however, was not
       obviously seasonal.  This may be caused by a delayed effect or
       could merely be a sampling artefact (see fig. 45).

(vii)  Mortality through desiccation at Westondale (fig. 47) was
       highest because of the harsh environment, especially in summer,
       in which the jointed cactus plants had to survive.  This feature
       must account for the low growth rate recorded and illustrated
       for Westondale in fig. 42.

(viii) D. austrinus became the key-mortality factor only during epidemic
       outbreaks at Centlivres and Middelburgplaas (figs  44 and 46).
       These mortalities coincided with the high rate of cochineal
       colonization illustrated in figs  40 and 41.

(ix)   Peaks in mortalities caused by D. austrinus were consistently
       recorded during the summer periods at Glen Ovis and Westondale
       (figs  45 and 47).

(x)    These peaks in mortalities caused by D. austrinus were not
       observed for Centlivres (fig. 46) where high mortalities occur-
       red in both winter and summer periods during the epidemic phase
       of D. austrinus outbreaks.

Small isolated cladodes and plants (B-category) were more vulnerable to
desiccation and cochineal insect feeding than large specimens.  However,
claims that isolated cladodes have near unlimited survival potential is a
gross exaggeration.  The extent of this significant abiotic mortality
factor which operates on jointed cactus populations, was hitherto unknown.

Fig. 44. 'Birth' rates and mortalities per 1 000 cladodes for jointed cactus populations caused by mainly desiccation and by feeding of D. austrinus in natural and insect-free jointed cactus cohorts at Middelburgplaas. F = February; M = May; A = August; N = November.

GLEN OVIS



Fig. 45.  'Birth' rates and mortalities per 1 000 cladodes for jointed cactus populations caused by mainly desiccation and by feeding of D. austrinus in natural and insect-free jointed cactus cochorts at Glen Ovis.  F = February; M = May; A = August; N = November.
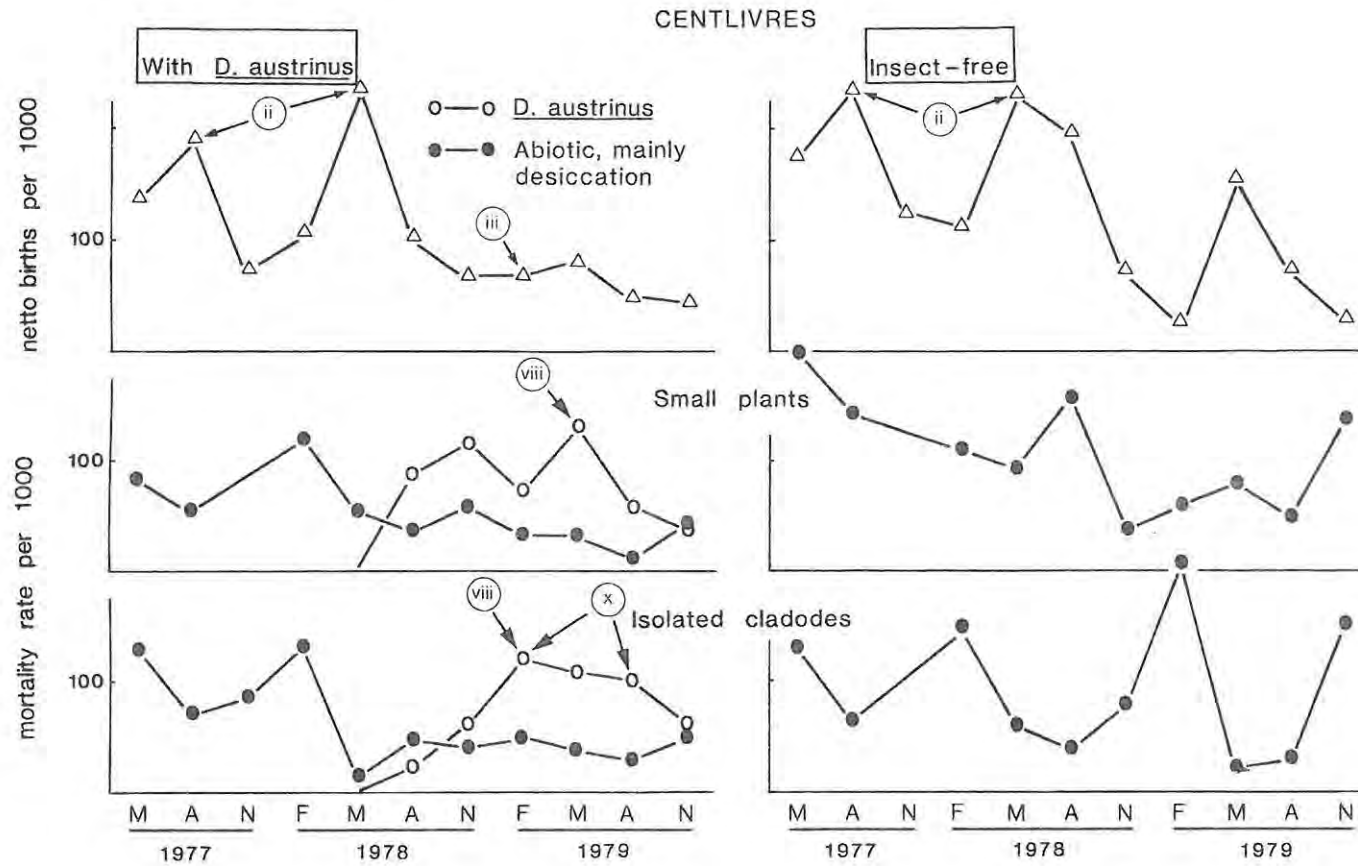
Fig. 46. 'Birth' rates and mortalities per 1 000 cladodes for jointed cactus populations caused by mainly desiccation and by feeding of D. austrinus in natural and insect-free jointed cactus cohorts at Centlivres. F = February; M = May; A = August; N = November.
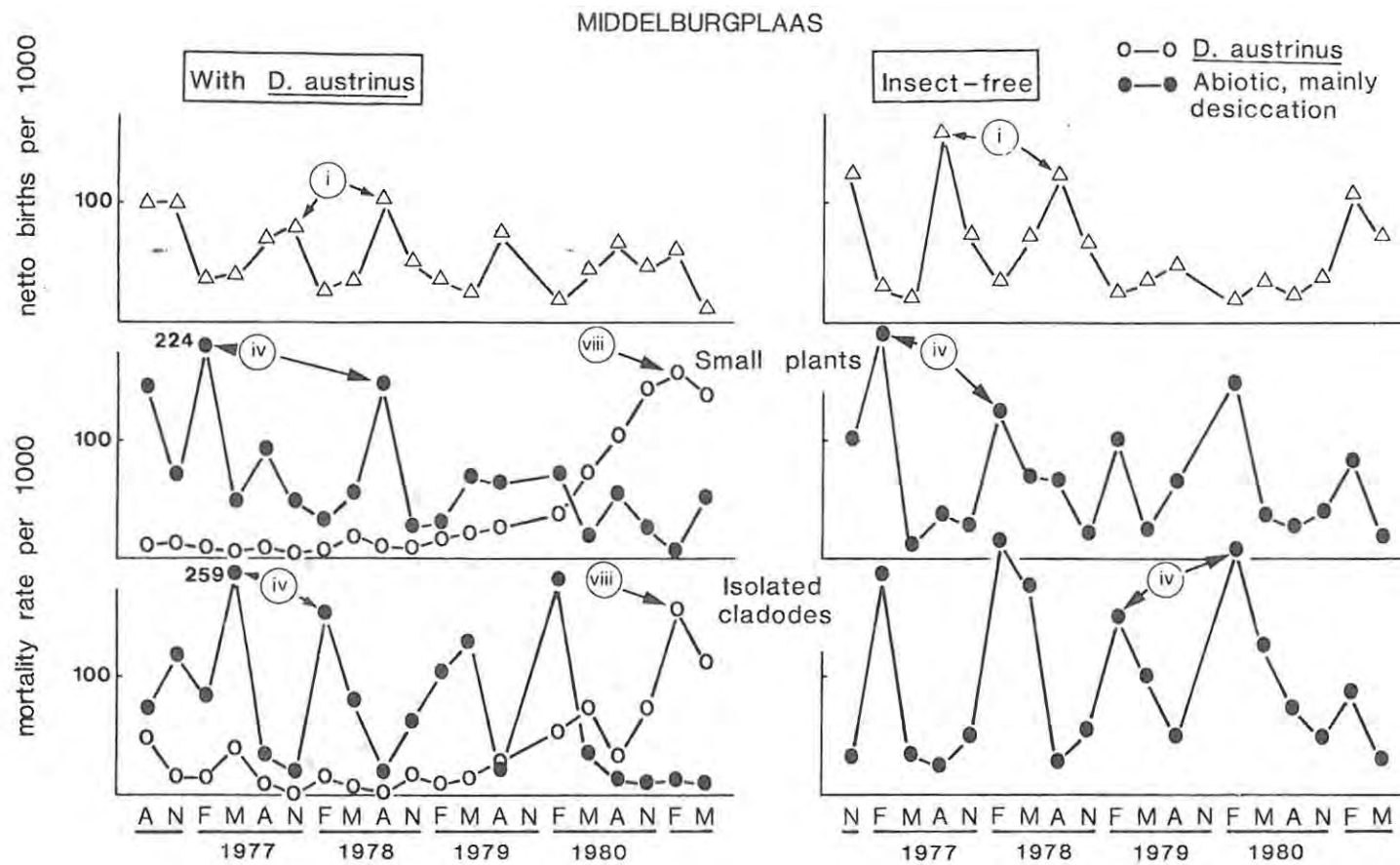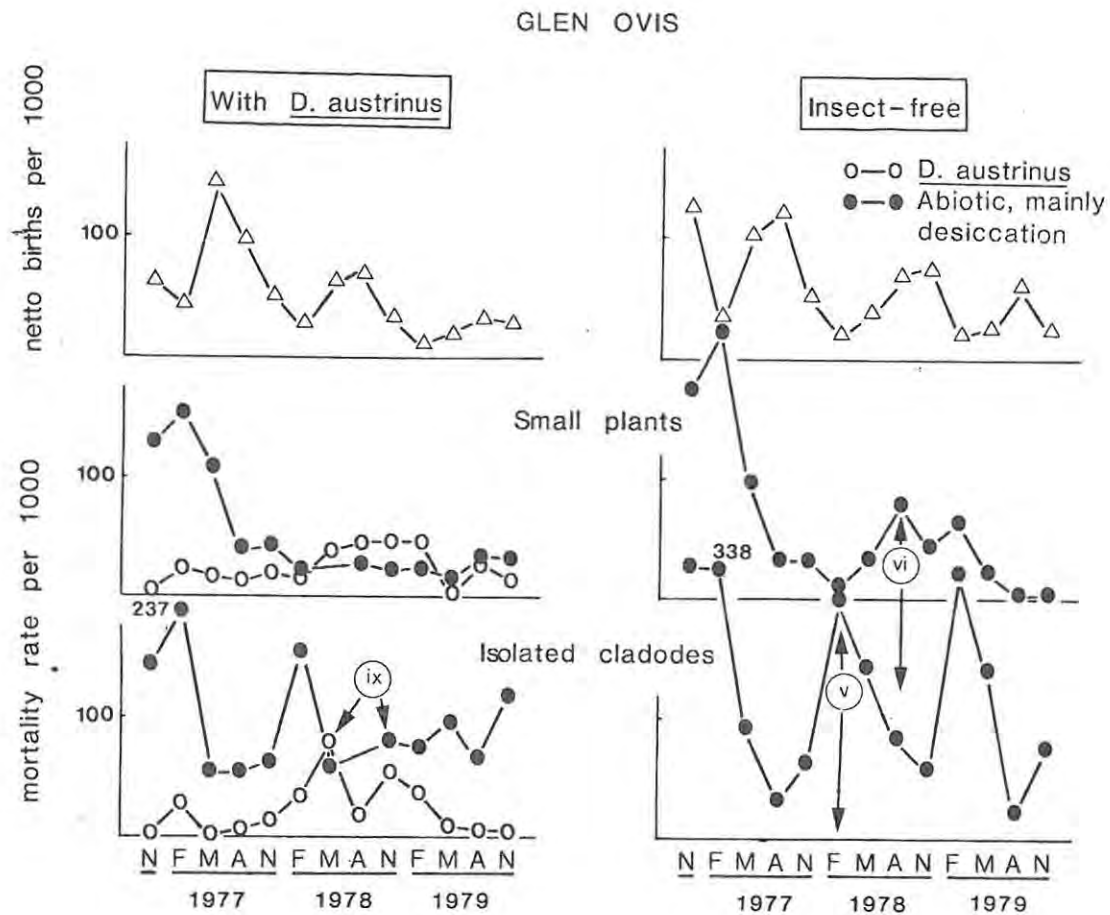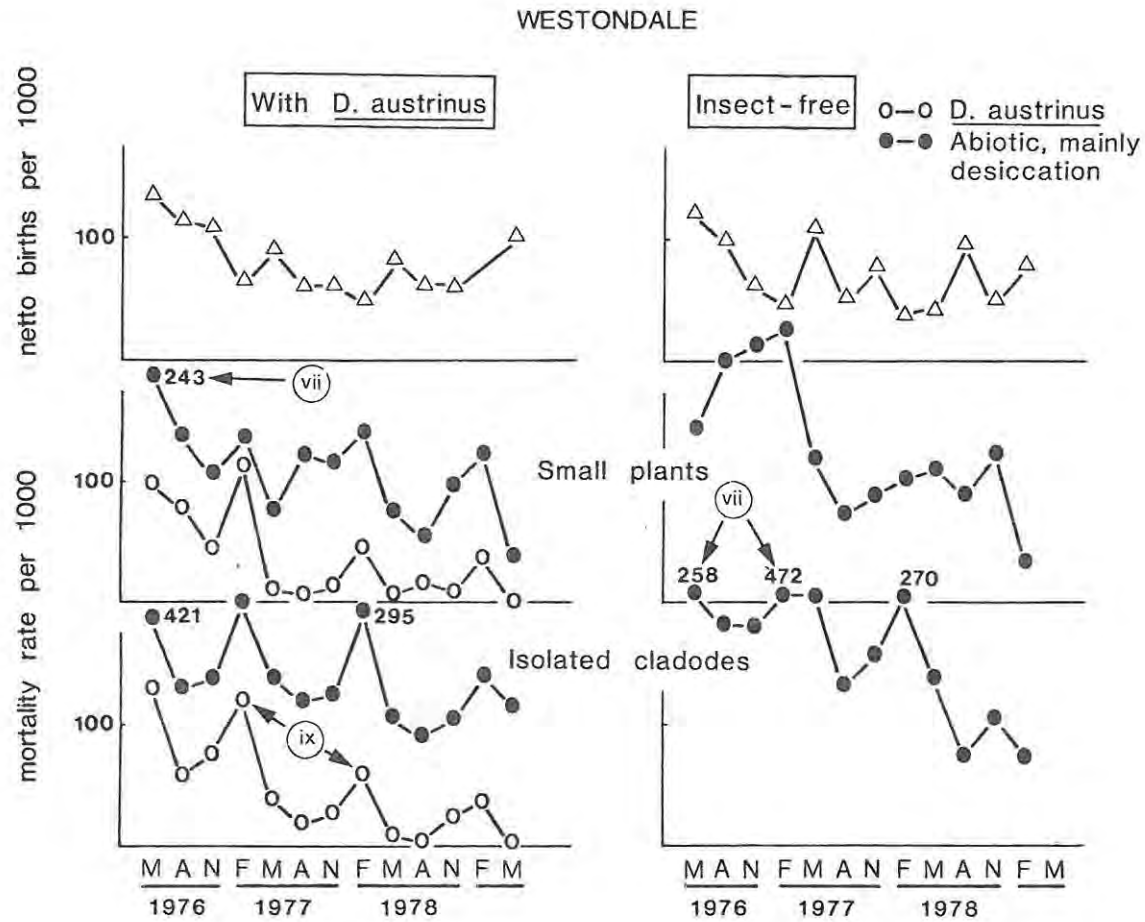
WESTONDALE



Fig. 47. 'Birth' rates and mortalities per 1 000 cladodes for jointed cactus populations caused by mainly desiccation and by feeding of D. austrinus in natural and insect-free jointed cactus cohorts at Westondale.  F = February; M = May; A = August; N = November.

Seasonal Changes in D. austrinus Populations

The emphasis in this chapter has been on the growth and mortality of jointed cactus plants with and without cochineal insects. Apart from the data in figs 39 - 41 very little has been said about D. austrinus population fluctuations although this is clearly central in considering jointed cactus performances in the field. Further, the data on cochineal populations in figs 39 - 41 are misleading because the measure of D. austrinus colonization is very crude : no distinction was made between a plant colonized with one or by many cochineal insects. Thus a plant was scored as being colonized with D. austrinus on the basis of one cochineal insect on one of the cladodes. A more sensitive measure of D. austrinus fluctuations would be to record the presence or absence of cochineal insects on each of the cladodes of the colonized host plant and these data are shown in figs 48 and 49.

Figures 48 and 49 show consistent increases in cochineal population numbers at all sites in December over a three year period as indicated by arrows in figs 48 and 49 (Westondale has one exception). These sudden increases in cochineal insect abundance are not obviously related to climate because, if the peaks represented merely a summer increase in population numbers, then there is little reason why high numbers should continue over a longer duration. Nor are these increases obviously related to rainfall (appendix 4), and it is tempting to suggest that these population increases are mediated by changes in the host plant itself, which are not yet understood. However, the peaks in cochineal population numbers coincide with peak growth of the host plant in December as shown in fig. 9.

All stages of D. austrinus, including large numbers of crawlers, were sampled on plants throughout the year and no synchrony of the developmental stages was observed with the onset of spring. This suggests that development and reproduction continues uninterrupted but at a slower rate during winter. This is understandable where mean day temperatures at 14h00 are between 19,9°C and 19,6°C for June, July and August (Anon. 1954) for representative localities where jointed cactus occurs. These temperatures are well above the minimum threshold temperatures necessary for development for D. austrinus (Karny 1972).
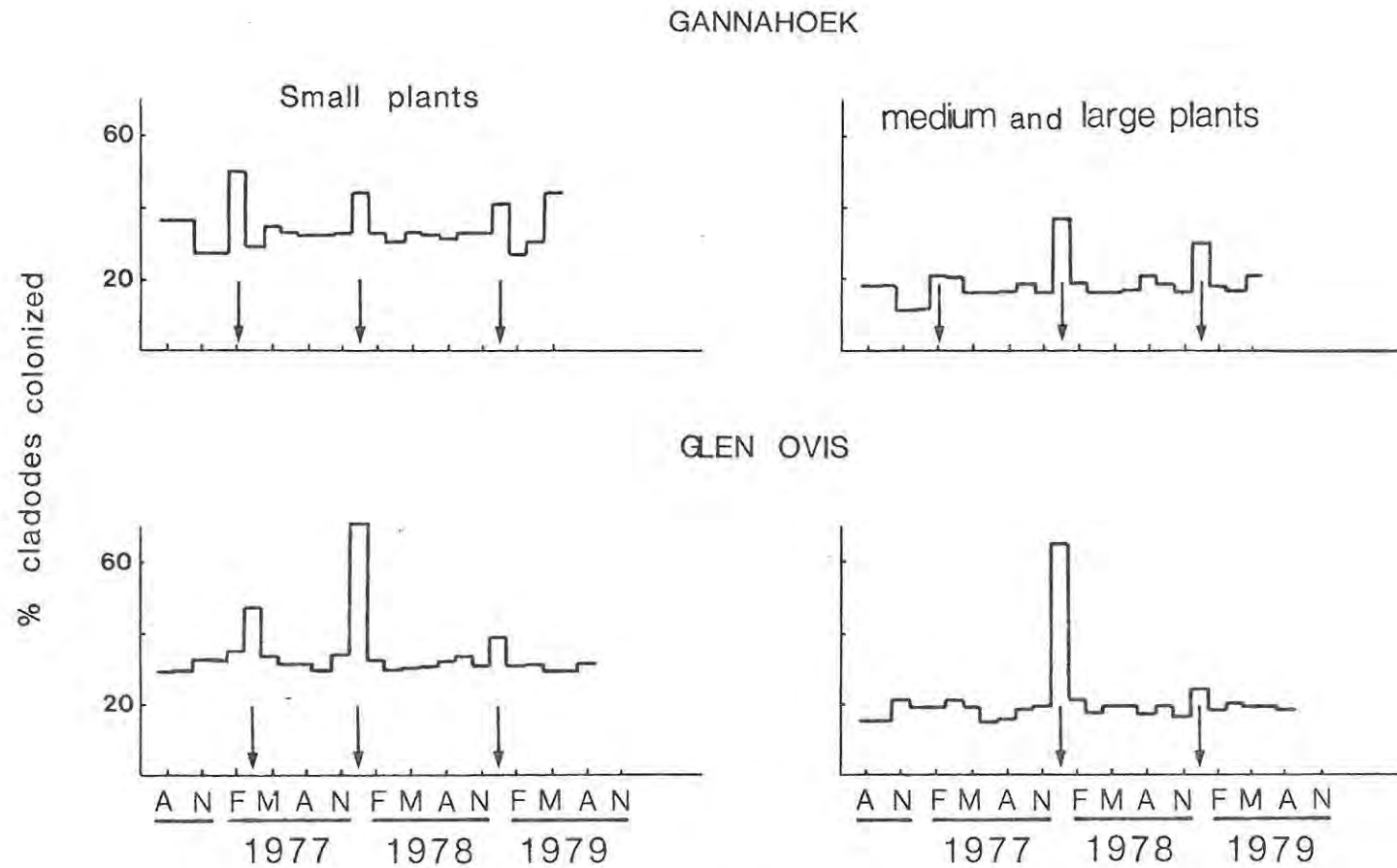
Fig. 48. Mean percentage of cladodes colonized by D. austrinus in 20 small (B-category) and 20 large (C + D category) O. aurantiaca plants observed at six week intervals at Gannahoek and Glen Ovis. F = February; M = May; A = August; N = November.

WESTONDALE

small plants

medium and large plants

MIDDELBURGPLAAS

A N F M A N F M A N F M A
1977 1978 1979

A N F M A N F M A N F M A
1977 1978 1979
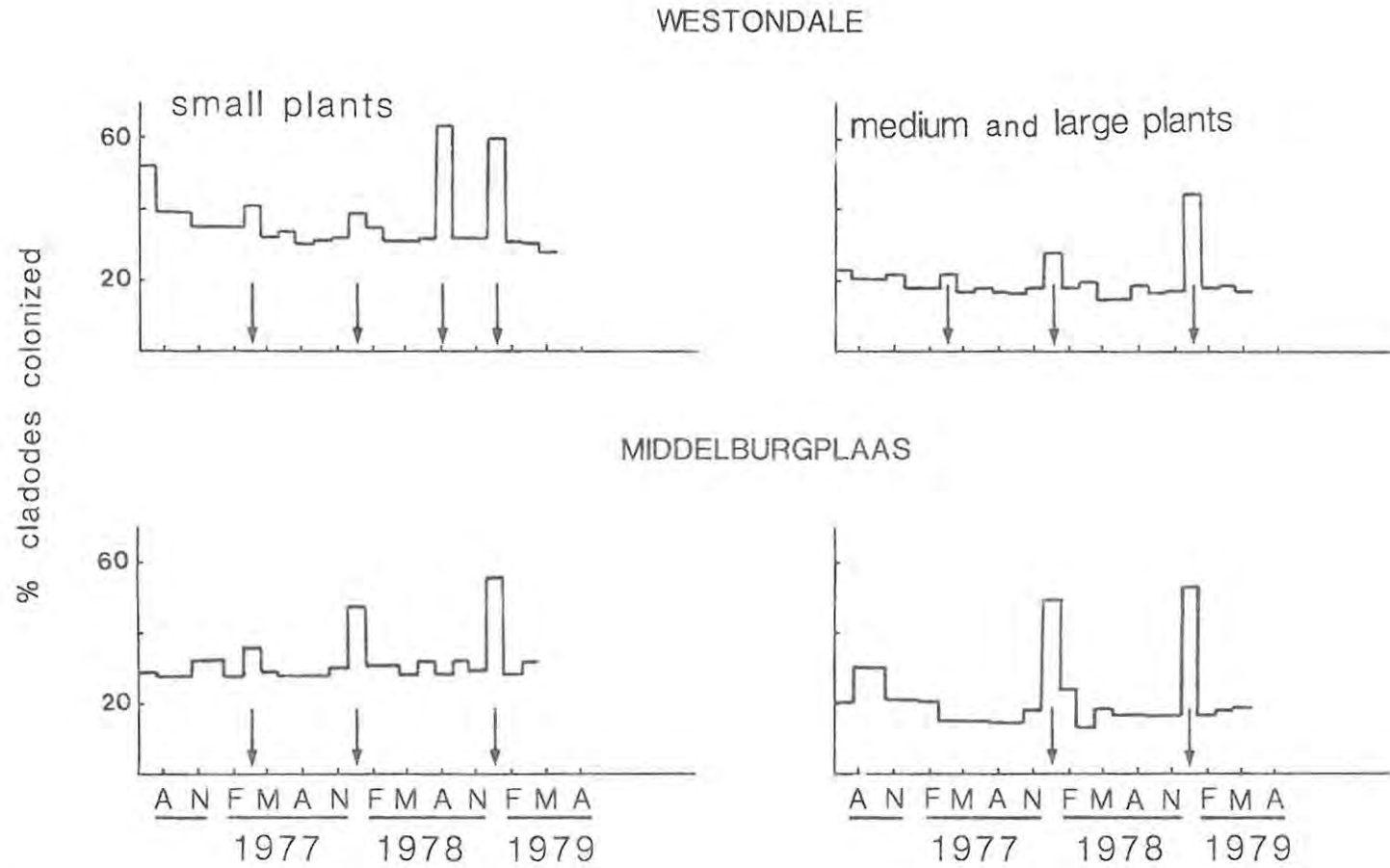
Fig. 49. Mean percentage of cladodes colonized by D. austrinus in 20 small (B-category) and 20 large
(C + D category) O. aurantiaca plants observed at six week intervals at Westondale and
Middelburgplaas. F = February; M = May; A = August; N = November.

## 12. DISCUSSION

The success of any biological control programme on a weed will depend on the interaction between the weed, its insect enemies and the environment (Groves et al. 1979) and the importance of understanding the ecology of the weed is therefore fundamental to any biological control study. In this study the distribution ecology of jointed cactus received considerable attention because of its effect on the success of chemical and biological control.

This study has far reaching implications for jointed cactus control in South Africa and these will be discussed under the following points : (i) survey techniques for both O. aurantiaca and D. austrinus populations; (ii) aggregation of the weed and its effect on chemical and biological control; (iii) integrated control strategies for jointed cactus; (iv) surveillance of jointed cactus infestations; (v) biotic and abiotic mortality factors in jointed cactus populations; (vi) the Westondale controversy; (vii) probable effect of the nutritional status of the plant and the effect on settling of cochineal crawlers and (viii) scope for future research.

The basis of this study was the development of an acceptable and reliable sampling method that could be used for host plant and insect population studies : the old empirical methods had to be replaced with more quantita-tive approaches.

The survey method adopted in this study relied on non-destructive cohort (= transect) surveys to relate mean and variance estimates to the true population parameters at pre-set reliability levels. The transect method was robust and versatile and was also used successfully to evaluate chemical control methods (see appendix 5) and to screen herbicides for jointed cactus control (Zimmermann et al 1981). The high coefficients of variance at all quadrat sizes is a reflection of the aggregated nature of jointed cactus populations encountered and explains why an excessively high number of random samples had to be used in destructive sampling methods. Such high variances are not rare in biological populations as most animals and plants are aggregated in nature (Southwood 1978).

The key population parameter that has the largest impact on jointed cactus and cochineal population dynamics in South Africa is the aggregated nature of the jointed cactus plant. Therefore the quantification of aggregation

and also its relation to the distribution of the cochineal insect has been
studied in some detail.

Aggregation of jointed cactus is positively related to the efficiency of
chemical and biological control of O. aurantiaca. This resulted inadver-
tently in the selective elimination of all those plants and clumps, during
spray operations, that carry the bulk of the cochineal insect population.
Twenty-four years of continuous application of herbicides in South Africa
has gradually and selectively eliminated cochineal insects from jointed
cactus infestations and this explains their low numbers in areas where
chemical spraying is rigidly applied. Consequently the impact of
D. austrinus on jointed cactus populations today is generally low.

Aggregation of jointed cactus populations is also a prerequisite for
successful dispersal of D. austrinus crawlers (Gunn 1979). The degree of
aggregation necessary for successful dispersal is normally associated with
high density jointed cactus infestation which often lies well above the
tolerable threshold level of 2 - 3 large (C+D) plants per 10 $m^2$.

It is now possible to explain the first ten years of events after
D. austrinus was released on jointed cactus in 1936 (Pettey 1948). The
pre-release infestations, then, were dense and highly aggregated according
to present criteria (Burger, pers. comm.). These dense infestations enabled
the cochineal insects to increase rapidly, destroying most clumps and large
plants, thus also eliminating their own host plant and points for further
dispersal. During the peak epidemic levels of D. austrinus all other
measures of control were discontinued and D. austrinus carried full respon-
sibility for control. As aggregation of the weed infestations decreased,
the increased interclump distance in the post-release and regrowth popula-
tions prevented subsequent dispersal of the cochineal insects. It then
became clear that equilibrium levels of jointed cactus following biological
control were unacceptably high and that the reinfestation of jointed
cactus regrowth with D. austrinus was delayed. Subsequently (in about
1947) it was decided to discontinue biological control and to reintroduce
mechanical and later chemical control. The failure of D. austrinus was
explained by means of ant and rodent predation and lack of "toxicity" of
D. austrinus. Studies and observations, not reported in this study,
showed that these are not limiting factors which hinder the increase of
D. austrinus in South Africa.

The spraying of jointed cactus regrowth i.e. at the endemic levels of cochineal infestation, drastically reduced cochineal abundance even further to the extent where D. austrinus became extinct in some areas. Unfortunately, the present jointed cactus control campaign leaves no alternative methods to explore which could prevent this selective elimination process of D. austrinus. It is impractical to instruct sprayers to leave the cochineal-bearing large plants and clumps un-sprayed in order to increase the cochineal reservoir in post-spray jointed cactus populations. Also the insecticidally effective paraffin based herbicide which has now been replaced with water based MSMA (Zimmermann & Malan 1981) and which exhibits no insecticidal effect on D. austrinus, will unfortunately not change this selective eliminating process because the sessile cochineal insect will inevitably die with the death of the host. Moran and Cobby (1980), however, have shown that cochineal females that are removed from their host cladodes at the end of the pre-oviposition period still produce their full complement of crawlers. Crawler dispersal should thus continue unabated in spite of the rapid desiccation of the host plant by MSMA. It is unlikely, however, that this will improve biological control in post-spray populations because of the elimination of the prime targets of D. austrinus crawlers, namely large plants and clumps. The residue cochineal inoculum in a post-spray infestation will be determined by the number of infested plants that have been overlooked by sprayers and these are always few.

Isaacson (1976) reported on an integrated control programme at State level for Senecio jacobaea L. management in Canada where the productivity level and the physical accessibility of the land dictates the type of control measure applied. Chemical control is justified in highly productive land whereas biological control provides satisfactory control in timber-land which is little affected by infestations of ragwort. These considerations are implemented in the State-wide control strategy. A similar approach for the management of jointed cactus in South Africa is justified and would entail the identification of areas where biological control could continue unhindered. Other areas can be set aside for "integrated" control where some jointed cactus infestations on the same property are chemically treated and where the prospects for successful biological control are less favourable. Some areas, on the same property, may be managed biologically. The artificial dispersal of cochineal crawlers as outlined by Gunn (1979) and discussed in this study, could enhance the dispersal of D. austrinus

in these areas. Other areas may be reserved entirely for chemical control where it has been shown that biological control is unsatisfactory. Highly productive grazing land may fall in this category. The delimitation of these areas would not be difficult and could largely be dictated by the different ecosystems present in the eastern Cape. Information on the phenology and growth of jointed cactus and the efficiency of D. austrinus in three of the ecological regions of the eastern Cape has already been obtained from this study and could form the basis for such a classification.

A prerequisite for the management of such an integrated control system as discussed above, would be to intensify and quantify the present surveil-lance scheme for jointed cactus and D. austrinus populations. The informa-tion gained would then dictate the control strategy to be followed in any particular area. To meet the need for a method of field assessments of jointed cactus populations a sequential sampling method was designed for use by the existing team of weed inspectors operating in the eastern Cape (see appendix 6). This will allow weed inspectors to assess jointed cactus populations quantitatively and on the basis of pre-set rules, then recom-mend the best control method.

The sequential inspection method proposed comprises a number of random 10 m walks or "transects". These transects are 2 m wide and each cover an area of 2 x 10 m (= 20 m²). The surveyor paces 10 steps in a straight line at random in the infested veld to be inspected while holding a T-shaped walking stick in front of him over the vegetation. The crossbar of the stick is 2 m long and all the medium (C) and large (D) category plants that pass underneath the bar, are counted. This survey is continued until, on the basis of the density of plants per 20 m², the degree of the infestation level can be estimated at a preset reliability level. Figure 50 represents such a sequential survey plan for jointed cactus, based on the calculations in appendix 6.

After 10 such transects are covered one of three decisions is made, namely:

(a)  the infestation is light ($<1$ plants per 20 m²) and no action is necessary for 18 – 24 months, depending on the region;

(b)  the infestation is medium (between 1 and 5 plants per 20 m²) and some action must be taken during the following 12 – 18 months when a subsequent inspection is due and
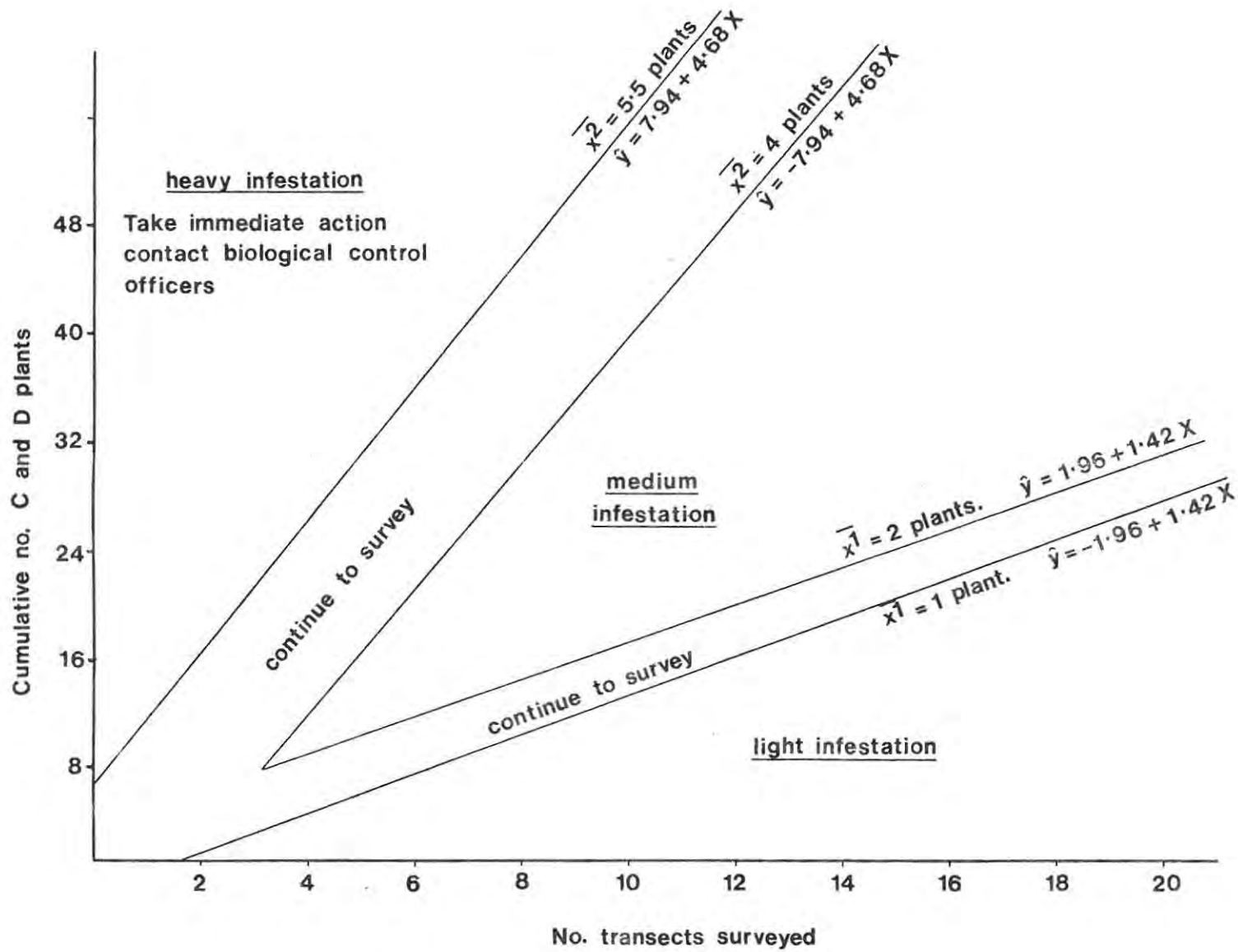
Fig. 50. Sequential graph for sampling C and D category plants for three infestation levels.

(c)   the infestation is heavy (> 5 plants per 20 m²) and calls for urgent
attention.  Such infestations must be reported to biological control
officers for further assessments because such dense infestations are
often suitable for biological control in which case it may also be neces-
sary to enhance the cochineal population by means of artificial dispersal.

Abiotic mortalities (mainly desiccation) are the key mortality factors
operating on small O. aurantiaca plant categories at all jointed cactus
population levels and is thus density independent.  This mortality was not
recognized before and all deaths were usually assigned to D. austrinus
because cochineal colonized plants are so conspicuous in infested veld.
As expected, desiccation was highest in dry areas and peaks were consis-
tently recorded for February when hot and dry midsummer conditions pre-
vailed.

Post-spray jointed cactus populations consist mainly of small category
plants which are continuously subjected to desiccation mortalities.
Bearing in mind the low efficiency of chemical control in these low density
and scattered small plant infestations, it would be futile and time and
money would be wasted in treating post-spray jointed cactus populations at
the recommended time of 6 - 8 months after spraying.  This study suggests
that residue post-spray jointed cactus populations could be left for 24 -
36 months to grow to more conspicuous plants before a follow-up operation
is done when most of these survivors will be efficiently killed (see
appendix 5).

The Westondale controversy needs to be highlighted because of the confusion
that surrounds the status of the weed and the efficiency of D. austrinus in
this and surrounding regions.

The owner of Westondale has always been reluctant to apply any recommended
control measure against jointed cactus other than biological control, in
spite of the fact that according to the Weeds Act of 1937, he is compelled
to spray all plants on his property.  Officials, however, realized that the
status of jointed cactus was less serious at Westondale than at other areas
but were nevertheless reluctant to admit that D. austrinus provided the
adequate control.  This controversy was one of the motivations behind this
study.

These populations studies have shown that: (a) growth of jointed cactus populations at Westondale was small compared to all other sites; (b) there is a very high rate of desiccation operating on the small category plants; (c) the mortalities caused by D. austrinus were small compared to desiccation mortalities, but nevertheless substantial and sufficient to prevent an increase of the jointed cactus population over the 39 month study period. Under these conditions the jointed cactus population equilibrium level is expected to remain well below any economic threshold level and it should be possible with very little input from chemical control, but with continued surveillance of plant populations, to keep the infestations at low levels. It should be stressed, however, that jointed cactus populations will behave slightly differently in the various habitats within the same area e.g. along river courses. A high cochineal inoculum level will have to be maintained for keeping the infestation under continued biological control.

In order to increase the impact of D. austrinus on dense jointed cactus infestations, dispersal of the insect can be enhanced by either "tower" releases of cochineal crawlers or by placing D. austrinus females on cladodes into large uncolonized plants or clusters, assuming that crawlers will then transfer to uninfested plants. Both methods have merits although the latter one is more practical and better suited for use by farmers because no equipment is needed and it can be applied equally well in all infestation types. Natural dispersal and "tower" dispersal of cochineal crawlers in the thick valley bushveld is very low because dispersing crawlers are effectively screened off by thick vegetation and seldom find their targets.

The limited dispersal of D. austrinus crawlers in valley bushveld is one of two reasons why biological control maintains a low profile in this habitat. Because of the extreme clumpiness of the infestations, the selective elimination of cochineal bearing large plants and clumps by chemical spraying, is intensified. This could explain why D. austrinus is totally absent from some of these areas. Results at Hankey and at Centlivres have shown that the mortalities caused by D. austrinus can be impressive if a sufficient cochineal inoculum is introduced although the valley bushveld has traditionally been earmarked as a poor biological control area. Therefore, hand-dispersal of D. austrinus could be of considerable advantage in infested valley bushveld.

Mass releases of D. austrinus crawlers did not produce the immediate increase in the cochineal population which suggests that other factors, including the nutritional level of the target plants, could have prevented host acceptance by the probing crawlers. There are several more similar observations from jointed cactus studies, listed below, which suggests that the nutritional levels of the host plant, e.g. the nitrogen levels (McNeill & Southwood 1978), could affect cochineal abundance.

The following observations highlight the need for further research on cochineal insects and host plant interrelationships with emphasis on the movement of essential nutrients or plant hormones in the plant :

(a) The short peak of the cochineal insect populations on colonized plants in December (see figs 48 and 49) mostly coincided with the onset of flowering which is often linked to an increase in nitrogen levels in the plants (McNeill 1973; Woodwell et al. 1975).

(b) D. austrinus has definite preferred feeding sites on O. aurantiaca (Gunn 1979), preferring mostly the stems and tubers which have a high starch content.

(c) Cochineal females reared on isolated cladodes were smaller and produced fewer crawlers than those reared from rooted plants (Gunn 1979).

(d) Zimmermann et al (1974) and Gunn (1979) stated that the spread of cochineal populations dependson the presence of large plants or clumps where the horizontal dispersal range exceeds the inter-plant distance. It has, however, frequently been observed that in two adjacent large plants only one remained colonized over extended periods suggesting that the uncolonized plant must have remained unsuitable for colonizing crawlers.

It may well turn out that inadequate dispersal of D. austrinus which has been identified as the weak link in the system is but a minor shortcoming, and that factors limiting host plant acceptance by the dispersing crawlers together with the selective elimination of cochineal populations by chemical spraying, prevent the full exploitation of this natural insect enemy in South Africa.

This study irrefutably showed that a thorough knowledge of the target plant is essential when trying to understand insect enemy and host weed inter-

actions.  <u>Ad</u> <u>hoc</u> and arbitrary decisions which are based on empirical observations have been part and parcel of decision making in the history of jointed cactus control in South Africa.  Both decisions, namely to discontinue all chemical and mechanical control methods, and secondly to shelve biological control completely 11 years later, carried no research support whatever and did the image of biological control immense harm. This provides a classical example of what should not have been done in a biological control programme.

## 13. SUMMARY

(1)    This study is about the interrelationships between the jointed
cactus weed Opuntia aurantiaca, in South Africa, and its prime natural
enemy Dactylopius austrinus and how this relationship is affected by the
chemical spraying of the weed.

(2)    The distribution of O. aurantiaca and the cochineal, D. austrinus,
was highly aggregated and this dictated that a large number of samples
was  required for a sample mean to remain within the 10% or 20% accuracy
levels.  It was more convenient to rely on non-destructive sampling and
this was achieved by means of 1 500 or 3 000 square metre samples strati-
fied into 30 randomly placed 2 m wide permanent transects.

(3)    O. aurantiaca distributions were best described by the negative
binomial distribution.  The variance/mean ratio, however, was the best
parameter to describe the degree of aggregation.  Aggregation always
increased with increase in density.  The diameters of aggregated plants
or clumps were always less than 1 m, but some clumps were compounded.

(4)    Efficiency of herbicidal spot spraying of O. aurantiaca is highly
correlated with the aggregation of the plant and because the distribution
of D. austrinus is also highly correlated with the aggregation level of
its host, spraying selectively eliminates cochineal populations from
infestations.  The result is that D. austrinus remains in low endemic
levels where chemical control of the weed is practised.

(5)    After chemical spraying, jointed cactus populations consist of
mainly evenly scattered small plants and isolated cladodes with a low
incidence of D. austrinus colonization.  Such endemic cochineal populations
are not correlated with aggregation.  Significant increases of D. austrinus
will depend on a minimum threshold density of the jointed cactus host
population and once this threshold has been reached, and provided condi-
tions are favourable, the abundance of the cochineal insect will again
become correlated with aggregation of the host plant.  Under ideal
conditions this may lead to an epidemic level where 40 - 80% of all plants
become colonized with D. austrinus resulting in high plant mortalities.
Because of chemical spraying, however, epidemic levels seldom occur
nowadays.

(6)    Regrowth of post-sprayed O. aurantiaca populations were unaffected by residue D. austrinus insects because of their very low numbers. A high mortality of small plants and isolated cladodes is the direct consequence of desiccation and this explains the initial slow increase of jointed cactus regrowth populations. Follow-up chemical treatment is recommended once the plants have grown to more conspicuous large plants when spray efficiency will again become high. This stage is reached some 24-36 months after spraying.

(7)    Growth of O. aurantiaca populations was highest in the coastal site, intermediate in three inland sites and low in the extreme hot and dry conditions at Westondale. Jointed cactus infestations at Westondale are subjected to a high desiccation of small plants and isolated cladodes and together with the biotic pressure from D. austrinus, are kept at an acceptable level of control with a minimum of chemical assistance.

(8)    Significant decreases of natural jointed cactus infestations caused by D. austrinus occurred only during epidemic outbreaks of the insect.

(9)    Desiccation of isolated cladodes and small plants was the key-mortality factor which operated density independently at all sites. Peak mortalities were consistently recorded for December to February.

(10)   There are no discrete generations of D. austrinus in the field and all stages of the insect were sampled throughout the year. There were, however, prominent peaks of short duration during December when cochineal insects suddenly increased on colonized plants. This and other observations suggest that host plant acceptance by the cochineal insect at different nutritional levels of the plant probably influences cochineal abundance.

(11)   This study suggests that control of the jointed cactus weed should be integrated by selectively applying chemical or biological control methods, whichever is most suited and effective. Infested areas can be delimited into three management zones where control relies on either biological control, integrated control or chemical control.

APPENDIX 1. Raw data sheet with survey results from a short 25 x 2 m transect. The small figures indicate the results of the previous survey and the large figures those of the present survey. The previous survey records were included on the data sheets in order to help the samplers to trace the plants and this method increased the accuracy of counts considerably.

farm: Glen Ovis       date: May 1978       transect: 8 Cochineal

(Note: in each cell the large figure is the present survey, the small figure — shown in parentheses — is the previous survey.)

**category — with D. austrinus (left)**

| # | A | | B | | C | | D | |
|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | | |
| 2 | 0(1) | | 2(1) | | | | | |
| 3 | | | | | | | | |
| 4 | | | 2(2) | | | | | |
| 5 | 1(1) | 1 | 3(4) | | 1 | | | |
| 6 | 4(1) | | 3(1) | | | | | |
| 7 | 1(1) | | 5(5) | | | | | |
| 8 | | | | | | | | |
| 9 | 28(27) | 8(7) | 30(29) | 6(6) | 1(2) | 0(2) | | |
| 10 | 28(26) | 6(7) | 30(30) | 6(5) | 1(1) | 1(1) | | |
| 11 | 9(9) | 0(7) | 25(23) | 0(4) | | | | |
| 12 | 0(3) | | 2(1) | 1(1) | | | | |
| 13 | 2 | | 5(3) | | | | | |
| 14 | | | | | | | | |
| 15 | 1 | | 2(2) | | | | | |
| 16 | 2(1) | | 1 | | | | | |
| 17 | | | 1 | | | | | |
| 18 | 0 | | 1 | | | | | |
| 19 | 1(1) | | 3(2) | | | | | |
| 20 | | | | | | | | |
| 21 | | | 1(1) | | | | | |
| 22 | 1 | | 10(4) | 1 | 1(2) | | | |
| 23 | 2 | | 0(1) | | | | | |
| 24 | 16(31) | 4(4) | 58(39) | 8(9) | 2(1) | 1(1) | | |
| 25 | 3 | | 2(5) | 1(2) | | | | |

**category — with D. austrinus (right)**

| # | A | | B | | C | | D | |
|---|---|---|---|---|---|---|---|---|
| 1 | | | 2(2) | | | | | |
| 2 | | | 5(3) | | | | | |
| 3 | | | | | | | | |
| 4 | 1(3) | | 2(1) | | 0(1) | | | |
| 5 | 2 | | 1(1) | | | | | |
| 6 | 0(1) | | 1 | | | | | |
| 7 | 1(1) | | | | | | | |
| 8 | 5(7) | 2 | 9(6) | 5(2) | 1(1) | 1(1) | | |
| 9 | 6(2) | 3(4) | 24(25) | 7(12) | 2(1) | 2(1) | | |
| 10 | 6(5) | 0(3) | 26(26) | 5(6) | 0(1) | 0(1) | | |
| 11 | 6(2) | 0(2) | 14(19) | 0(6) | 0(1) | 0(1) | | |
| 12 | 1(1) | | 2(2) | | | | | |
| 13 | 1(2) | 0(1) | 4(5) | 0(4) | 0(1) | 0(1) | | |
| 14 | | | | | | | | |
| 15 | (1) | | 1 | | | | | |
| 16 | 5 | 5 | 6(7) | 4(6) | | | | |
| 17 | 1(1) | 0(1) | 1 | | | | | |
| 18 | | | | | | | | |
| 19 | 9(6) | 4(2) | 28(24) | 5(4) | 1(1) | 1(1) | | |
| 20 | 4(1) | 0(1) | 3(3) | 0(3) | 1(1) | 1(1) | | |
| 21 | 47(45) | 42 | 21(19) | 6(13) | 3 | 3 | 1(1) | 1(1) |
| 22 | 3(2) | 0(1) | 11(11) | 2(6) | | | | |
| 23 | 1(1) | | 1(1) | | | | | |
| 24 | 13(12) | 6(10) | 11(11) | 5(10) | | | | |
| 25 | 23(29) | 8(9) | 36(33) | 14(25) | 2(2) | 2(2) | 0(1) | 0(1) |

APPENDIX 2.  Mortalities and births calculated from raw data sheet.  (see Appendix 1).

farm _ Glen Ovis _          date   February 1978 – May 1978

transects  8  Cochineal

| metre | BIRTHS | MORTALITY category A coch | A Abiot | B coch | B Abiot | BIRTHS | MORTALITY category A coch | A Abiot | B coch | B Abiot |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 |  |  |  |  |  |  |  |  |  |  |
| 2 |  |  |  |  |  | 2 |  |  |  |  |
| 3 |  |  |  |  |  |  | 2 |  |  |  |
| 4 |  |  |  |  |  |  |  |  |  |  |
| 5 |  |  |  |  |  | 2 |  |  |  |  |
| 6 | 5 |  |  |  |  |  |  |  |  |  |
| 7 |  |  |  |  |  |  |  |  |  | · |
| 8 |  |  |  |  |  | 1 |  |  |  |  |
| 9 | 1 |  |  |  |  |  |  |  |  |  |
| 10 | 2 |  |  | 5 | 1 | 1 |  |  |  |  |
| 11 | 2 |  |  |  |  | 4 |  |  | 6 |  |
| 12 |  |  | 2 |  |  |  |  |  |  |  |
| 13 | 4 |  |  |  |  |  | 1 |  | 2 |  |
| 14 |  |  |  |  |  |  |  |  |  |  |
| 15 | 1 |  |  |  |  |  |  |  |  |  |
| 16 | 2 |  |  |  |  | 5 |  |  | 1 |  |
| 17 | 1 |  |  |  |  | 1 |  |  |  |  |
| 18 |  |  |  |  |  |  |  |  |  |  |
| 19 | 1 |  |  |  |  | 7 |  |  |  |  |
| 20 |  |  |  |  |  | 3 |  |  |  |  |
| 21 |  |  |  | 1 |  | 7 |  |  |  |  |
| 22 | 6 |  |  |  |  | 1 |  |  |  |  |
| 23 | 2 |  |  |  | 1 |  |  |  |  |  |
| 24 |  | 4 | 1 |  |  | 1 |  |  |  |  |
| 25 | 3 |  |  | 2 | 7 |  | 4 |  |  |  |
| total | 30 | 4 | 3 | 7 | 3 | 35 | 5 | 2 | 9 | 0 |

APPENDIX 3. The mean and variance of transformed and untransformed
counts of isolated cladodes of O. aurantiaca at Gannahoek.
The tranformation log (x + 1), where x is equal to the
observed count, was best able to stabilize the variance
and mean dependency as shown in fig. 17, indicated by the
value of r = 0,33 ( P = < 0,01).

| | TRANSFORMED COUNTS | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Trans-ect Number | Original Counts | | Log (x + 1) | | Log (x + k/2) | | Log x .46 | |
| | Mean | Var. | Mean | Var. | Mean | Var. | Mean | Var. |
| 1. | 1,18 | 6,6 | 0,18 | 0,10 | 0,29 | 0,30 | 0,06 | 0,02 |
| 2. | 1,38 | 2,8 | 0,29 | 0,07 | 0,05 | 0,26 | 0,07 | 0,01 |
| 3. | 2,70 | 11,3 | 0,42 | 0,13 | 0,14 | 0,35 | 0,14 | 0,03 |
| 4. | 1,52 | 4,5 | 0,31 | 0,09 | 0,06 | 0,29 | 0,08 | 0,02 |
| 5. | 2,06 | 7,8 | 0,34 | 0,12 | 0,02 | 0,37 | 0,11 | 0,02 |
| 6. | 1,76 | 4,8 | 0,33 | 0,10 | 0,01 | 0,31 | 0,10 | 0,02 |
| 7. | 1,58 | 7,8 | 0,25 | 0,12 | 0,17 | 0,36 | 0,08 | 0,02 |
| 8. | 1,42 | 6,7 | 0,23 | 0,11 | 0,25 | 0,27 | 0,07 | 0,02 |
| 9. | 0,78 | 1,3 | 0,18 | 0,06 | 0,26 | 0,22 | 0,04 | 0,01 |
| 10. | 1,80 | 5,8 | 0,34 | 0,10 | 0,01 | 0,30 | 0,09 | 0,02 |
| 11. | 1,44 | 4,5 | 0,29 | 0,08 | 0,05 | 0,26 | 0,07 | 0,01 |
| 12. | 1,10 | 4,3 | 0,20 | 0,09 | 0,25 | 0,29 | 0,06 | 0,01 |
| 13. | 2,60 | 10,7 | 0,41 | 0,13 | 0,14 | 0,33 | 0,13 | 0,03 |
| 14. | 1,56 | 7,1 | 0,26 | 0,11 | 0,15 | 0,34 | 0,08 | 0,02 |
| 15. | 2,10 | 10,0 | 0,32 | 0,14 | 0,04 | 0,40 | 0,11 | 0,03 |
| 16. | 2,60 | 7,3 | 0,45 | 0,10 | 0,22 | 0,27 | 0,14 | 0,02 |
| 17. | 4,12 | 16,6 | 0,57 | 0,50 | 0,30 | 0,39 | 0,20 | 0,04 |
| 18. | 1,06 | 2,7 | 0,28 | 0,22 | 0,16 | 0,24 | 0,05 | 0,01 |
| 19. | 2,14 | 7,0 | 0,36 | 0,11 | 0,07 | 0,31 | 0,11 | 0,02 |
| 20. | 1,94 | 9,4 | 0,31 | 0,12 | 0,06 | 0,36 | 0,10 | 0,02 |
| | r = 0,9 | | r = 0,33 | | r = 0,41 | | r = 0,86 | |

APPENDIX 4 : Rainfall for the duration of the trials at four sites.
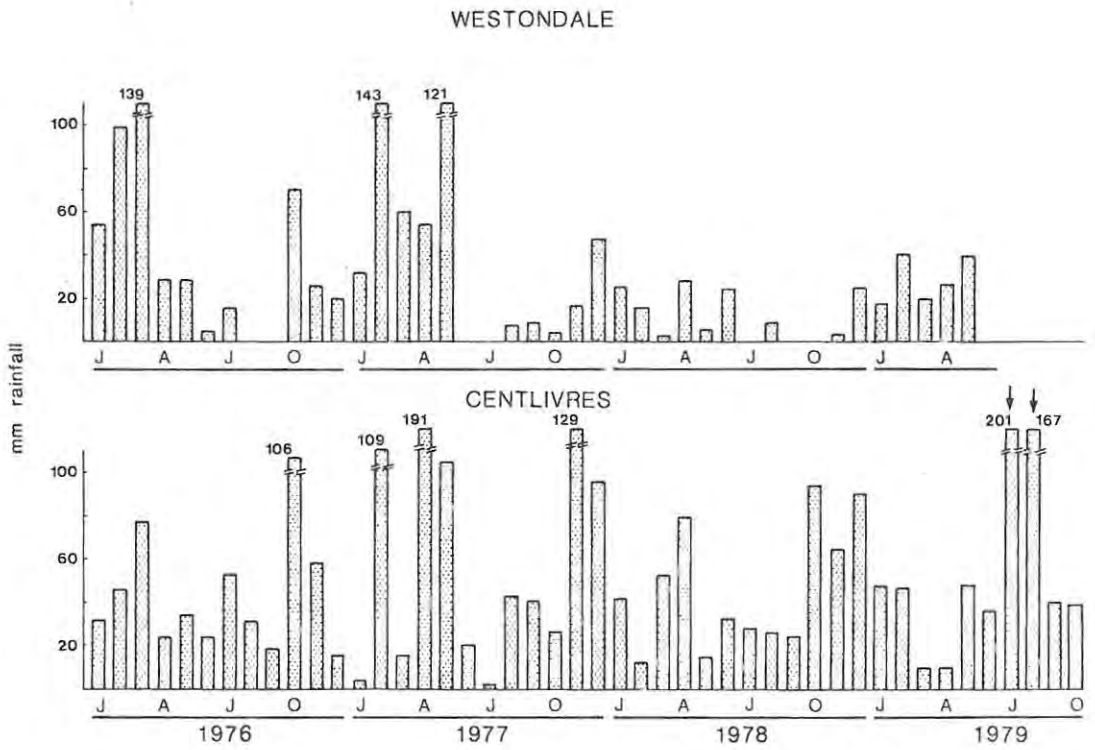
GLEN OVIS



MIDDELBURGPLAAS

APPENDIX 4 : (continued)



WESTONDALE

CENTLIVRES

mm rainfall

# A MODIFIED TECHNIQUE FOR THE HERBICIDAL CONTROL OF JOINTED CACTUS, OPUNTIA AURANTIACA LINDLEY, IN SOUTH AFRICA

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## ABSTRACT

Keywords: *Opuntia aurantiaca*, spray efficiency; savings; dose; plant size

A modified technique of applying a herbicide for the control of jointed cactus was developed in order to economise on materials and labour. When operators moved through an infested area in about half the normal time, not delaying to search for inconspicuous plants, there was a 35–47% saving in total costs. Efficiency dropped slightly among loose joints and isolated small plants but the difference was negligible in view of the natural mortality of these small category plants.


## *Uittreksel*

### *'N GEMODIFISEERDE TEGNIEK VIR DIE CHEMIESE BEHEER VAN LITJIESKAKTUS, OPUNTIA AURANTIACA LINDLEY IN SUID-AFRIKA*

*Sleutelwoorde:* Opuntia aurantiaca; *doeltreffendheid van bespuiting; besparings; dosis; plantgrootte*

*'n Gemodifiseerde tegniek van onkruiddodertoediening vir die beheer van litjieskaktus is ontwikkel met die oog op besparings van spuitstof en arbeid. Waar toedieners teen die helfte van die normale tempo gespuit het, sonder die onnodige vertragings deur na versteekte plante te soek, was daar 'n algehele besparing van 35–47% in totale koste. Die afname in doeltreffendheid van bespuiting van los litte en geïsoleerde klein plante was gering en die verskil is onbeduidend in die lig van die natuurlike mortaliteit wat in hierdie klein plantkategorieë voorkom.*


## *Résumé*

### *UNE TECHNIQUE MODIFIÉE POUR LA LUTTE HERBICIDE CONTRE LE CACTUS OPUNTIA AURANTIACA LINDLEY EN AFRIQUE DU SUD*

*Une technique modifiée d'application d'herbicide pour la lutte contre le cactus* Opuntia aurantiaca *a été développée afin d'économiser les produits ainsi que le travail et la main d'oeuvre. Quand les opérateurs se déplacèrent à travers une région infestée en un temps moitié moindre que la normale, ne perdant pas de temps à chercher les plantes peu visibles, une économie de 35–47% fut réalisée sur le coût total. L'efficience diminua légèrement pour les plantes détachées ainsi que pour les petites plantes isolées mais la différence fut négligeable quand on considère la mortalité naturelle de cette catégorie de petites plantes.*

## INTRODUCTION

The present herbicidal control programme against jointed cactus, *Opuntia aurantiaca* Lindley, comprises spot-spraying with a hormonal herbicide carried in illuminating paraffin. The formulated herbicide is provided by the Department of Agriculture and Fisheries to landholders whose properties are infested. The cost of a 200 dm³ drum of mixed herbicide rose from R35 in 1978 to R80 in 1979. The increasing expenditure is of grave concern to authorities in view of the large volume of herbicide that is used annually for jointed cactus control in the eastern Cape Province (Moran & Annecke, 1979).

For many years farmers have received the herbicide free of charge but recently a nominal fee of R2 per drum has been levied. The cost of application must be borne by the farmers themselves. Workers in spray teams are employed to search for every plant or joint in an infested area; progress is therefore slow and it is not uncommon for a labourer to spend 20 man hours on the treatment of one hectare with a medium to heavy infestation of jointed cactus. Even then, searching efficiency has been found to be low because sprayers fail to locate many of the small, isolated joints and plants. Searching efficiency is highest in highly aggregated infestations of jointed cactus because the bulk of the population of joints occurs in clumps and around large plants which are easily detected and sprayed (Zimmermann, 1979).

An attempt was made to reduce the cost of herbicidal control by adopting a modified technique of

spraying that permits a saving on both herbicide and labour without significantly sacrificing efficiency. This paper reports on the results of this attempt.

## MATERIALS AND METHODS

Experimental sites were chosen at three localities in the Eastern Cape Province, near Grahamstown, Somerset East and Adelaide. The vegetation at each site consisted of grass and low-growing shrubs dominated by *Pentzia incana* (Thunb.) Kuntze, known as "false karroid broken veld" (Acocks, 1975). At each site 1 ha of jointed cactus infested pasture was divided into two halves. In one half the spray team was instructed to perform a normal treatment, i.e. to search for and spray as much of the jointed cactus as possible. In the other half the spray team performed a fast treatment, i.e. they were instructed to move through the plot in about half the normal time, spraying only the jointed cactus that they detected at their increased pace. The team consisted of six experienced spray operators but they were unaware of the objectives of the experiment.

The herbicide was the iso-octyl ester of picloram with illuminating paraffin as carrier. Waxolene oil solvent red dye (1 g/dm³) was added to the spray solution. By comparing numbers of dyed and undyed plants the efficiency of the two treatments could be compared. Counts were made shortly after spraying in thirty randomly selected transects each 25 m long and 2 m wide. Each of the 50 meter squares per transect was assessed individually using a 2×1 m frame divided across the centre and moved along the transect as counting progressed (see Zimmermann, 1979).

Jointed cactus plants were divided into four size categories for the purpose of counting:

(i) individual, unrooted joints which had been dislodged from the parent plant;

(ii) small rooted plants each with less than five joints;

(iii) medium-sized plants each consisting of 5 to 10 joints, and

(iv) large plants with more than 10 joints each.

A second experiment was conducted in an infested area near Uitenhage to ascertain the actual volumes of herbicide mixture normally sprayed on jointed cactus plants of different sizes. For the purpose of this investigation six categories of plant size were chosen: 1 joint (unrooted), 1–5, 4–6, 7–10, 11–15 and 16–20 joints per plant, respectively. Each operator was instructed to spray only selected and marked plants in a particular category. By recording the total volume sprayed as well as the number of plants sprayed, the mean volume of herbicide sprayed per joint in each category of plant size was calculated. Determinations were made on eight replicate groups of 40 plants for each category.

Confidence limits were calculated according to the formula $\pm t\ 0,05\ (n-1)\ \dfrac{s}{\sqrt{n}}$, where $t\ 0,05\ (n-1)$ represents the t-value from a two-tailed t-table at $0,05$ probability and $n-1$ degrees of freedom, s the standard deviation and n the number of samples.

## RESULTS

The data in Table 1 shows that the normal, slow method of searching for jointed cactus plants resulted in an average of $10,1\%$ of isolated, single joints being overlooked at the three sites. The figures for overlooked small and medium plants, respectively, were $13,2\%$ and $4,9\%$. Operators were almost $100\%$ efficient in locating large plants. These data confirm the results of Zimmermann (1979).

The fast treatment resulted in more of the single joints, small and medium plants being overlooked. In the case of large plants, however, efficiency was still close to $100\%$. Spraying efficiency on single joints, small and medium plants was found to have decreased overall by $7,02\%$ ($95\%$ confidence limit$=\pm 2,8\%$).

TABLE 1 Efficiency of spray teams in treating *O. aurantiaca* plants with herbicide after normal treatment and fast treatment methods at three localities: A=Adelaide; B=Grahamstown; C=Somerset East
TABEL 1 *Doeltreffendheid van spuitspanne vir die beheer van* O. aurantiaca-*plante met onkruiddoder na normale en vinnige bespuitingsmetodes by drie lokaliteite: A=Adelaide; B=Grahamstad; C=Somerset-Oos*

| Normal treatment *Normale metode* | Single joints *Enkel litte* | | | Small plants *Klein plante* | | | Medium plants *Medium plante* | | | Large plants *Groot plante* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | A | B | C | A | B | C | A | B | C |
| No. of plants in 1 500 m² prior to treatment *Aantal plante in 1 500 m² voor behandeling* | 6 044 | 2 497 | 2 657 | 2 380 | 2 006 | 2 167 | 389 | 282 | 363 | 67 | 92 | 186 |
| No. of palnts untreated *Aantal onbehandelde plante* | 773 | 240 | 210 | 377 | 184 | 316 | 18 | 17 | 21 | 0 | 0 | 1 |
| % untreated plants % *onbehandelde plante* | 12,8 | 9,6 | 7,9 | 15,8 | 9,2 | 14,6 | 4,6 | 4,4 | 5,8 | 0 | 0 | 0,5 |
| Mean % untreated plants *Gemiddelde % onbehandelde plante* | 10,1 | | | 13,2 | | | 4,9 | | | 0,2 | | |
| Fast treatment *Vinnige metode* | | | | | | | | | | | | |
| No. of plants in 1 500 m² prior to treatment *Aantal plante in 1 500 m² voor behandeling* | 6 340 | 2 629 | 2 856 | 3 585 | 1 910 | 3 199 | 550 | 377 | 502 | 61 | 109 | 211 |
| No. of plants untreated *Aantal onbehandelde plante* | 1 908 | 406 | 353 | 1 045 | 309 | 545 | 95 | 38 | 66 | 0 | 2 | 2 |
| % untreated plants % *onbehandelde plante* | 17,3 | 15,4 | 12,4 | 29,2 | 16,2 | 17,0 | 17,2 | 10,1 | 13,1 | 0 | 1,8 | 0,9 |
| Mean % untreated plants *Gemiddelde % onbehandelde plante* | 15,0 | | | 20,8 | | | 13,5 | | | 0,9 | | |

TABLE 2 Cost analysis per hectare for chemical control of *O. aurantiaca* for "normal" and "fast" treatments, at three localities
TABEL 2 *Kosteberekening per hektaar van chemiese beheer van* O. aurantiaca *met "normale" en "vinnige" behandeling by drie lokaliteite*

| | Adelaide | | Grahamstown | | Somerset East | |
|---|---|---|---|---|---|---|
| | Normal *Normaal* | Fast *Vinnig* | Normal *Normaal* | Fast *Vinnig* | Normal *Normaal* | Fast *Vinnig* |
| Litres sprayed/*Liters gespuit* | 196 | 116 | 160 | 108 | 277 | 146 |
| Time (minutes)/*Tyd (minute)* | 160,3 | 81,3 | 176 | 82,5 | 208,7 | 110 |
| Total costs (R)/*Totale koste (R)* | 88,02 | 51,26 | 74,56 | 48,15 | 123,56 | 65,08 |
| % savings with fast treatment/% *besparings met vinnige metode* | 41,8 | | 35,4 | | 47,3 | |

Taking the cost of herbicide mixture as R0,40 per dm³ and labour at R0,60 per man hour, a cost analysis of the two spraying strategies was made. The fast treatment resulted in a saving of 41,8% at the Adelaide site, 35,4% at the Grahamstown site and 47,3% at Somerset East (Table 2).

Fig. 1 shows the wastage of herbicide that occurred when single joints and small plants were sprayed. Single joints were heavily overdosed and received, on average, far higher volumes of spray (11,4 cm³) compared with joints which were part of larger plants. Joints in a clump received only 0,5 cm³ each. The overdose applied to single joints and small plants is a result of poor volume control with the spray pumps and because of the large fan-shaped spray patterns that cover a far greater area than required to wet a single cladode or small plant.
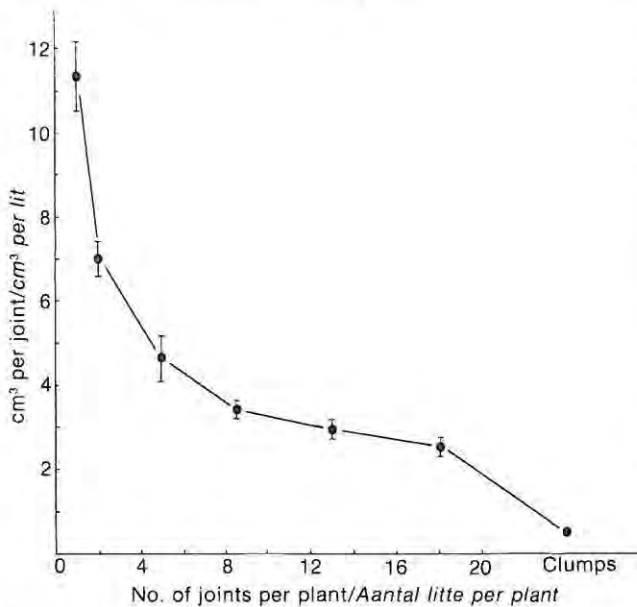


FIG. 1 Volumes of herbicide mixture applied per joint in different plant size categories of *O. aurantiaca*. The 95% confidence intervals are shown

FIG. 1 *Die volume onkruiddoder per lit toegedien aan die onderskeie plantgroottes van O. aurantiaca. Die 95% betroubaarheidsgrense word aangetoon*

## DISCUSSION

The present study has indicated that teams spraying jointed cactus should be encouraged to increase their walking pace so that approximately double the area is covered in the same time. This does not necessarily entail more physical work on the part of the operators but restricts searching for inconspicuous plants and tends to concentrate attention to the large plants and clumps. Although a small decrease in efficiency can be expected, this is a minor disadvantage when the saving in both herbicide and labour costs is taken into account. Overlooking unrooted, single, isolated joints may not be a particularly serious disadvantage with the fast method because as many as 20% of the isolated joints die of exposure during the hot, dry summer months (Zimmermann, unpublished data). Most of the remaining survivors will be efficiently killed during any follow-up operation once they have grown into conspicuous plants. While spraying it might also be advisable to collect loose joints and small plants and treat them collectively with herbicide, but this method can only be advocated where labour is abundant and cheap.

The large differences in the volume of herbicide applied to plants of different size, expressed as the dose per joint, emphasizes the care necessary in the evaluation of herbicides. Herbicidal efficacy should be judged on plants of equal size thus ensuring uniform doses. Inconsistent results may otherwise be attributable to unintentional overdosing of small plants.

## ACKNOWLEDGEMENTS

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APPENDIX 6.  Sequential Sampling Plan for Opuntia aurantiaca infestations

## Introduction

The regular inspections of jointed cactus populations by weed inspectors
is of fundamental importance to obtain some estimate of the infestations
in the eastern Cape and Karoo.  Inspection records are kept on each camp
or paddock of every infested farm and recommendations are made on the basis
of the available information derived from these inspections.  Progress of
treatment or any changes in the infestations are checked during subsequent
inspections.  In very extreme cases landowners may be summonsed to appear
in court if their progress in controlling jointed cactus is unsatisfactory.

Nel (1962) published guide lines for weed inspectors to assess the degree
of infestations quantitatively.  His criteria were :

  (1)  Light   : One or less plants per 18,6 sq. m.
  (2)  Medium : Two to five plants per 18,6 sq. m.
  (3)  Heavy   : Six or more branched plants per 18,6 sq. m.

His description of a plant was not defined but could possibly have been
plants with 5 or more cladodes because these category plants or larger
ones are conspicuous in the vegetation.  The method of assessment was not
described and one can only assume that inspectors had to decide on a
figure based on very general scanning of the infested veld.

Slabber (1964) refuted this method of assessment claiming that thick
colonies (clumps) often found in infested veld would make such a method
unreliable.  He obviously recognized the aggregated distribution pattern of
jointed cactus populations but gave no statistical evidence why Nel's
method was unreliable.

Serfontein (1961) agreed with Slabber and did not believe that a quantita-
tive figure could describe the degree of infestation satisfactorily.  He,
instead, drew up a different, non-quantitative classification system which
is still in use today.  The infesation classes are described as follows :

(1)  Light infestation

  (a)  Plants sparsely distributed and concealed.

  (b)  Large proportions of plants with less than 3 cladodes and
       no isolated cladodes.

(c)     Chances of dispersal by grazing stock (mainly
        domestic) is minimal.

(2)  Medium infestation

(a)     Plants occur at regular intervals and are obvious.

(b)     Mainly small plants (3 to 5 cladodes) with occasional
        large plants with isolated cladodes scattered in between.

(c)     The chances of dispersal by animals are good.

(3)  Heavy infestation

(a)     The infestation must hinder the movements of man and
        animals.

(b)     Large plants with numerous isolated cladodes which are
        also inclined to occur in clumps, are common.  The
        grazing value of heavy infested veld is decreased.

(c)     A dangerous level of dispersal is reached because of
        cladodes which adhere to animals or which are trans-
        ported by flood waters.

The disadvantage of this classification lies in the interpretation of
these definitions which varies between the different weed inspectors and
this explains why identical infestations are so often dissimilarly classed
by different assessors.  The diversity of vegetation types in which
jointed cactus is found, e.g. thick bush or in open karoo-veld, makes
population estimates based on such generalities difficult.

A Suggested Surveillance Method

Evaluation of any campaign, in this case biological, chemical or integrated
control will depend largely on the accuracy and reliability of population
assessments.  The following criteria are suggested for a surveillance
plan :

(1)     the survey must be simple and practical under all conditions
        and infestation classes;

(2)     it must be quantitative with preset confidence limits and
        sensitive enough to show important changes in the populations
        over time.

A new method of inspection is proposed by means of sequential surveys comprising a number of random 10 m walks or transects. These imaginary transects are 2 m wide and each cover an area of 20 m². The surveyor paces 10 steps at random in a straight line while holding a T-shaped walking stick in front of him over the vegetation. The crossbar of the stick is 2 m long and all the C and D category (= medium and large) plants that pass underneath the bar, are counted. A number of such random transects are surveyed until, on the basis of the progressive information gained, the degree of infestation can be estimated at a preset reliability level. Only a few transects will be surveyed at light and heavy infestations. At medium infestations the number of surveys may have to be increased to a point where a decision becomes possible.

On the basis of this information one of three decisions are made namely that :

(1)     the infestation is light and no action is necessary for the following 18 - 24 months, depending on the region;

(2)     the infestation is medium and action must be taken during the following 12 - 18 months when the next inspection is due;

(3)     the infestation is heavy and calls for urgent attention.

Such dense jointed cactus infestations must further be brought under the attention of biological control officers for further assessment because dense infestations are often suitable for biological control. Follow-up inspections should be on a regular 6 monthly basis.

Materials and Methods

Sequential sampling is extensively used in forest entomology (Morris 1954; Waters 1955; Reeks 1956; Stevens & Stark 1962) also in scouting for injurious insects on vegetables (Onsager 1974; Wolfenbarger et al. 1975) and in cotton insect and other crop surveys (Ingram & Green 1972; Sevacherian & Stern 1972; Pieters & Sterling 1974; Sterling 1976; Harcourt & Guppy 1976). No reference could be found of this method used in weed control.

Extensive data are needed to construct a sequential survey plan namely :

(1)  A practical and reliable survey technique is necessary to assess the density of the weed as described above.  This has been dealt with in chapter 4.

(2)  The acceptable levels, $\alpha$ and $\beta$ , of the risks associated with incorrect classification of the infestations should be obtained e.g. when the jointed cactus infestation is classified as heavy when it is supposed to be medium.  With insect scouting this risk level ( $\alpha$ and $\beta$ ) is set at 0,5 or 1,0.  Fortunately the risks of incorrect classification in weed inspection surveys is relatively small and probability factors can be set much higher compared to insect surveys.  In this case the level of $\alpha$ and $\beta$ was set at 3,0.  This means that the possibility of making a wrong decision is 30% in both directions.

(3)  The density levels of C and D category plants at the different infestation levels must be known.  These levels are determined only after extensive field surveys, inspections and consultations with weed inspectors and farmers.  The two hypotheses ($h_0$ and $h_1$) to determine the type of infestation are :

   (a)   To distinguish between heavy and medium infestations :

$$h_0 = 4 \text{ to } 2 \text{ plants per } 20 \text{ m}^2 .$$

$$h_1 = 5,5 \text{ plants or more per } 20 \text{ m}^2 .$$

   (b)   To distinguish between light and medium infestations :

$$h_0 = 1 \text{ or less plants per } 20 \text{ m}^2$$

$$h_1 = 2 \text{ to } 4 \text{ plants per } 20 \text{ m}^2 .$$

Table 1 gives means of C and D category plants per 20 m² transects at various localities.  The infestations were classified according to Serfontein (1961).

(4)  The nature of the frequency distribution of the plant population that is surveyed must be known using the 20 m² transect as the survey unit. The type of distribution will determine the formulae that should be used

for calculating the survey plant. The C and D category plants at different densities conformed well to the negative binomial distribution except for one locality namely Maastrict, April 1977 where the observed and calculated frequencies differed significantly ($P > 0,05$). The k-values are listed in Table 1.

(5) A single common k-value (kc) must be obtained for all the data. With jointed cactus data it was found that there were significant differences between the values of k from the different localities (Table 1).

Calculations for kc were achieved using the moment of regression method as described by Bliss and Owen (1958), Bliss (1958) and Southwood (1978) using the two statistics

$$x^1 = \bar{x}^2 - \frac{(S^2)}{(N)} \qquad \text{and}$$

$$y^1 = S^2 - \bar{x}$$

where $\bar{x}$ = the mean, $S^2$ = the variance and $N$ = the number of individual counts on which $\bar{x}$ is based. When a kc-value is to be estimated from several samples of size N and different means, an estimate of $\frac{1}{k}$ can be obtained by calculating the slope of the regression line of $y^1$ upon $x^1$. The approximation of kc is then given by

$$\frac{1}{kc} = \text{slope of line} = \frac{y^1}{x^1}$$

In this case

$$\frac{1}{kc} = 0,4261$$

$$kc = 2,3596$$

The values that are necessary for these calculations are shown in Table 1 and the regression of $y^1$ upon $x^1$ and the slope of the line is shown in fig. 1. Ingram and Green (1972) and Southwood (1978) suggest that the points that lie completely outside the main trend may be omitted and they doubt whether the kc derived from including them would be meaningful.

If $\frac{1}{k}$ is plotted against the mean (fig. 2) for the different localities, neither a trend nor any significant clustering (r = 0,02) could be detected and thus the fitting of kc is justified and valid and kc may be taken as constant for all the densities. This method was suggested by Bliss and Owen (1958).

## Calculation of a Sequential Survey Plan

The calculation of this sampling plan is based on methods by Oakland (1950), Morris (1954), Waters (1955), Ingram and Green (1972), Onsager (1974) and Sterling (1976) applied the same method.

Table 1.   Mean and k-values of C and D category plants per 20m$^2$ transects at different infestation levels.

| Locality | Date of survey | Mean | Variance | k-value | N | Infestation level according to Serfontein (1961) |
|---|---|---|---|---|---|---|
| Glen Ovis | Feb 77 | 8,12 | 32,79 | 2,48 | 153 | heavy |
| " | Feb 78 | 6,44 | 16,60 | 3,04 | 68 | heavy |
| " | Jun 79 | 4,69 | 9,86 | 1,65 | 80 | medium/heavy |
| " | Jun 79 | 0,5 | – | 4,04 | – | light |
| Maastricht | Apr 77 | 2,07 | 5,32 | 0,79 | 60 | medium |
| " | Apr 79 | 1,39 | 2,73 | 1,23 | 62 | light/medium |
| " | Oct 79 | 4,0 | – | 1,64 | – | medium |
| " | Apr 79 | 0,69 | 0,95 | 1,17 | 61 | light/medium |
| " | Dec 77 | 0,48 | – | – | – | light |
| Middelburg-plaas | Jun 76 | 2,57 | 4,11 | 4,27 | 56 | medium/heavy |
| | Feb 79 | 7,66 | 26,64 | 2,24 | 74 | heavy |
| " | Apr 79 | 9,36 | 41,97 | 1,60 | 47 | heavy |
| Gannahoek | Aug 76 | 2,76 | 10,42 | 0,90 | 150 | medium |
| " | Feb 77 | 6,06 | 19,43 | 1,99 | 68 | heavy |
| "    * | Feb 79 | 11,24 | 35,70 | 3,99 | 76 | heavy |
| Rietmond | May 76 | 3,79 | 11,09 | 1,50 | 62 | medium |
| " | Mar 77 | 1,42 | 3,50 | 0,62 | 60 | light/medium |
| " | Feb 78 | 1,75 | 3,66 | 1,03 | 65 | light/medium |
| " | Jan 79 | 4,84 | 19,84 | 0,78 | 67 | medium/heavy |
| Centlivres | Aug 77 | 4,81 | 18,50 | 1,11 | 70 | medium/heavy |
| " | Aug 78 | 5,57 | 25,06 | 1,00 | 67 | heavy |
| " | Nov 76 | 4,03 | 21,45 | 0,62 | 153 | medium/heavy |

*omitted from calculations for common k.
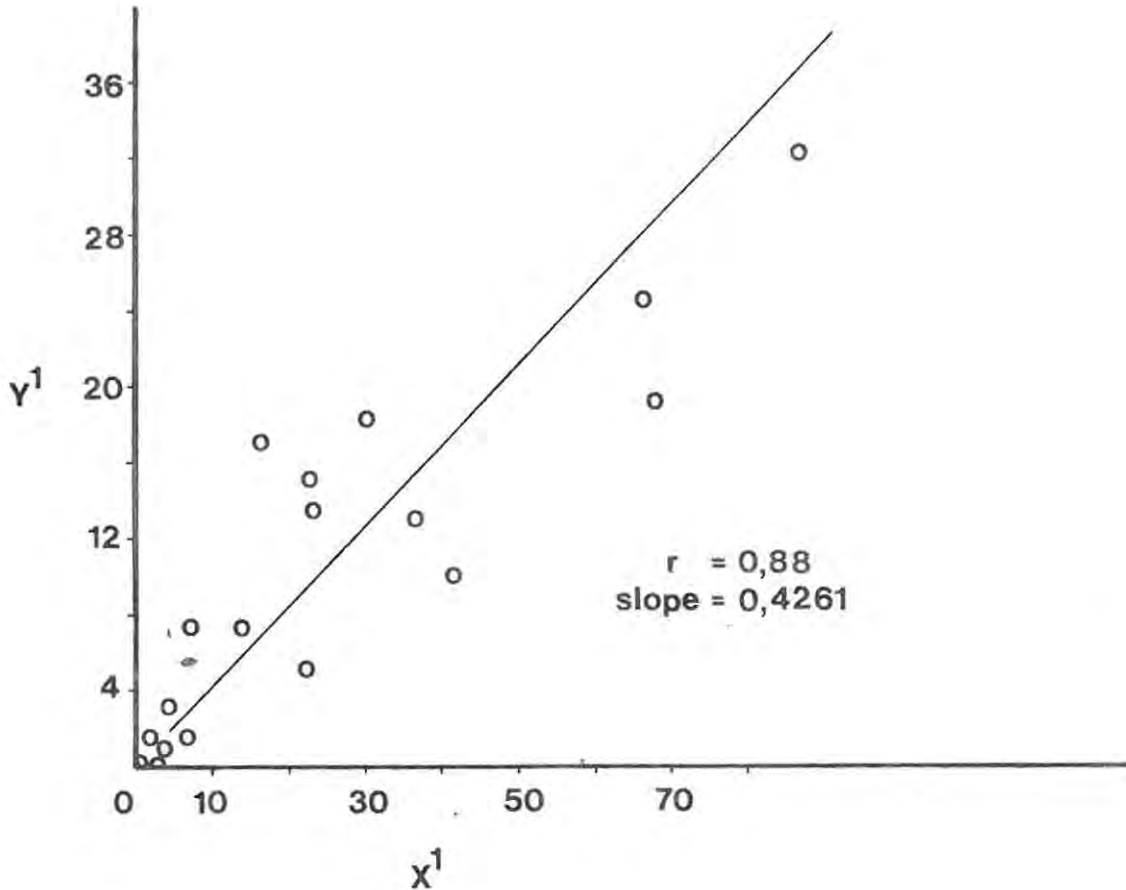
Fig. 1. The regression estimate for a common k for C and D category plants (see text). Each point is based on 47 to 153 observations.

The probabilities of errors, i.e. $\alpha$ and $\beta$, of accepting $h_1$ (lower level of infestation) when $h_o$ (higher level of infestation) is actually true or accepting $h_o$ when $h_1$ is true, was taken at 0,3 for reasons already given. The formulae for the acceptance and rejection lines are

$$d = S_n + h_o \quad \text{and} \quad d = S_n + h_1$$

where d = commulative number C + D plants and N = number of transects.

$$S = \text{slope} = \frac{k. \log (q_1/q_o)}{\log (p_1 q_o/p_o q_1)}$$

$$h_o = \text{intercept} = \frac{\log B}{\log (p_1 q_o/p_o q_1)}$$

$$h_1 = \text{intercept} = \frac{\log A}{\log (p_1 q_o/p_o q_1)}$$

where $A = \dfrac{1 - \beta}{\alpha}$ and $B = \dfrac{\beta}{1 - \alpha}$

where $\alpha$ and $\beta$ are probability risk levels and $\bar{x}_o$ at $h_o$ for the light/ medium infestation = 1; $\bar{x}_1$ at $h_1$ = 2; $\bar{x}_o$ at $h_o$ for the medium/heavy

infesation = 4 and $\bar{x}_1$ at $h_1$ = 5,5

$$p_1 = \frac{\bar{x}_1}{k} \quad \text{and} \quad q_1 = 1 + p_1 :$$

$$p_2 = \frac{\bar{x}_2}{k} \quad \text{and} \quad q_2 = 1 + p_2$$

where $\bar{x}$ = mean and k = common k of the negative binomial. These values are shown in Table 2.
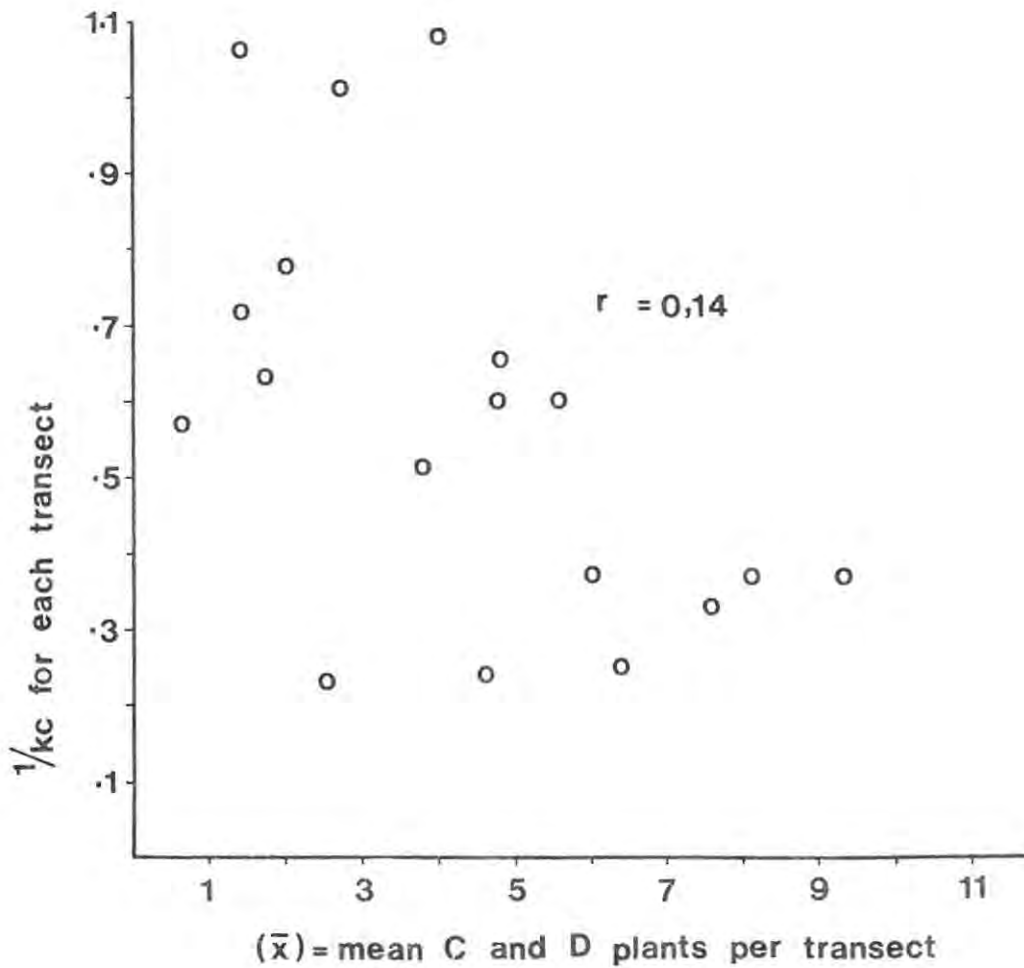


Fig. 2. The regression of $\frac{1}{k}$ to the mean of C and D category plants for various localities combined.
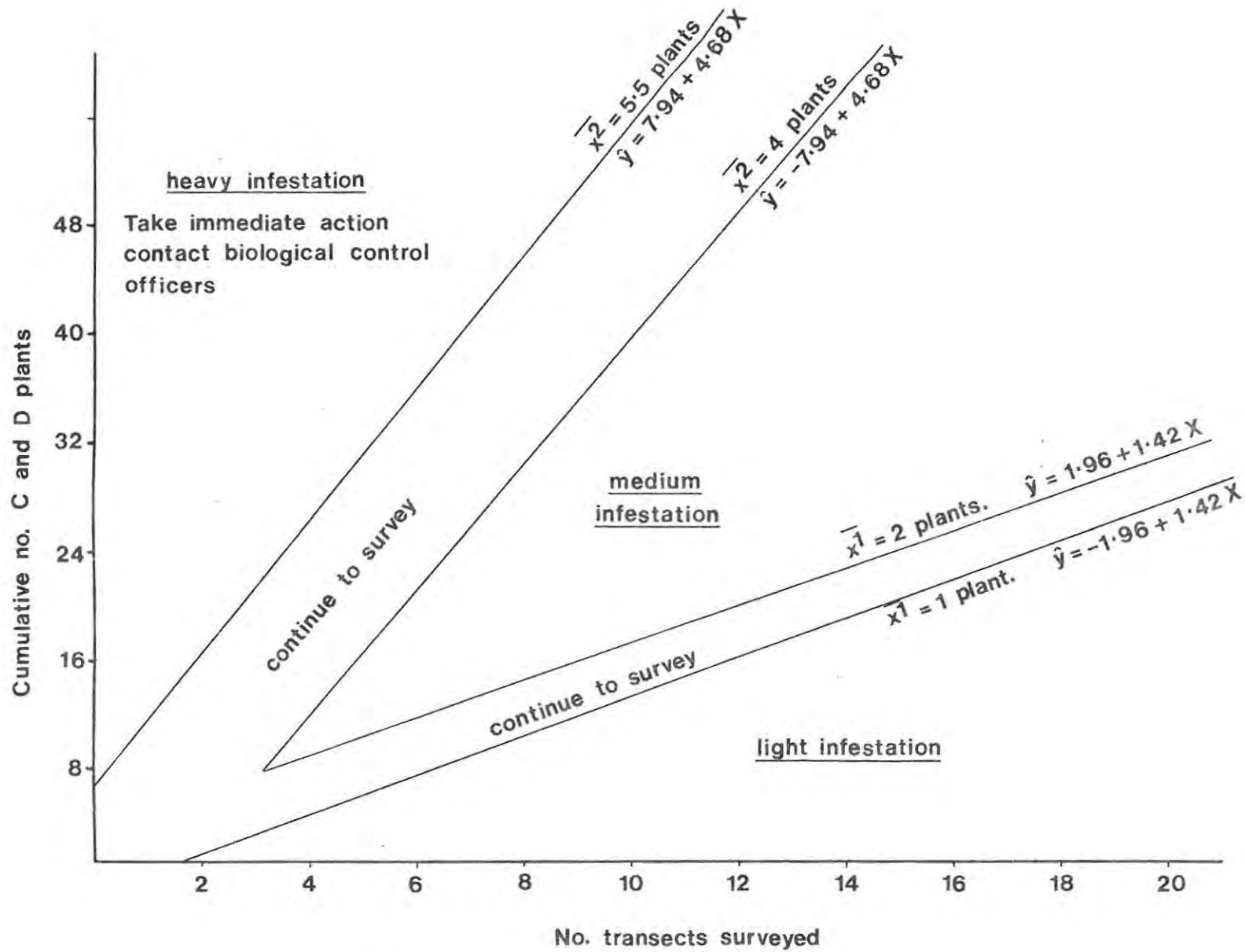
Fig. 3. Sequential graph for sampling C and D category plants for three infestation levels.

Table 2.  Values to calculate the acceptance and rejection lines under the $h_o$ and $h_1$ hypothesis.

| Constant | Infestation | | Infestation | |
| --- | --- | --- | --- | --- |
| | Light $h_o$ | Moderate $h_1$ | Moderate $h_o$ | Heavy $h_1$ |
| $\bar{x}$ | 1 | 2 | 4 | 5,5 |
| $p = (\frac{\bar{x}}{k})$ | 0,4237 | 1,8475 | 1,6949 | 2,3305 |
| $q = (1 + p)$ | 1,4237 | 2,2975 | 2,6949 | 3,3305 |
| $h_1$ | -1,9582 | 1,9582 | -7,9408 | 7,9508 |
| A | 2,3330 | | 2,3330 | |
| B | 0,4286 | | 0,4286 | |
| S | 1,4212 | | 4,6838 | |

For light or medium infested transects we accept $h_o$ if $d \leq 1{,}4158n - 2{,}2975$ and $h_1$ if $d \geq 1{,}4158n + 2{,}2975$ where $d$ is the cumulative number of C and D category plants and $n$ the number of transects.  For medium to heavy transects we accept $h_o$ if $d \leq 4{,}46799 - 10{,}3968$ and $h_1$ if $d \geq 4{,}6799 + 10{,}3968$.  These lines are shown in fig. 3.  These lines determine how many transects should be surveyed to classify an infestation within the accepted limits of $\alpha$ and $\beta$.  According to the lines in fig. 3, a minimum of two transects are needed to identify a light infestation (provided the mean is not higher than 0,8) and one transect to identify a heavy infestation should the number of plants exceed 13 or more.  If the cumulative number of plants for example reached 16 after 4 transects they fall inside the "continue" band between the heavy and medium bands and the survey must be continued.  The survey is continued until the cumulative number falls outside the parallel lines.

## Operating Characteristic Curves

It is necessary to know the probability of making the correct classification at the various C + D plant density levels.  For example, if 1 or less plants per transect are classified as a light and 2 to 4 as a medium infestation at $\alpha$ and $\beta = 0{,}3$, then the probability of correctly calling an infestation  light when there is an average of 1 plant per transect, is

0,7 and the probability of calling it light when there are two plants per transect is 0,3. These probabilities are demonstrated in fig. 4 where the operating characteristic curves show all the probability levels for the different densities.

The following formulae were used to calculate the values for the operating characteristic curve which are listed in Table 3.

$$L(p) = \frac{A^h - 1}{A^h - B^h} \quad \text{and}$$

$$p = \frac{1 - \frac{(p_0)^h}{(q_1)}}{\frac{(p_1 q_0)^h}{(p_0 q_1)} - 1}$$

where h is a "dummy variable" and other values are explained above.
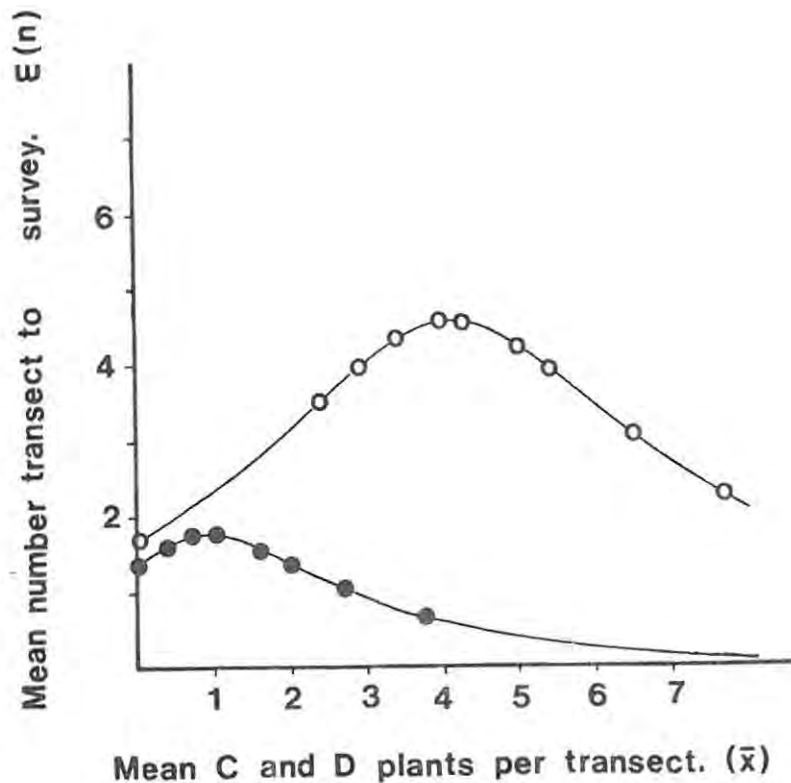


Fig. 4. The average sample-number-curves to indicate the mean number of transects to be sampled for light to medium (closed circles) and medium to heavy infestations (open circles).

## Average Sample Number

It is possibe to calculate the average sample number expected at different population densities as outlined by Waters (1955) and Onsager (1974). This is shown in fig. 5. These values are used to establish the feasability of the sampling system. Should the average sample number at normal operating densities be unpractical, the $\alpha$ and $\beta$ values may be changed. The peaks in the curves occur where infestations are borderline cases between light and medium (closed circles) and medium and heavy levels (open circles).

The number of transects to be surveyed (n) at the different densities is calculated from the following formula and values are included in Table 3.

$$(n) = \frac{h_1 + (h_o - h_1) \cdot (p)}{\bar{x} - S}$$

where L(p) is the operating characterisitc curve $h_o$, $h_1$ and S values are discussed above.

At a mean density of 4 plants per transect, which falls inside the medium-heavy infestation level (open circles in fig. 3) a mean maximum of 5 transects will have to be surveyed. The actual number of transects necessary may however, be substantially more than 5.

## Acceptance and Rejection Table

It is more convenient when inspecting infestations to use field charts to classify infestations rather than to read from the acceptance and rejection lines. The values in the field chart (see Table 4) are derived from the rejection and acceptance line formulae shown in fig. 3.

Should it happen that the infestations tend to remain between the heavy and medium infestation line for 10 or more transects it then becomes impractical to continue and a decision can be made depending in which half of the "continue" zone the cumulative number lies. This limit can be set at 10 transects. Although some reliability is sacrificed, any incorrect classification carries no serious consequences.

Table 3. Values to establish the operating characteristic curves (L(p))
and the average sample number ((n)).

| | P | | ($\bar{x}$) | | L(p) | (n) | |
|---|---|---|---|---|---|---|---|
| | 1* | 2 | 1 | 2 | 1 + 2 | 1 | 2 |
| | 0 | 0 | 0 | 0 | 1 | 1,3778 | 1,6954 |
| 0,5 | 0,5058 | 1,8330 | 1,1937 | 4,3259 | 0,6044 | 1,8409 | 4,6327 |
| -0,5 | 0,7153 | 2,1493 | 1,6881 | 5,0723 | 0,3957 | 1,5001 | 4,2637 |
| 1 | 0,4237 | 1,6945 | 1 | 4 | 0,7000 | 1,8838 | 4,6451 |
| -1 | 0,8475 | 2,3298 | 2 | 5,4983 | 0,3000 | 1,3408 | 3,8997 |
| 2 | 0,2952 | 1,4511 | 0,6967 | 3,4246 | 0,8448 | 1,8779 | 4,3488 |
| -2 | 1,1811 | 2,7433 | 2,7874 | 6,4742 | 0,1552 | 0,9845 | 3,0585 |
| 3 | 0,1719 | 1,2462 | 0,4057 | 2,9410 | 0,9270 | 1,6556 | 3,8911 |
| -3 | 1,6305 | 3,2391 | 3,8480 | 7,6443 | 0,0730 | 0,6876 | 2,2906 |
| 4 | 0,1394 | 1,0730 | 0,3290 | 2,5323 | 0,9670 | 1,6829 | 3,4472 |

* Column 1 = values for light/medium infested transects and
  Column 2 = values for medium/heavy infested transects.



($\bar{x}$) mean C and D plants per transect
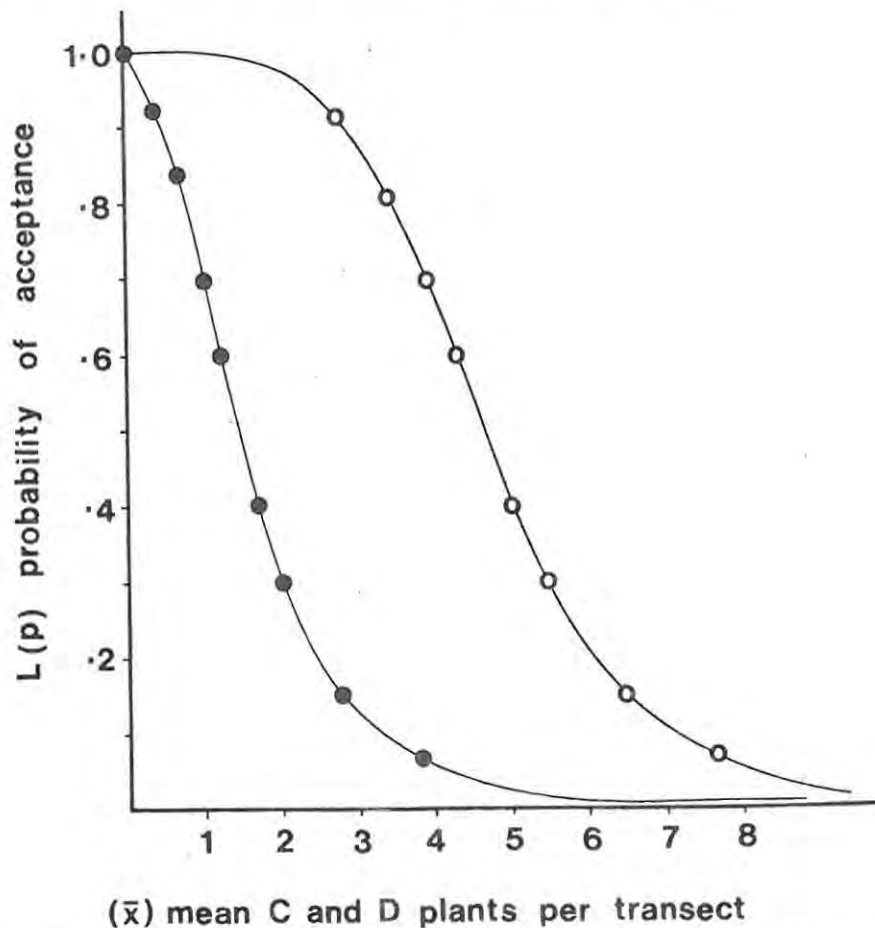
Fig. 5. The operating characteristic curve for light vs. medium (closed
circles) and medium vs. heavy (open circles) infestations. L(p)
is the probability of accepting the $h_o$ hypothesis at different
mean densities of plants.

Table 4.  Sequential chart for use by weed inspectors to classify jointed cactus infestations in the veld.

| No. Transects | Cumulative C and D plants per 20 m² transects surveyed | | | | |
|---|---|---|---|---|---|
| | (1) Zone Light | Continue | (2) Zone Medium | Continue | (3) Zone Heavy |
| 1 | |     −   − | − | −   − 12,6 | ≥ |
| 2 | ≤ | 0,8 −   − | − | −   − 17,3 | |
| 3 | | 2,3 −   − | − | −   − 21,9 | |
| 4 | | 3,7 − 7,6 | ≥   ≤ | 10,8 − 26,7 | |
| 5 | | 5,1 − 9,1 | | 15,5 − 31,3 | |
| 6 | | 6,6 − 10,5 | | 20,2 − 36.0 | |
| 7 | | 8,0 − 11,9 | | 24,8 − 40,7 | |
| 8 | | 9,4 − 13,3 | | 29,5 − 45,4 | |
| 9 | | 10,8 − 14,7 | | 34,2 − 50,1 | |
| 10 | | 12,2 − 16,2 | | 38,9 − 54,8 | |

Surveys are continued until the cumulative result fall in one of the three zones.

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