DISPERSAL OF THE COCHINEAL INSECT *DACTYLOPIUS AUSTRINUS* DE LOTTO (HOMOPTERA: DACTYLOPIIDAE)

BY

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1. RESUME

Dispersal of the cochineal insect Dactylopius austrinus De Lotto, introduced into South Africa in 1932 as a biological control agent against jointed cactus Opuntia aurantiaca Lindley, was investigated. Zimmermann et al. (1974) suggested that the apparent failure of this insect to control jointed cactus infestations is due to limited dispersal of the first instar nymphs (hereafter referred to as crawlers).

Studies on crawler morphology have shown a clear sexual dimorphism in the pattern and development of filaments on the head, thorax and abdomen of male and female crawlers. This enabled differentiation between the sexes with respect to terminal velocities, behaviour and survival of crawlers which have shown that the crawlers, especially the females, are well adapted to dispersal. Long filaments on the head, thorax and abdomen of the female crawlers, that are restricted to dispersal in the crawler stage (as later instars are sessile) and a behaviour directed towards "take-off" enhance the potential for dispersal. The more sedentary males, with long filaments restricted to the abdomen, are able to disperse as winged adults.

The principal factors influencing the timing of dispersal and number of crawlers blown from the host plant are wind and temperature; the latter determining the number of crawlers moving on the host plant. Dispersal is confined to the period between 06h00 and 20h00 and it was possible to correlate the pattern of crawler dispersal with wind patterns. The general equation of Taylor (1978) provided an adequate description of horizontal distribution of D.austrinus crawlers in all directions.

Wind dispersal of the apterous crawlers is restricted by the low height of jointed cactus plants. Horizontal distribution is limited (generally less than 10 m) although a small proportion of crawlers carried vertically upwards by turbulence or convection currents are sufficiently hardy to survive long range displacement. It is suggested that the small size of the host plant will also reduce effective colonization as the canopy area provides a small target for the wind-blown crawlers.

The limitation on dispersal due to the low height of the host plant suggested a system for artificially enhancing crawler dispersal from elevated towers in the field. Evaluation of this system confirmed that it would be practical to augment or introduce cochineal into jointed cactus infestations

to enhance the biocontrol potential of this insect. This offers an alternative to chemical control, that has so far failed to control the spread of jointed cactus despite an intensive and expensive herbicide program.

2. INTRODUCTION

To provide the reader with a background to this study on dispersal of D.austrinus it is necessary to introduce (i) the insect, (ii) the host plant O.aurantiaca, (iii) the role of D.austrinus in biological control of jointed cactus, and with this perspective it is appropriate to consider (iv) the topic of dispersal in a wider context. The introduction is detailed to enable a clear evaluation of this study.

2.1. The insect.

The cochineal insects belong to the genus Dactylopius, proposed type genus of the family Dactylopiidae (Miller 1974). Morphologically, cochineal insects are similar to mealybugs (Pseudococcidae) (De Lotto 1974). There are two features which characterise the genus. The body contents have a red pigment used extensively, prior to the introduction of artificial pigments, as a dyestuff (Baranyovits 1978); and Dactylopius species are specific "...to cactaceous plants, particularly of the genus Opuntia." (De Lotto 1974). The genus has been revised by De Lotto (1974) who recognises nine species of which six have been introduced into South Africa. Prior to this revision, D.austrinus was referred to as Dactylopius sp. near confusus (Dodd 1940; Pettey 1948; Mann 1969) and as species 'J' (Karny 1972).

D.austrinus is indigenous to central and western Argentina (Mann 1969). In South America D.austrinus, like other Dactylopius species, has a range of host plants (Table 1). All the host plants, on which D.austrinus has been positively identified, are low growing cacti. Although D.austrinus breeds easily on O.aurantiaca, the distribution of insect and plant in Argentina do not overlap (Zimmermann pers. comm.) and this plant is not a host for D.austrinus in Argentina.

In South Africa O.aurantiaca is the only host plant of D.austrinus. Although populations of D.austrinus have been reared with difficulty on O.tardospina (Pettey 1948; Karny 1972), O.megacantha and O.vulgaris (Karny 1972); this insect has not been recorded on these plants in the field.

The adult male and female of D.austrinus, in common with other species of the Coccoidea, are morphologically very different. The females are paedogenetic and resemble the earlier instars; while the male undergoes a pupal stage and emerges as a delicate adult with a single pair of wings.

Table 1. Host plants of *D.austrinus* in Argentina and Uruguay (South America). Classification of host plants as in Britton and Rose (1919). Source of reference in brackets after host name.*

Family Cactaceae

Genus *Opuntia*

Subgenus *Tephrocactus*

- *Opuntia russellii* Britton and Rose 1919 (Mann 1969)
- *Opuntia weberi* Spegazzini 1905 (Mann 1969)

Subgenus *Platyopuntia*

- *Opuntia sulphurea* G. Don 1830 (Dodd 1940; Mann 1969; Zimmermann *et al*. 1979)
- *Opuntia discolor* Britton and Rose 1919 (Dodd 1940; Mann 1969; Zimmermann *et al*. 1979)
- *Opuntia canina* Spegazzini 1905 (Zimmermann *et al*. 1979)
- *Opuntia retrosa* Spegazzini 1905 (Zimmermann *et al*. 1979)
- *Opuntia utkilio* Spegazzini 1905 (Dodd 1940; Zimmermann *et al*. 1979)

*Mann (1969) lists *O.wetmorei* as a host plant but Britton and Rose (1919) do not list this plant. In addition *Cereus aethiops* and *Echinopsis intricatissima* (Mann 1969) and *O.palmadora* (Zimmermann pers.comm.) have been suggested as host plants, but specimens from these plants have not been positively identified as *D.austrinus* (De Lotto pers. comm.).

The adult female is characterised by a fluffy white cover (Fig. 1), formed by a secretion of fine curly wax filaments. The females are ovoviviporous and lay 0,5 mm long eggs singly or in chains, depending on the rate of production. The first instar crawlers hatch at intervals varying from less than a minute to several hours (personal observations). Karny (1972) described the hatching process after which there is a delay while the newly emerged nymph (crawler)(Fig. 2) retracts the long stylets into the body. Approximately one hour after oviposition the young crawlers emerge from beneath the female.

Mann (1969) gave a generalised account of the life cycle of the cochineal insects, in which he stated "The habits and life histories of the various species appear to be very similar...". Karny (1972) detailed the life cycles of the females of three *Dactylopius* species including *D.austrinus*,

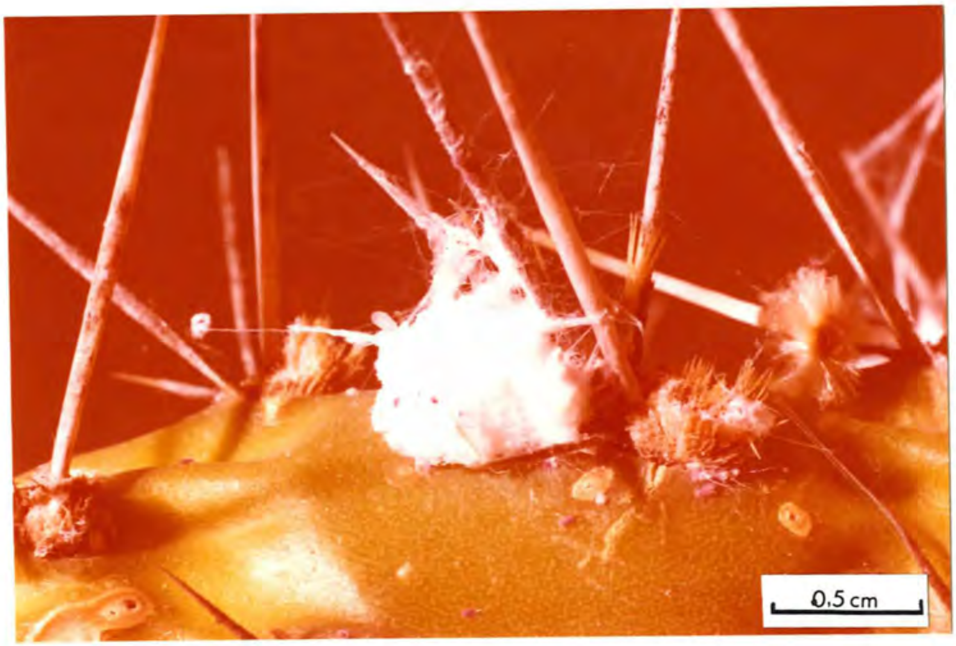


Fig. 1. Cladode of O. aurantiaca with a single adult D. austrinus female, characterised by a covering of fine curly wax filaments. Several crawlers can be seen on the cladode surface close to the parent female.

Fig. 2. First instar crawler emerging from chorion. Note the long stylets which are withdrawn soon after emergence is completed.

but made little comment on that of the males. The most detailed study of the life cycle of *D.austrinus* is the recent account by Moran and Cobby (1979) which is summarised in the table below.

Table 2. Summary of the life cycle of *D.austrinus* (Moran & Cobby 1979)

	Instar	Duration (days)	Size (mm)
a) Male	1st (crawler)	18	0,4 - 0,6
	2nd	8	1,65
	Prepupa	4	1,9
	Pupa	7	1,9
	Adult	3 - 4	1,9
b) Female	1st (crawler)	20	0,4 - 0,6
	2nd	13	0,8 - 1,5
	Adult Preoviposition	23	1,7 - 4,0
	Oviposition	50	

Although newly emerged male and female crawlers are indistinguishable, differences between the two sexes are evident once the crawlers are 24 h and older. These differences and details on crawler behaviour will be dealt with in context in the thesis. Moran and Cobby (1979) have shown that unfertilised females can survive for up to 80 days. The adult females, which may be fertilised at any stage after the second moult has been completed, undergo preoviposition and oviposition periods of the same duration regardless of age at the time of fertilisation.

Dispersal of females is limited to the first instar crawlers, as the second instar and adult are sessile. In the male life cycle there are two dispersive stages; the crawler and the winged adult. The fragile adult males are ephemeral and function only to fertilise the females.

There are no discrete generations in the field and all instars of *D.austrinus* are found on the host plant all year round (Zimmermann pers. comm.). However during winter, low temperatures retard growth and population increase. With the onset of warmer weather in September and October populations build up and lightly infested plants rapidly become covered with *D.austrinus*.

It appears that phytotoxins in the saliva of *D.austrinus* cause deterioration and destruction of jointed cactus plants. Although above ground growth may be completely destroyed, the tuberous root may survive and give rise to regrowth.

No parasites were found in D.austrinus cultures and the absence of parasitism is confirmed by Zimmermann (pers. comm.).

2.2. The host plant.

O.aurantiaca is a low growing cactus, one of eight species in the Series Aurantiacae forming part of the subgenus Platyopuntia (Britton & Rose 1919). This plant consists of one or more spiny, jointed stems growing from a tuberous root (Fig. 3). A feature of the joints (cladodes) is the presence of numerous aeroles bearing between one and seven barbed spines, 1 - 3 cm long. Although the plant produces a characteristic yellow flower, Archibald (1939) reported seed sterility at 99,95% eliminating seeds as a source of new plants. However individual cladodes readily detach from the plant, root and form new plants.

Fig. 3. Jointed cactus (O.aurantiaca) plant, showing the spiny jointed branching stems.

This plant is indigenous to South America where it shows a restricted and discontinuous distribution in Argentina and Uruguay (Moran *et al*. 1976). There has been confusion as to the identity and origin of this plant. Moran *et al*. (1976) suggested the West Indies might be the "...centre of evolution for the fragile-jointed cacti, similar to *O.aurantiaca*..." and that *O.aurantiaca* may have been recently introduced to Argentina and Uruguay. However a recent survey of the cactus flora of the West Indies found no evidence for this suggestion (Hoffmann pers. comm.). Arnold (1977) put forward an alternative suggestion; that on the basis of seed sterility, pollen morphology, cytology, insect associations, morphology and distribution *O.aurantiaca* is a hybrid taxon with *O.salmiana* and *O.discolor* the "...two most likely putative parents.". The insect fauna associated with *O.aurantiaca* is sparse and the spread of this plant in South America is limited by fungal diseases and competition with perennial grasses (Moran *et al*. 1976).

Moran (pers. comm.) has suggested that *O.aurantiaca* was introduced into South Africa in the early 1840's as an ornamental plant in the Ludwigsberg gardens in Cape Town where it was first recorded by McGibbon in 1858 (Moran *et al*. 1976). The plant subsequently spread into the Eastern Cape with smaller infestations in Natal, Transvaal and the Orange Free State (Fig. 4). Pettey (1948) points out that the initial spread of this plant was probably facilitated by its suitability as an ornamental plant in cemeteries and its protective function as a hedge. Subsequently, movement of stock, floodwaters and wind played a continuing part in the spread of cladodes and increase in the distribution and density of the jointed cactus population (Pettey 1948).

Today jointed cactus is considered the most important weed in South Africa (Neser & Annecke 1973). Despite intensive control programmes the invasion area of the plant increased from 43,000 ha in 1924 (Pettey 1948) to over 1,500,000 ha in 1973 (Neser & Annecke 1973). Large parts of the invasion area are used for stock farming and stock deaths (due to loss of condition), lameness and depreciation in the value of wool and hides result from the presence of or damage by jointed cactus spines (Pettey 1948).

In South Africa jointed cactus populations are not uniformly dispersed, as the plant is highly aggregated (Zimmermann 1977). In open areas the plant rarely exceeds 0,4 m in height although larger plants can be found in dense bush where the surrounding vegetation supports the jointed stems. There are no indigenous insects associated with jointed cactus. A degree of damage is caused by the introduced phycitid moth Cactoblastis cactorum (Berg), a biological control agent against prickly pear Opuntia ficus-indica (L.) Miller.

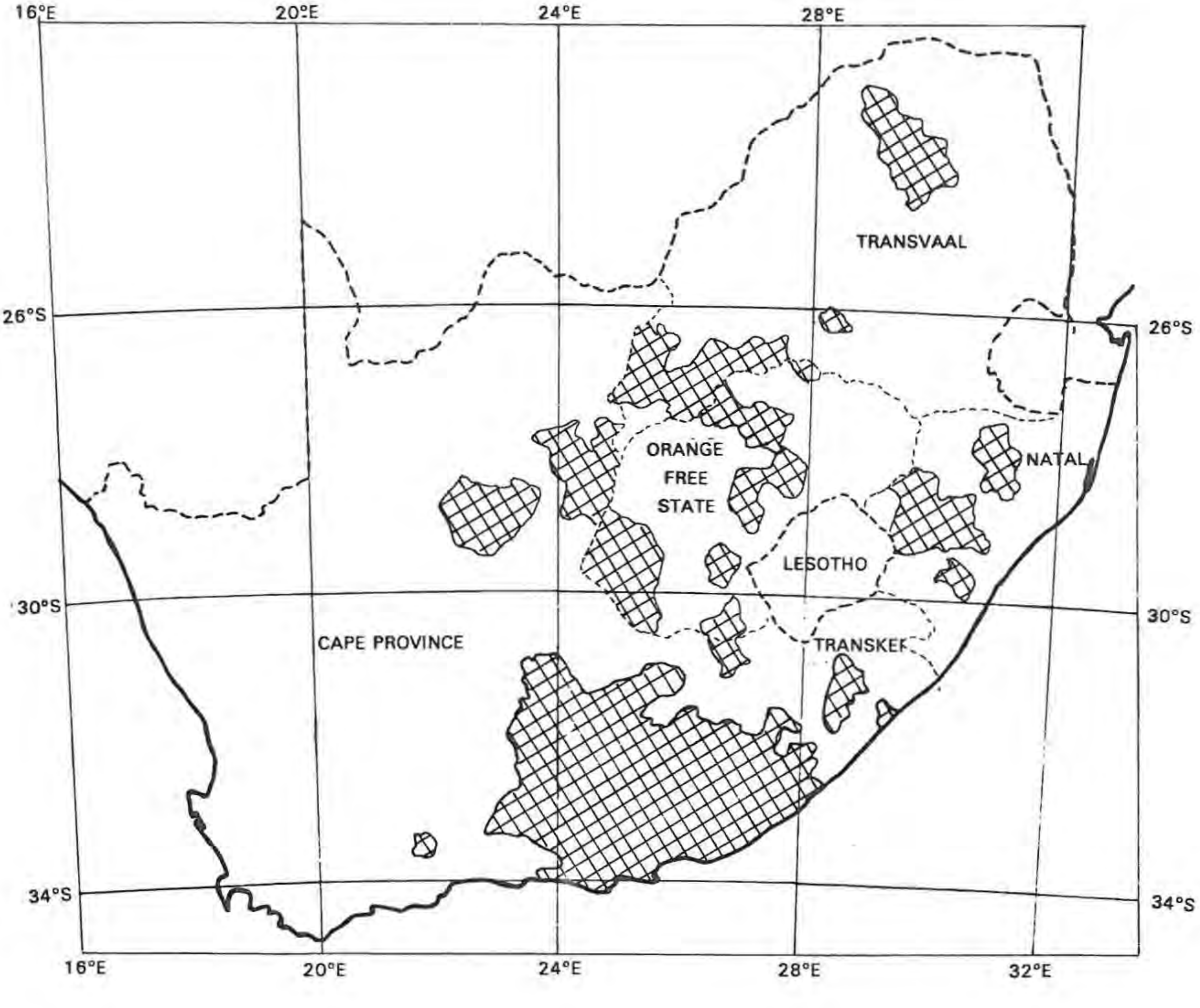


Fig. 4. Distribution of O. aurantiaca in South Africa. International boundaries (- -); provincial boundaries (----); area of jointed cactus infestation (XXX).

2.3. The role of *D.austrinus* in biological control of *O.aurantiaca*.

The problem *O.aurantiaca* posed for stock farmers was recognised before the turn of this century (Pettey 1948), but it was not until 1928 that ordinance was passed to control this plant using existing mechanical and chemical control measures.

In 1932, part of a shipment of *D.austrinus* en route to Australia was obtained by the South African authorities. Dodd (1940) reported the original host plant of this material "...was an unidentified prickly pear, possibly a relation of *sulphurea*, found in the province of Catamarca [Argentina]". The cochineal was transferred from this plant to *O.sulphurea* and then to *O.aurantiaca* for shipment to Australia (Dodd 1940).

Pettey (1948) reported that within two years of the release of *D.austrinus* in 1936 there was extensive destruction of above ground growth of jointed cactus over the whole area of infestation. The cochineal was released over wide areas by placing cladodes infested with *D.austrinus* in amongst the jointed stems of healthy plants. The success of the biological control programme using *D.austrinus* was such that in 1938 mechanical and chemical control measures were discontinued (Pettey 1948).

However, subsequent regrowth of jointed cactus in scattered localities was not destroyed by the cochineal insect, and the failure to follow up the initial success with further release of *D.austrinus* or mechanical and chemical control measures led to further large scale increases in jointed cactus infestations (Pettey 1948).

As a result, chemical and mechanical control measures were reintroduced in 1947 (Zimmermann *et al*. 1974). Despite an intensive control programme since 1947, including the use of sophisticated herbicides such as 2,4,5-T and Tordon 40 which has cost the authorities at least R7,000,000 (Neser & Annecke 1973), jointed cactus populations have continued to spread (Neser & Annecke 1973 and Zimmermann *et al*. 1974). This has led to a renewed interest in the biological control potential of *D.austrinus* and the recent importation of several candidate biological control agents from South America.

Pettey (1948) attributed the apparent failure of *D.austrinus* to control jointed cactus, following the initial success, to reduction in cochineal populations by a complex of natural enemies; competition with the phycitid moth *Cactoblastis cactorum* and a fungal disease *Empusa lecanii*. The complex of natural enemies included rodents, two predatory coccinellid beetles Exochomus flavipes Thunb. and Cryptolaemus montrouzieri Muls and the flesh-eating ant Anoploplepis steingröveri For.. Zimmermann et al. (1974) reported, that apart from limited damage by rodents in bushveld areas, these factors have little effect on cochineal populations.

Dispersal of D.austrinus, as in other coccoid species, is limited to the first instar crawlers. Zimmermann et al. (1974) suggested that the dispersal potential of the apterous crawler stage is limited preventing large scale distribution of cochineal, especially in areas where jointed cactus population densities have been lowered by the previous action of cochineal or the herbicide control programmes.

2.4. Dispersal.

Southwood (1962) defines dispersal as "...a scattering, an increase in the mean distance between individuals, and may be used...for movements within the population territory [trivial] movement , as well as for those away from it [migratory movement] .". The distinction between the two types of movement is important in terms of the ecological significance of migration. The hypothesis (Southwood 1962) that there is a high level of migratory movement in species which utilise temporary habitats and require to locate new habitats to avoid extinction has been widely accepted (Wilson 1968; Den Boer 1970; Gadgil 1971; Vlijm 1971; Dingle 1972; Greathead 1972; Hawkes 1972 and Roff 1977).

Our present concept of migration takes no account of the mechanism of the dispersive movement i.e. whether the organism disperses actively or passively; but characterises migration on features of the behaviour of the migrating organism (Kennedy 1961 and Johnson 1969), timing of the migratory movement (Johnson 1969) and the ecological significance of the movement (Southwood 1962).

Several modes of dispersal have been suggested for the apterous, free-living crawler stage of the Coccoidea. Movement of crawlers on plant material or nursery stock (Quayle 1911; Stofberg 1937; Stafford & Barnes 1948; Cumming 1953 and Williams 1970), on insects, birds and other animals (Stofberg 1937; Mathis 1947; Marek 1952; Cumming 1953; Hoy 1961; Husseiny & Madsen 1962; Samarasinghe & Le Roux 1966 and Williams 1970), on wind-blown leaves (Schweig & Grunberg 1936), or agricultural equipment or workers (Quayle 1911; Stofberg 1937; Mathis 1947; Gentile & Summers 1958; Avidov & Harpaz 1969 and Williams 1970) and livestock (Hoy 1961). Strickland (1950), Cornwell (1958), Gentile & Summers (1958),Hoy (1961) and Avidov and Harpaz (1969) have suggested or shown dispersal by movement of crawlers from one plant to another via interlocking canopies. It is agreed that dispersal across ground is limited by the small size of the crawlers (Quayle 1911; Stofberg 1937; Mathis 1947; Bodenheimer 1951; Cornwell 1956 and Gentile & Summers 1958).

Beardsley and Gonzalez (1975), in a review on the biology and ecology of armoured scale insects, state "Air currents have long been recognised as being of probable importance in dispersal of armoured scale crawlers, at least over short distances (as within orchards).". The first analysis of wind dispersal in scale insects was by Quayle (1916) on the black scale Saissetia oleae Bern. Subsequent studies on wind dispersal of a variety of coccoid species (Table 3) have clearly demonstrated the importance of air currents in dispersal of crawlers. Although Kennedy (1961) stated, in regard to migrant behaviour "...there may be no more locomotion than that involved in leaving the feeding or hibernation site and releasing the foothold..."; Southwood (1962) considered that coccoid crawlers "...are vagrants, not migrants, for like lepidoterous larvae, but unlike spiders, they do not 'take-off', but are knocked off when branches clash in windy weather.".

Southwood's (1962) statement suggests that there is a low level of migratory movement in the Coccoidea. The requirement for location of new habitats, as ultimately all habitats are impermanent (Wilson 1968), is satisfied by the chance location of new sites by accidently dispersing individuals. The implications of this suggestion, in terms of the biological control potential of D.austrinus are obvious: effective control will not be possible using an insect with a low level of dispersal.

However, Southwood's (1962) assessment of coccoid dispersal must be viewed in the context of the literature available at that stage, which was limited to studies of species infesting deciduous trees or conifers; i.e. relatively permanent habitats. More recently Greathead (1972) has shown behaviour of crawlers of the sugar-cane scale Aulacaspis tegalensis (Zhnt.) directed towards "take-off", enhancing the possibility of dispersal, a feature of passively dispersed spiders which are rated as migrants (Duffey 1956; Southwood 1962 and Van Wingerden & Vugts 1974).

Table 3. Studies on wind dispersal of species of the Coccoidea.

Family Coccidae		
Coccus hesperidum L.	Soft brown scale	Hoelscher (1967)
Gascardia (=*Ceroplastes*) *destructor* (Newst.)	White wax scale	Hely (1960)
Physokermes hemicryphus Dalm	Small spruce axil scale	Pechhacker (1971)
Saissetia oleae Bern.	Black scale	Quayle (1916)
Toumeyella numismaticum (Pettit and McDaniel)	Pine tortoise scale	Rabkin and Lejeune (1954)
Family Diaspididae		
Aonidiella aurantii (Mask.)	Red scale	Jones (1936)
Aonidiella aurantii (Mask.)	Red scale	Willard (1974, 1976)
Aulacaspis tegalensis (Zhnt.)	Sugar-cane scale	Greathead (1972)
Chrysomphalus ficus Ashm.	Black scale	Schweig and Grunberg (1936)
Parlatoria pittospori Mask.	-	Timlin (1964)
Phenacaspis pinifoliae (Fitch)	Pine needle scale	Brown (1958)
Quadraspidiotus perniciosus Comst.	San Jose scale	Mathys (1953)
		Maksimova (1973)
Family Eriococcidae		
Eriococcus orariensis Hoy	-	Hoy (1961)
Family Pseudococcidae		
Pseudococcus aonidium (L.)	Long-tailed mealybug	Browning (1959)
Pseudococcus njalensis Laing	Cacao mealybug	Strickland (1950)
		Cornwell (1958, 1960)

The toxic feeding action of D.austrinus rapidly destroys the plant and thus jointed cactus must class as a relatively temporary habitat for the cochineal. This suggests that maintenance of populations of cochineal on the host plant will require a high level of migratory movement in the species. Pettey (1948) observed that large numbers of D.austrinus crawlers concentrated on the spines of the terminal cladodes of jointed cactus plants in the field. This points to a behavioural component to enhance crawler dispersal. Limitation of the dispersal potential, with respect to biological control, may not be as a result of the biology of the insect but due to features of the host. Southwood (1977) emphasised the importance of both the temporal and spatial characteristics of the habitat in determining the ecological strategies of insect species adapting to their habitats.

Jointed cactus plants are small in comparison to the host plants of other species studied (Table 3) which are trees and grasses which form large 'target' areas against or on which wind dispersed crawlers may be deposited. The dispersal range of wind-blown crawlers is determined by the sinking speed (terminal velocity) of the crawler, wind velocity and the height from which the crawler is dispersed (Brown 1958), according to the formula:

Distance dispersed = Wind velocity/Terminal velocity x height above surface.

The effect of host plant height on dispersal distance emphasises the importance of the physical characteristics of the host plant as a platform for dispersal. Crawlers of species which inhabit trees or tall grasses are launched from a height sufficient for them to be carried considerable distances before sinking to the ground. By contrast O.aurantiaca is a low growing host plant, rarely more than 50 cm high, which limits the release height. Jointed cactus plants are frequently scattered in amongst the surrounding vegetation. Frictional drag between the ground and the air body moving over it reduces air velocity and this braking effect is transmitted upwards (Taylor 1960), and most evident below 2 m. Vegetation cover in effect "raises" the ground level and will further reduce wind velocities at the level of the jointed cactus plants. The low height of O.aurantiaca plants and the reduction in wind velocities will combine to reduce the dispersal distances.

Other related species of *D.austrinus*, the two cochineal insects *D.opuntiae* (Cockerell) and *D.tomentosus* (Lamark), have been successfully used in South Africa as biological control agents against *O.ficus-indica* and *O.imbricata* (Haworth) respectively. These plants are large and tall, up to 5 m in height, providing a high dispersal platform. Pettey (1948) stated that *D.opuntiae* crawlers were carried long distances by air currents.

I have suggested (Gunn 1974, 1977) that the small size of the host plant *O.aurantiaca*, will be the limiting factor in the dispersal and subsequent colonization of new host plants, reducing the effectiveness of *D.austrinus* as a biological control agent against jointed cactus.

A brief review of previous studies on crawler dispersal will enable the reader to assess the status of this work and the variety of aspects of dispersal that have been investigated. The majority of studies have been limited to a demonstration of the importance of wind as a dispersal agent, without a detailed analysis of this mode of dispersal. However there have been three comprehensive studies on dispersal of coccoid crawlers.

Cornwell (1956, 1958 and 1960) reported on ground movement, canopy movement and wind dispersal of the crawlers of the cacao mealybug *Pseudococcus njalensis* Laing, a vector of swollen shoot virus of cacao in Ghana. He concluded that wind dispersal was the principal mode of dispersal and gave details of the influence of weather variables on dispersal, horizontal and vertical distribution of wind dispersed crawlers and colonization of new host plants by the crawler stage.

The work of Greathead (1972), on dispersal of the sugar-cane scale *Aulacaspis tegalensis* (Zhnt.) in Tanzania, centred on the horizontal and vertical dispersal of crawlers with details on crawler behaviour and survival. His conclusion with regard to crawler behaviour and long range dispersal have an important bearing on this subject.

Willard (1974 and 1976) made a detailed study of wind dispersal of the red scale *Aonidiella aurantii* (Mask.) in South Australia, with data on horizontal and vertical distribution of wind dispersed crawlers together with an analysis of the importance of certain weather variables in the dispersal process. These studies were supplemented by his previous work (Willard 1972a, 1972b, 1973a and 1973b) on adult reproduction, the rate of crawler emergence and the wandering period and survival of crawlers.

In addition to these studies, the horizontal distribution of the wind dispersed crawlers of the black scale *Saissetia oleae* Bern. (Quayle 1916), the pine tortoise scale *Toumeyella numismaticum* (Pettit and McDaniel) (Rabkin & Lejeune 1954), the pine needle scale *Phenacaspis pinifoliae* (Fitch) (Brown 1958), apple scale *Parlatoria pittospori* Mask. (Timlin 1964), the soft brown scale *Coccus hesperidum* L. (Hoelscher 1967), small spruce axil scale *Physokermes hemicryphus* Dalm. (Pechhaker 1971) and the San Jose scale *Quadraspidiotus perniciosus* Comst. (Maksimova 1973) have been examined. However, there is little additional information on crawler dispersal in these studies.

The study of dispersal of any insect species cannot be limited to an assessment of the physical characteristics of this process but must include, as stressed by Vlijm (1971) and Dingle (1972), studies on the morphological, behavioural and physiological features of the individual which influence dispersal. I have therefore separated the study of dispersal of *D.austrinus* into several sections. The first section, which I have titled "Features of the individual", covers features of the biology of *D.austrinus* crawlers and adults which influence dispersal. The next three sections deal with the process of dispersal: laboratory studies of physical factors affecting dispersal, crawler dispersal from a single host plant and dispersal of field populations of cochineal. This is followed by a section detailing the evaluation of a system to augment field populations of *D.austrinus*.

In sections of this study where a variety of different aspects have been investigated using several experimental techniques it was inappropriate to use the conventional headings "materials and methods" and "results". Therefore to ensure continuity I have described the general materials and methods used and then detailed individual experimental techniques and results with an evaluation of their relevance under appropriate sub-headings.

This diversity of information is summarised and placed in perspective in a general discussion.

3. GENERAL MATERIALS AND METHODS

Insect and plant material used in this study was collected from three localities; the farms Maastricht (33.04S 26.07E), Glenovis (33.02S 26.09E) and Thursford (33.12S 26.24E) in the Albany district of the Eastern Province. Comparison of slide mounted immature 3rd instar females (for method see Appendix 1) with the description of *D.austrinus* (De Lotto 1974) confirmed that populations of cochineal on *O.aurantiaca* plants in all these localities were all *D.austrinus*.

During the period of study, cultures of *D.austrinus* were reared and maintained on *O.aurantiaca* plants grown in pots or loose cladodes of *O.aurantiaca*. The potted plants were grown from tuberous roots collected in the field, or cladodes placed in the soil which rooted to form plants. New cultures of *D.austrinus* were obtained by placing cladodes, infested with mature *D.austrinus* females in amongst the jointed stems of the potted plants or on top of loose cladodes. Crawlers produced by the mature females either dropped onto or wandered onto the new plant material where they settled and began feeding.

Crawlers and adult females used in laboratory experiments were obtained from cultures maintained in a controlled environment (C.E.) room. Standard C.E. room conditions were: 14 h light, temperature 25° ± 2°C, relative humidity 50 ± 3%; 10 h dark, temperature 18° ± 2°C, and 70 ± 3% R.H. To obtain known-aged batches of crawlers, mature females were removed from the cladodes and stripped of their waxy covering by rolling the wax threads onto a needle. The females were then placed in petri dishes, and the crawlers produced in a two-hour interval collected with an aspirator.

Batches of crawlers were held in paper lined petri dishes covered with a finely perforated plastic wrapping to prevent them moving out of the dishes. The perspex dishes also served as holding containers during studies on crawler survival.

All laboratory studies were carried out in the Department of Zoology and Entomology at Rhodes University, Grahamstown. Dispersal studies were undertaken at the Tick Research Unit (Department of Zoology and Entomology) and on the farm Maastricht (33.04S 26.07E) and Table Farm (33.16S 26.25E) in the Albany district.

4. DISPERSAL: FEATURES OF THE INDIVIDUAL

Studies on the morphology, terminal velocities, behaviour and survival of D.austrinus crawlers together with the parthenogenetic status and fecundity of the adult and sex ratios of the offspring are detailed. These aspects have a profound effect on the number of individuals dispersed and the potential spread of this species.

4.1. Morphology.

D.austrinus crawlers closely resemble crawlers of other scale insects. The dorsoventrally flattened body is oval shaped, approximately 0,5 mm long, with well developed legs and six segmented antennae. Compound eyes are reduced to a single facet and ocelli are absent. The body is a distinctive carmine colour, typical of cochineal insects. There is no clear differentiation between head, thorax and abdomen. A characteristic feature of the crawlers is the presence of long wax filaments on the dorsal and dorsolateral surface of the body.

Pettey (1948) commented on the presence of these filaments which he considered facilitated wind distribution. Karny (1972) stated "About 13 - 25 of these 'wax bristles' protrude from the body in a straight upright position; with progressive development their length but not their density is increased.".

The number and pattern of D.austrinus filaments contrast strikingly with the single pair of caudal filaments characteristic of crawlers of other families of the Coccoidea. This feature has been noted in the Asterolecaniidae (Kehat & Amitai 1967), Coccidae (Smith 1944; McConnell & Davidson 1959; Husseiny & Madsen 1962; Phillips 1962; Bedford 1968; Chatterji & Datta 1974 and El-Minshawy & Moursi 1976), Diaspididae (Avidov & Harpaz 1969), Eriococcidae (Patel 1971) and Pseudococcidae (Avidov & Harpaz 1969).

Hoelscher (1967) commented on the posterior bristles of the soft brown scale (C.hesperidum) which flex forward over the body of the crawler and Azab et al. (1968) mentioned the six long (1,5 x body length) caudal filaments of Icerya aegyptica (Douglas) crawlers. Although the crawlers of these two species have a greater number of long filaments than the majority of species they do not compare with D.austrinus. Hulley (1962) suggested the anal filaments of Lepidosaphes beckii Newm. served to right overturned crawlers or might act as a parachute during wind dispersal.

An additional observation during routine handling of D.austrinus crawlers showed the presence of two patterns of filament development evident in crawlers 24 h or older. One group of crawlers developed long filaments on the head, thorax and abdomen while the other group only developed long filaments on the abdomen.

72 h old crawlers were used in a rearing experiment to confirm that dimorphism in filament development represented a sexual difference, as the two categories are clearly distinct at this age (Gunn 1978). 400 crawlers with long filaments on the head, thorax and abdomen were reared on cladodes separately from 400 crawlers with filaments only on the abdomen. Once adult the number of males and females in each group were counted (Table 4).

Table 4. Sex of D.austrinus adults reared from (A) 72 h old crawlers with long filaments on the head, thorax and abdomen and (B) crawlers with long filaments restricted to the abdomen.

Category	No. crawlers released in culture	No. adults recovered	Number of females : males
A	400	252	250 : 2
B	400	150	3 : 147

The crawlers which develop long filaments on the head, thorax and abdomen are female; the males have long filaments restricted to the abdomen. In addition to the sexual dimorphism in filament development there are other minor variations between the sexes. The males appear slightly darker and less active than the females but these characters have not been quantified and cannot be used to distinguish the sexes.

Two techniques were used to determine the number and position of the wax filaments on the bodies of male and female crawlers. Firstly, crawlers were examined using a Joel JSM V3 scanning electron microscope. Preparative techniques did not include vacuum coating with gold paladium since this method damaged the filaments. During examination a low accelerating voltage (8 kv) was used to prevent 'charging' of the uncoated specimens.

Secondly, crawlers were slide mounted for light microscope examination.

De Lotto (1974) recognised 10 abdominal segments in the adult female and I have followed his plan in describing more detailed features of the anatomy of the crawler stage. The long rigid wax filaments produced by the crawlers are not found in the later instars of males or females. The wax extruded in the later instars forms dense masses of curly elastic threads which function as a protective cover. Meinwald et al. (1975) analysed the chemical composition of the wax covering of D.opuntiae and found it was formed from a C_{30} ketoacid and a C_{34} keto-alcohol forming a C_{64} di-keto ester. The wax filaments of D.austrinus crawlers may have a similar composition.

The crawler filaments develop from setae similar to those described by De Lotto (1974) on the adult female which are a diagnostic feature of the species. Figure 5 shows a filament in the early stages of development, and it appears as a hollow white tube, approximately 6 μm in diameter, surrounding the seta.

The number and position of the filaments on the bodies of male and female crawlers are similar except for minor variations. Figure 6 is an idealised representation of the position of the filaments on the dorsal and dorsolateral surfaces of a female crawler. Two classes of filaments are shown in this representation which distinguishes filaments showing extensive development from those which show more limited growth. Filaments are found on all segments except for abdominal segment X. There are eight filaments on each segment with the exception of the prothoracic segment and abdominal segment II which have six filaments. Disregarding the head, there are three longitudinal rows of filaments on either side of the midline; mid-dorsal, dorsal and dorsolateral. The dorsal and mid-dorsal longitudinal rows have a single filament on each segment and the dorsolateral rows have two, except on the prothoracic segment and abdominal segment II, where there is only one. There is also a pair of filaments ventrally on abdominal segment IX but which is obscured in Figure 6. This pattern is similar in the male except that there may be less than eight filaments on the head. All the filaments lengthen after the crawlers hatch although some grow longer than others.

To monitor filament development, groups of known aged crawlers were held in petri dishes in the C.E. room. At 24 h intervals, up

Fig. 5. Wax filament of D. austrinus crawler at the early stage of the extrusion of wax which surrounds the basal seta.

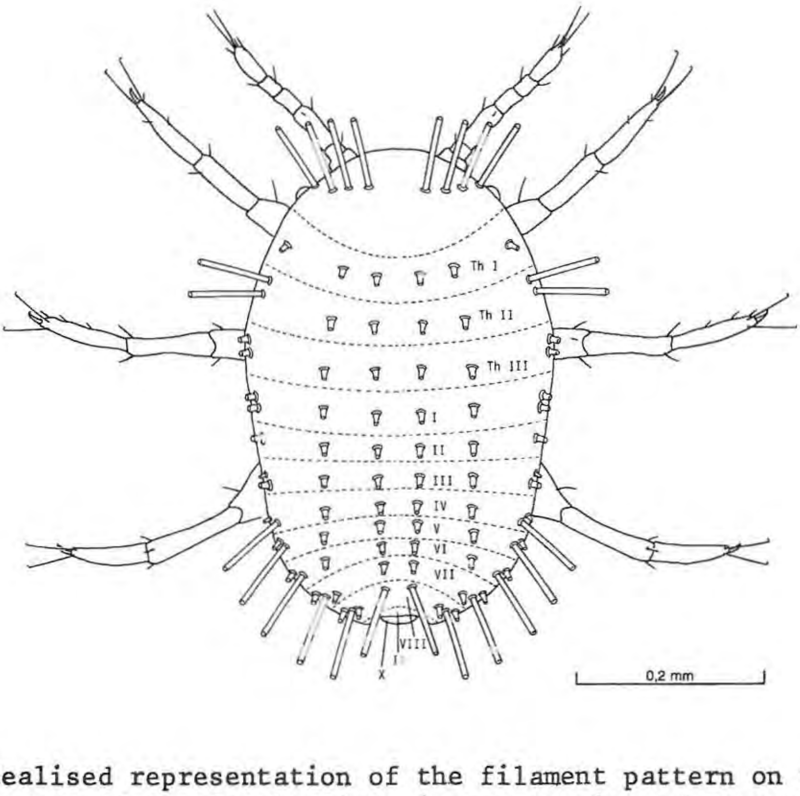


Fig. 6. Idealised representation of the filament pattern on the dorsal surface of the female first instar crawler of D. austrinus. Filaments which show the greatest development are lengthened in the diagram; Th 1 - Th 111 thoracic segments, I - X abdominal segments.

to 168 h, the longest filament on the head, mesothorax and abdomen of 30 male and 30 female crawlers were measured. This provided a measure of the overall trend of development. The absence of filaments on newly-emerged crawlers prevented separation of males and females of this age group and measurements of filaments of a single sample of 30 crawlers were used to represent filament development of both male and female crawlers.

In the female three groups of filaments develop extensively (Fig. 6): (i) the eight head filaments, (ii) the dorsolateral mesothoracic filaments and (iii) the posterior filament in the dorsolateral pair on abdominal segments IV - VIII and the dorsal filaments of segment VIII. By contrast in the male only the filaments in the abdominal group, i.e. the posterior filament in the dorsolateral pair on abdominal segments IV - VIII and the dorsal filaments of segment VIII, grow extensively.

Measurements of the longest filament on the head, thorax and abdomen of eight age groups of 30 female crawlers (Table 5) show rapid development of all three groups of filaments after the crawlers hatch. A Fmax test (Sokal & Rohlf 1973) showed heterogeneity in sample variances for all three groups of filaments. This probably resulted from measurement of the longest filament, rather than a specified filament and in addition filaments may have been damaged prior to measurement. Therefore the 10 longest measurements in each sample were used as a measure of maximum potential development and this data (Fig. 7) showed that all three sets of filaments develop continuously for at least 168 h.

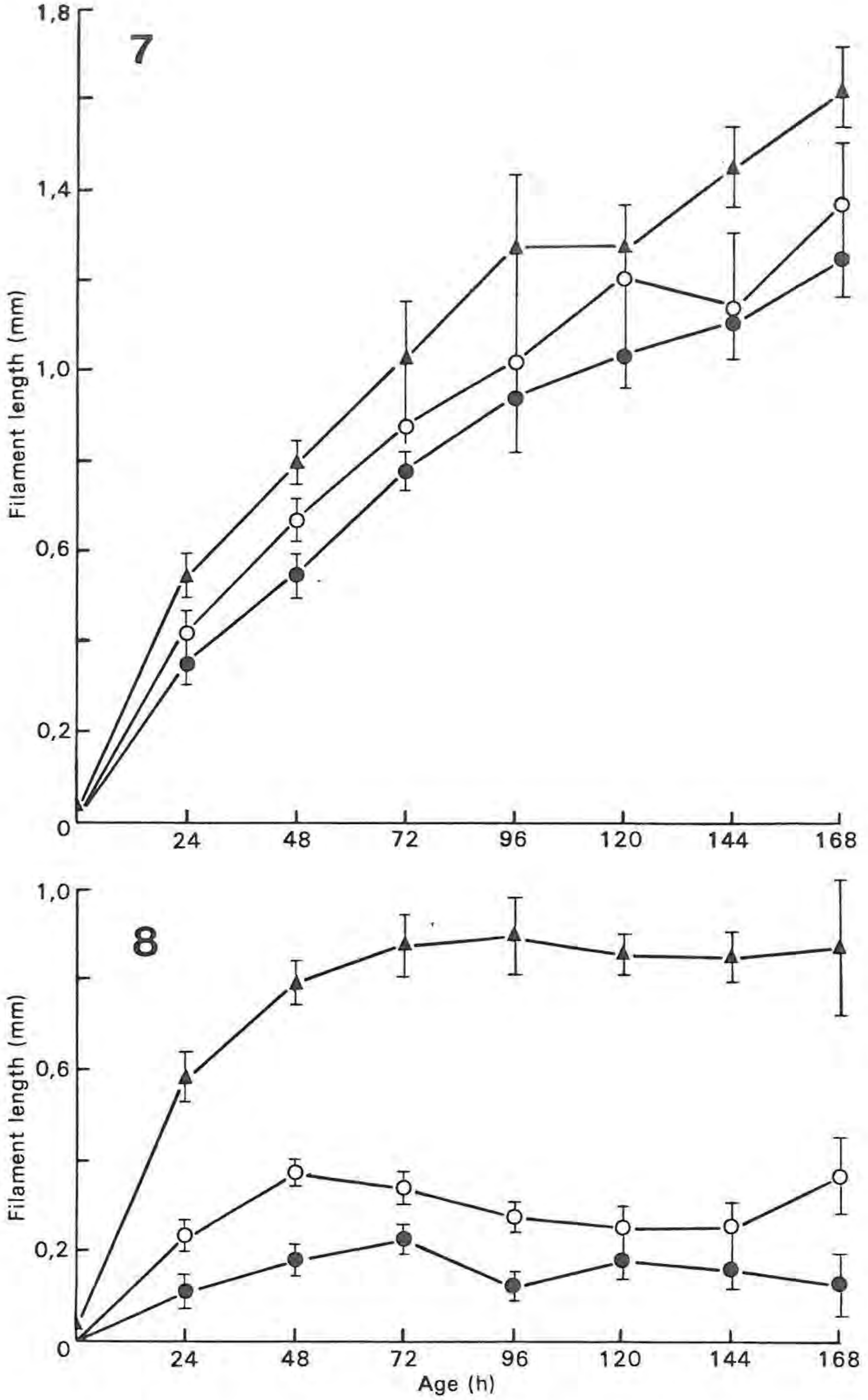
By contrast in the male (Table 5; Fig. 8) only the abdominal filaments show extensive growth. The filaments on the head and dorsolateral surfaces of the mesothoracic segment show limited development, similar to other filaments on the body.

There is a similar increase in the length of the abdominal filaments for the male and female crawlers for the first 48 h but

Table 5. Length (mm) of the longest filament on the head, thorax and abdomen of eight age classes of male and female *D.austrinus* crawlers. The mean and standard error for 30 measurements in each age class are shown. *Single sample of newly-emerged crawlers represents filament lengths of both males and females.

Female

			Filament length (mm)	
Age (h)	N	Head	Mesothoracic	Abdominal
NE*	30	-	-	0,03 ± 0,005
24	30	0,27 ± 0,012	0,31 ± 0,017	0,45 ± 0,017
48	30	0,46 ± 0,018	0,54 ± 0,023	0,68 ± 0,021
72	30	0,64 ± 0,022	0,79 ± 0,022	0,94 ± 0,032
96	30	0,68 ± 0,041	0,82 ± 0,047	0,95 ± 0,054
120	30	0,84 ± 0,045	0,89 ± 0,055	0,99 ± 0,045
144	30	0,83 ± 0,042	0,81 ± 0,054	1,13 ± 0,054
168	30	0,94 ± 0,047	1,00 ± 0,059	1,26 ± 0,062
Male				
NE*	30	-	-	0,03 ± 0,005
24	30	0,08 ± 0,006	0,16 ± 0,014	0,45 ± 0,024
48	30	0,13 ± 0,007	0,27 ± 0,019	0,62 ± 0,027
72	30	0,16 ± 0,011	0,25 ± 0,015	0,74 ± 0,027
96	30	0,11 ± 0,013	0,19 ± 0,018	0,61 ± 0,046
120	30	0,11 ± 0,012	0,17 ± 0,017	0,60 ± 0,036
144	30	0,08 ± 0,012	0,13 ± 0,018	0,63 ± 0,036
168	30	0,07 ± 0,011	0,20 ± 0,029	0,69 ± 0,037



Figs 7 and 8. Filament development in eight age classes of D.austrinus crawlers. 7. Females. 8. Males. Means ± 2 standard errors for 10 crawlers in each age class. ▲ - Posterior abdominal filaments; ○ - mesothoracic filaments; ● - filaments on the head.

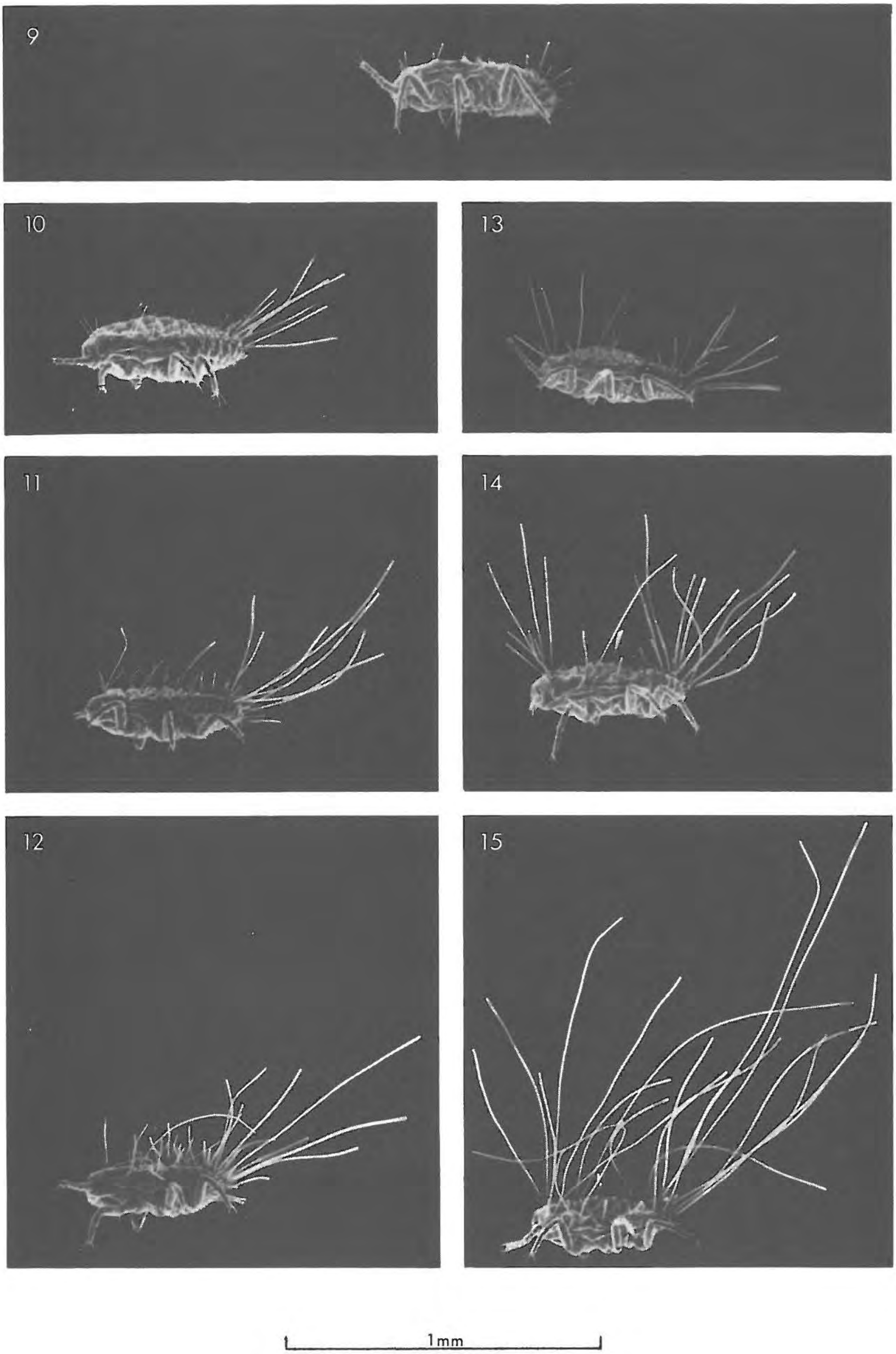
thereafter there is little growth in the male abdominal filaments.

Scanning electron micrographs (Figs. 9-15) of newly emerged, 24, 48 and 120 h old crawlers demonstrate the clear difference in filament development between male and female crawlers. This is the first time that clear sexual dimorphism has been noted in the crawlers of the Dactylopiidae. Many authors (Jones 1936; Mathis 1947; Das *et al*. 1948; Cumming 1953; Husseiny & Madsen 1962; Phillips 1962; Richards 1962; Avidov & Harpaz 1969; Mann 1969; Williams 1970; Patel 1971; Ghose 1971 and Ghose & Paul 1972) have commented on the absence of features distinguishing the sex of first instar crawlers of species of the Diaspididae, Eriococcidae, Coccidae and Pseudococcidae. In only one case among the many species of diaspine scale that have been studied world wide has a reliable method been developed for sexing young crawlers. Bennett and Brown (1958) reported that the white peach scale *Pseudaulacaspis pentagona* (Targioni Tozzetti) shows colour differences in the eggs and crawlers: their studies were based on the pioneering but unpublished work of E.C.G. Bedford on this species in Bermuda.

Tippins and Howell (1973) and Stoetzel and Davidson (1974) have also noted sexual dimorphism in the crawlers of diaspine scales, but it is impractical to use their criteria to sex living crawlers. Sexual dimorphism in the crawlers of two lac insects (Lacciferidae) has been demonstrated by Mahdihassan (1964) but the differences are only manifested once the crawlers have settled on the plant and begun feeding.

The sexual dimorphism in filament development provided a simple and reliable method of separating male and female crawlers and for distinguishing the sexes in studies on behaviour, survival and dispersal.

In comparison to the number and development of filaments reported for other species (references cited previously in this section), these features of *D. austrinus* crawlers clearly suggest a role in wind dispersal. Silk threads are known to assist in dispersal of "ballooning" spiders and mites (Ebeling 1934; Fleschner *et al*. 1956 and Nishiki 1966). The effect of



Figs 9-15. Filament development in D.austrinus crawlers. 9. Newly emerged crawlers; the sexes are indistinguishable at this stage. 10-12. Males 24 h, 48 h, 120 h old respectively. 13-15. Females, 24 h, 48 h, 120 h old respectively.

the presence of structures such as silk threads and filaments will serve to increase the effective surface area of the body which will affect the terminal volocities of dispersed organisms. According to the formula of Brown (1958), altering the terminal velocity of D. austrinus crawlers will have a marked effect on the dispersal range.

4.2. Terminal velocities

The terminal velocities of male and female D. austrinus crawlers will determine the distance they are carried by air currents before sinking to the ground. The terminal velocity of an object is the maximum velocity it reaches falling through the air i.e. the velocity at which there is no further acceleration. At terminal velocity, "the upward resisting force of the air equals the weight of the falling object, so the resultant force is zero and no further acceleration is experienced." (Shortley & Williams 1967). At low terminal volocities, the resistive force of the air is a function of the velocity and the size and shape of the moving object (Stephenson 1960).

An increase in the surface area will increase the resistive force of the air, thereby equalling the weight at a lower velocity. Obviously a simultaneous loss in weight will result in a lower terminal velocity. Thus terminal velocities will be lowered by an increase in surface area and a decrease in weight, and the smaller an object the greater will be the surface area in relation to weight. Apterous crawlers, dependant on air currents for dispersal, are characteristically very small (generally less than 0,5 mm) and flattened providing a large surface area in relation to their weight. The term bouyancy is used in this context, the more bouyant an insect the larger the ratio of surface area to weight (Wolfenbarger 1945). Glick (1939) expressed bouyancy quantitatively as the "aerostatic coefficient".

The terminal velocities of eight age groups (newly emerged, 24, 48, 72, 96, 120, 144 and 168 h) of 20 male and 20 female D. austrinus crawlers were obtained by timing the drop of individual crawlers down a 1,58 m long glass tube (diameter 20 cm). Willard (1973b) found that the crawlers of red scale, A. aurantii, reached terminal velocity in a very short distance and the height of drop did not influence the result. Accurate drop times were obtained using two stopwatches, the one started at the beginning of the drop and the other as the crawler arrived at the base of the tube. The watches were stopped simultaneously and the difference in readings used as the drop time. Drop times of crawlers which touched the side of the tube during the fall were discarded.

The terminal velocities of both sexes (Table 6) decrease with age. A "t" test (Sokal & Rohlf 1973) on the terminal velocities of 24 h old crawlers shows the males have a significantly higher terminal velocity ($t = 4,75$; $p < 0,01$ for 38 degrees of freedom (d.f.)) and this difference increases as the crawlers age.

Table 6. Mean terminal velocities (± 1 standard error) for eight age classes of 20 male and 20 female D. austrinus crawlers. *Single sample used to represent both males and females.

Age (h)	Terminal velocity (m)	
	Male	Female
NE*	0,62 ± 0,04	0,62 ± 0,04
24	0,51 ± 0,04	0,46 ± 0,04
48	0,44 ± 0,04	0,38 ± 0,06
72	0,43 ± 0,04	0,35 ± 0,06
96	0,39 ± 0,04	0,29 ± 0,04
120	0,37 ± 0,03	0,23 ± 0,03
144	0,35 ± 0,03	0,22 ± 0,05
168	0,31 ± 0,03	0,23 ± 0,05

It may be argued that as the crawlers are non-feeding, the decrease in terminal velocities reflects loss in weight as the crawlers desiccate rather than filament development. However the decrease in weight is matched by a decrease in length (Table 7) and presumably surface area, and male and female crawlers are of similar size from 96 h onwards. Therefore the decrease and difference in terminal velocities between the sexes must be explained by filament development.

The effect of differing filament development on the range of wind dispersal of male and female crawlers was determined in a wind tunnel. A 1,9 m long wind tunnel (Fig. 16), 40 x 40 cm in cross section, was constructed of hardboard and perspex. The base and sides were made of hardboard with a removable perspex top cover which allowed access to the dispersal chamber and observation during the experiment. The top cover was held in position on a foam seal by two weights providing an airtight seal. A 17 cm suction fan was centrally mounted on a hardboard cover at one end of the wind tunnel. The air inlet and air outlet to the 1,1 m

Table 7. Mean body length (± 1 standard error) for eight age classes of 20 male and 20 female *D.austrinus* crawlers. "t" values comparing males and females of the same age are shown.
* Single sample representing males and females.

	Body length (mm)			
Age (h)	Males	Females	"t" Value	Probability for 58 d.f.
NE*	0,52 ± 0,004	0,52 ± 0,004	-	
24	0,49 ± 0,003	0,51 ± 0,003	3,22	P < 0,01
48	0,48 ± 0,002	0,49 ± 0,002	2,14	0,05 > P < 0,01
72	0,46 ± 0,003	0,47 ± 0,003	2,28	0,05 > P < 0,01
96	0,45 ± 0,004	0,46 ± 0,003	1,42	P > 0,1
120	0,45 ± 0,003	0,45 ± 0,002	1,02	P > 0,2
144	0,45 ± 0,003	0,45 ± 0,002	0,19	P > 0,5
168	0,44 ± 0,002	0,44 ± 0,003	0,96	P > 0,2

long dispersal chamber, with the same diameter as the suction fan, were filled with 5 cm long drinking straws. The straws, placed parallel to the airstream provided laminar air flow. A metal bracket, mounted on one side of the dispersal chamber 10 cm from the air inlet, anchored a metal clamp used to hold a roughened perspex dispersal platform (10 x 2 cm), horizontally in the airstream. Crawlers blown off the dispersal platform, were trapped on a vaseline-covered perspex sheet placed in the base of the dispersal chamber. This sheet could be removed to count the number of crawlers dispersed and measure the distances they were blown.

Wind velocities in the dispersal chamber were measured using a Lambrecht Type 641 bN thermistor anemometer. The measured velocities (Fig. 17) showed the suction fan set up a core of moving air with a velocity of 1,7 m sec^{-1}. The air velocity did drop slightly down the length of the chamber, but this was inevitable due to turbulence at the interface of the column of moving air and dead air space.

Wind tunnel dispersal distances for 96 h male and 96 h female crawlers were compared. At this age the filaments of the males are fully developed (Fig. 8) enabling a clear comparison between the sexes. A group of 150 crawlers of one sex were collected with an aspirator and released on the dispersal platform. Once the crawlers had spread out on the platform, it was clamped into position in the dispersal chamber. The fan was then

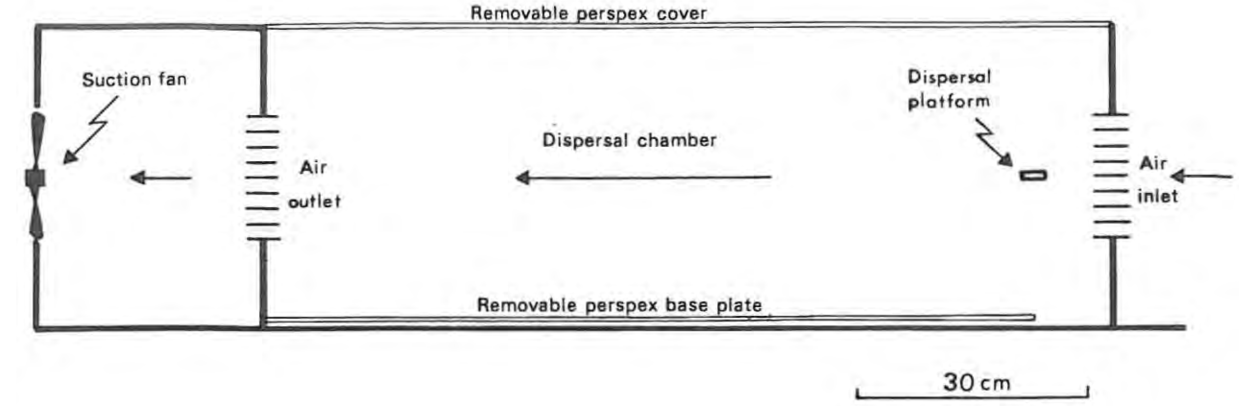


Fig. 16. Longitudinal plan of wind tunnel. Straight arrows indicate direction of air flow.

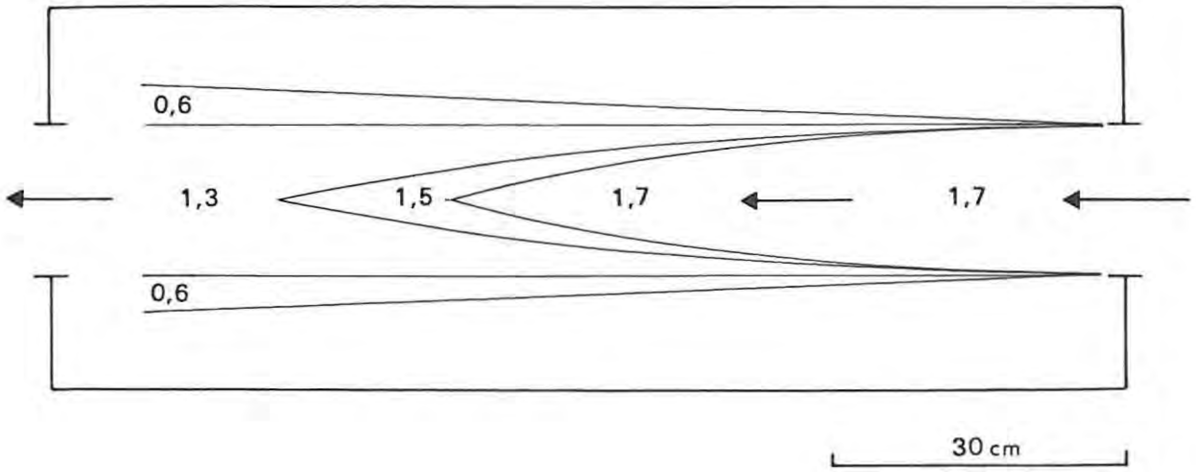


Fig. 17. Air velocities (m sec^{-1}) in dispersal chamber of wind tunnel. Arrows indicate direction of air flow.

switched on for a 30 min period, after which the base sheet was removed and counts made of the number of crawlers found at 5 cm wide distance intervals down the length of the sheet. This procedure was repeated for five groups of each sex. The number of crawlers remaining on the dispersal platform was also recorded.

The mean dispersal distance (using the upper value of the distance intervals) for male crawlers was 36,05 cm and 46,06 cm for females. Maximum numbers of dispersed males were recovered 30 - 35 cm from the dispersal point with overall dispersal up to 70 cm; the equivalent values for female crawlers were 40 - 45 cm and 90 cm respectively (Fig. 18).

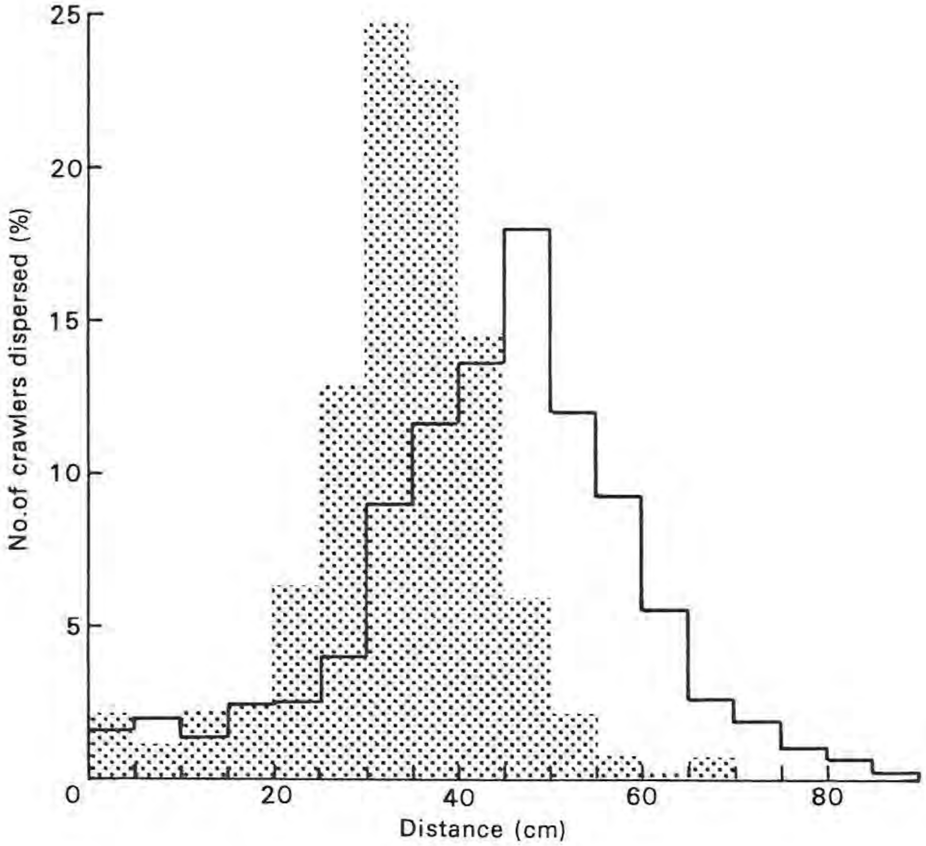


Fig. 18. Percentage number of 96 h male (░) and 96 h female (☐) *D.austrinus* crawlers in 5 cm class intervals up to 90 cm from the dispersal point in a wind tunnel. Means of 5 replications for both sexes are shown.

The dispersal formula of Brown (1958) was used to calculate the expected dispersal distances for 96 h crawlers in the wind tunnel. The dispersal platform was centred in relation to the 17 cm diameter air inlet so that the effective release height in the core of moving air was 8,5 cm. The height, the measured value for air velocity (1,7 m sec^{-1}) and terminal velocities for 96 h male and 96 h female crawlers (Table 6) were used in the formula (Section 2.4) to calculate the expected dispersal distances; 37,05 cm and 49,83 cm for male and female crawlers respectively. The calculated values are not significantly different from the observed mean dispersal distances of 36,05 cm and 46,06 cm (χ^2 = 0,3122; $p < 0,5$ for 1 d.f.). The difference in dispersal distances between the sexes would be more pronounced with an increased release height and wind velocity. However, it is clear that the females, with lower terminal velocities, are more bouyant than the males.

A significant feature of the results was the greater number of males remaining on the dispersal platform (Table 8). A G-test (Sokal & Rohlf 1973) showed a significantly greater number of females were dispersed from the platform (G = 9,73; $p < 0,005$ for 1 d.f.). The long filaments on the head, thorax and abdomen of the female will present a large surface area to air currents flowing around the host plant. The buffeting action of the air currents will enhance the possibility of removal of female crawlers in comparison to male crawlers.

Table 8. Number of 96 h male and 96 h female *D.austrinus* crawlers remaining on a dispersal platform in a wind tunnel and dispersed from the platform by air currents.

Sex	Number on platform	Number dispersed
Male	82	625
Female	45	621

Newly emerged *D.austrinus* crawlers have a high terminal velocity (0,62 m sec^{-1}) in comparison to the measured terminal velocities of three diaspine scale crawlers (Table 9). This is explained by the smaller size of the crawlers, with a greater surface area to weight ratio. By contrast 96 h old *D.austrinus* female crawlers have comparable terminal velocities even though they are larger. The reduction in the sinking

Table 9. Terminal velocities and length of three diaspidid species and of 96 h old D.austrinus female crawlers. All terminal velocities calculated using a similar method.

Species	Terminal velocity (m $\sec^{-1}$)	Length (mm)	Authors
Aonidiella aurantii (Mask.)	0,37	0,25	Willard 1973b
Aulacaspis tegalensis (Zhnt.)	0,20	0,30	Greathead 1972
Phenacaspis pinifoliae (Fitch)	0,30	0,30	Brown 1958
Dactylopius austrinus De Lotto	0,29	0,46	This study

speed will be accounted for by the presence of the long filaments. The relevance of these findings is clearer when discussed in relation to crawler behaviour.

4.3. Behaviour

Pettey (1948) noted the large numbers of D.austrinus crawlers which collected on the terminal cladodes of O.aurantiaca plants on hot windless days. The movement of crawlers to the spines of cladodes on the upper part of the host plant would facilitate wind dispersal. A similar behaviour pattern was noted for the crawlers of the sugar-cane scale A.tegalensis (Greathead 1972). During the morning, newly-emerged A.tegalensis crawlers move out from the leaf sheath, under which the parents had settled, on to the leaf blade where there is a greater chance of dispersal. By evening, the crawlers which remain on the leaf blade move back beneath the leaf sheath and settle. Greathead (1972) demonstrated the movement of crawlers from beneath the leaf sheath was in response to light. Day old crawlers showed a weaker response to light which suggested the behavioural pattern was restricted to the newly-emerged crawlers.

There is a clear difference in the behaviour of newly-emerged male and female D.austrinus crawlers. The first instar males settle and begin feeding beneath or in the immediate vicinity of the parent. Moran and Cobby (1979) showed that large numbers of first and second instar males are found beneath the ovipositing adult: a feature of populations of D.austrinus is the accumulation of male pupal cocoons around and above the adult females (Fig. 19).

Fig. 19. Clusters of pupal cocoons of D. austrinus around and over the parent females.

By contrast, first instar females emerge, move away from the parent and wander around the cladode, probing the surface with their mouthparts. Accumulation of crawlers (Fig. 20) on the spines of terminal cladodes is a common occurrence on plants with heavy infestations of cochineal. Crawlers move onto and up the spines, and after a variable period of time move back down to the cladode surface. However as the number of crawlers on a single spine increases, mutual interference prevents crawlers moving back down the spine and causes aggregations of crawlers at the tip.

In the field, movement of crawlers on the plant may place the crawlers in contact with surrounding vegetation. On one occasion I found a dense mass of crawlers clustered on the tip of an old flower stalk of Aloe tenior (Haworth) (Fig. 21). At the base of the aloe there was a heavily infested jointed cactus plant; the source of the crawlers which had moved to the tip of the flower stem. Close observation of crawlers on the spines of cladodes showed that these crawlers were females and the long filaments pointed to the advanced age of individuals displaying this behaviour. To verify this observation, the movement of crawlers to the spines of the terminal cladodes of an infested jointed cactus plant was further monitored.

Fig. 20. Accumulation of D.austrinus crawlers on the terminal spines of a cladode of O.aurantiaca.

Fig. 21. Jointed cactus (O.aurantiaca) growing at the base of an Aloe tenior (Haworth) plant. D.austrinus crawlers moved from cladodes of the host plant and clustered on the tip of an old flower stalk of the aloe (arrowed).

A large potted jointed cactus plant was placed in an air conditioned greenhouse with day temperature (06h00 - 20h00) at 25°C and night temperature (20h00 - 06h00) at 15°C. The spines on four terminal points of the plant were marked and crawlers found on the spines were removed with an aspirator every hour from 06h00 to 20h00 over a four day period. These crawlers were sexed on the basis of filament development.

The aggregation of the crawlers on the spines of the terminal cladodes showed a consistent pattern over the four day period (Fig. 22). With the increase in temperature and light intensity from 06h00 onwards, the number of crawlers moving on to the spines increased rapidly with peak numbers found between 08h00 and 10h00. Thereafter the number accumulating declined rapidly.

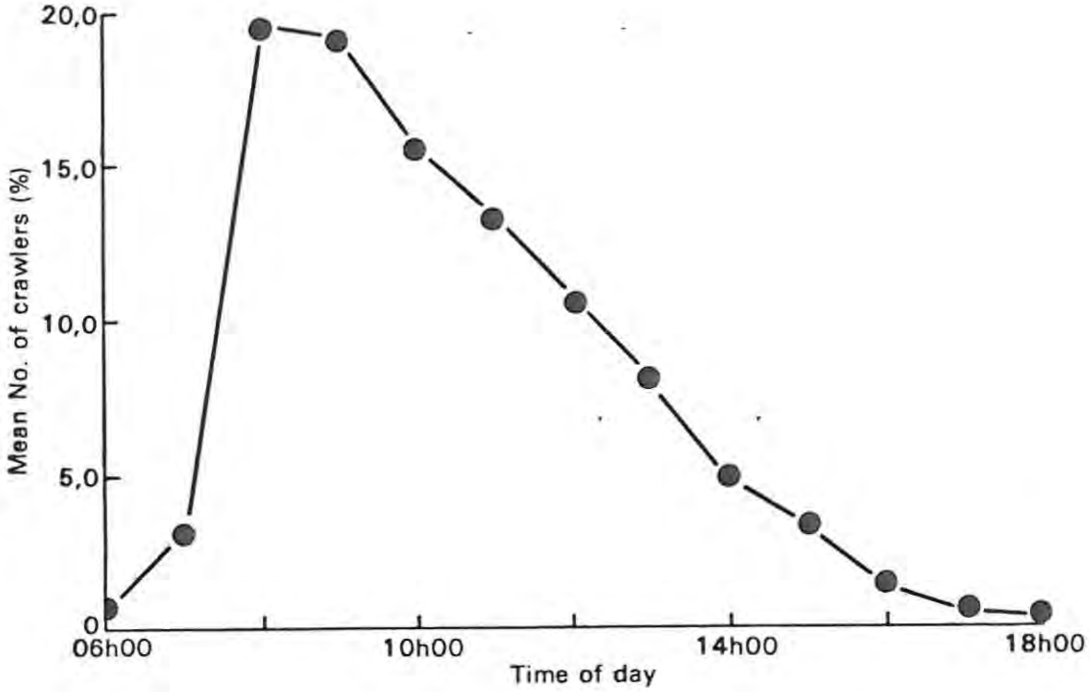


Fig. 22. The mean percentage number of D.austrinus crawlers recovered from the spines of four terminal cladodes of a single O.aurantiaca plant at hourly intervals over a four day period.

Both Cornwell (1960) and Willard (1973a) showed synchronization between peak crawler movement on foliage and the increase in diurnal wind velocity for the crawlers of P.njalensis and A.aurantii respectively. To confirm a similar synchronization for D.austrinus the average hourly wind velocity in the field (Maastricht farm) from September 1975 to April 1976 (including the summer months) was calculated (Fig. 23). The increase in wind velocity from 06h00 onwards to a peak between 14h00 and 18h00, coincided with the build up of crawlers on the spines, and this synchronization will enhance the possibility of dispersal.

Of 978 crawlers collected from the spines over the four day period 98,7% were female and this confirmed the field observations. The longest filament on the head, thorax and abdomen of 100 females, selected at random from amongst the crawlers recovered from the spines, was measured to provide an estimate of the mean age of the crawlers (Table 10).

Table 10. Mean length (± 1 standard error) of the longest filament on the head, thorax and abdomen of 100 female D.austrinus crawlers collected from spines on four terminal cladodes of an O.aurantiaca plant. For purposes of comparison the equivalent measurements for 48 h and 72 h old female crawlers (Table 5) are shown.

	Filament length (mm)		
Category	Head	Thorax	Abdomen
Crawlers collected on spines	0,55 ± 0,019	0,65 ± 0,022	0,80 ± 0,022
48 h crawlers	0,46 ± 0,018	0,54 ± 0,023	0,68 ± 0,021
72 h crawlers	0,64 ± 0,022	0,79 ± 0,022	0,94 ± 0,032

Comparison of these measurements with those of 48 h and 72 h old crawlers (Table 5) suggests that the crawlers were about 60 h old. The small standard errors indicates that the female crawlers on spines were approximately the same age.

There appears to be a close tie-up between filament development and the behaviour of female crawlers. Newly-emerged crawlers, with short filaments, would not present a large surface area to air currents, minimising the chance of removal from the host plant, while in search of a feeding site. The older crawlers (about 60 h) which fail to locate a feeding site and move to the spines of terminal joints have long filaments which enhances the possibility of dispersal.

Movement of crawlers on the cladodes surface and accumulation of crawlers on the spines in the morning and early afternoon means that the crawlers will be subject to high temperatures and low humidities which will reduce their survival time both on the host plant and once dispersed.

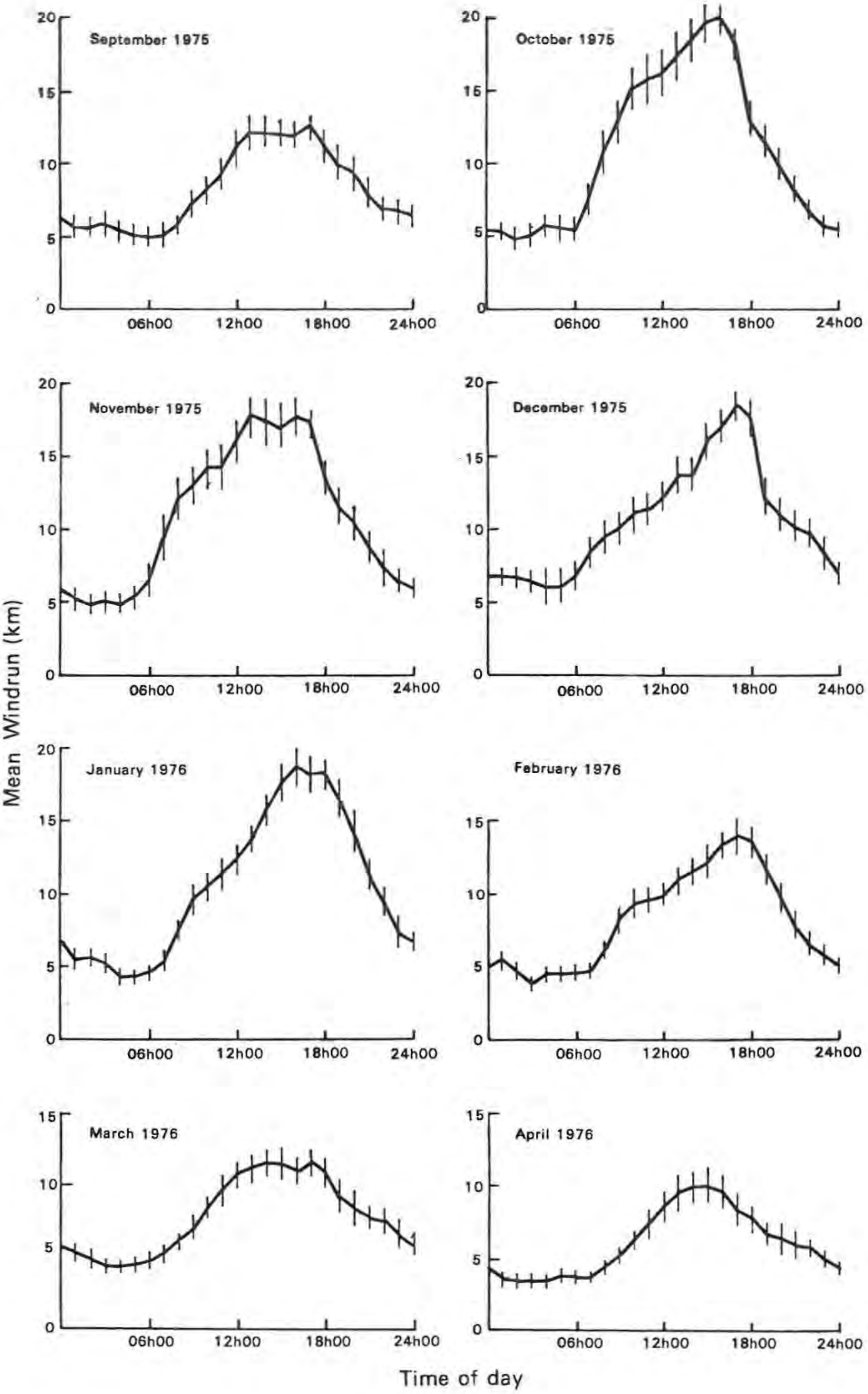


Fig. 23. Mean hourly wind velocities (± 1 standard error) for eight months (September 1975 to April 1976) on the farm Maastricht.

Karny (1972) remarked on the tolerance of young crawlers to high temperatures stating " The crawlers could withstand a temperature of 45°C for up to 24 hours...". The survival time of non-feeding crawlers will determine (i) the time crawlers are available for dispersal and (ii) the possibility of surviving long distance dispersal by air currents.

4.4. Survival

As mentioned earlier, the advantage of a large body surface area in relation to weight in dispersal of D.austrinus crawlers must be offset against increased risk of desiccation. The tolerance of D.austrinus crawlers to high temperatures was investigated in a series of laboratory experiments to determine the survival times of non-feeding crawlers. Tolerance to low temperature was limited to a single experiment for reasons which will be discussed later in this section.

Abdelrahman (1974) drew attention to the comment of Bursell (1964) on the applicability of data obtained under laboratory conditions of constant temperature to insect populations, which in normal environments are subject to fluctuating diurnal temperature cycles. I have used both fluctuating and constant temperature conditions to determine the survival time of D.austrinus crawlers. The use of constant temperature conditions enables comparison with other data.

Temperature data recorded in a Stevenson screen at the farm Maastricht during summer, from September 1975 to March 1976, were analysed and the longest period temperatures remained continuously above 20°C, 25°C, 30°C, 35°C and 40°C respectively were recorded (Table 11).

Table 11. Maximum duration (h) of high temperatures above five temperature levels at Maastricht.

Temperature (°C)	20	25	30	35	40
Time (h)	65	14	11	7	4

Standard temperatures (Stevenson screen) may be an underestimate of the air temperatures to which crawlers are exposed. However crawlers will have access to cooler positions (e.g. shaded areas) of the host plant where temperatures will be more consistent with Stevenson screen recordings which provide a means of comparison with other data.

On the basis of the data in Table 11 four daily temperature regimes were simulated in the C.E. room (Fig. 24). Humidity levels and light settings were similar in all four replicates as was the night temperature (20^{o}C).

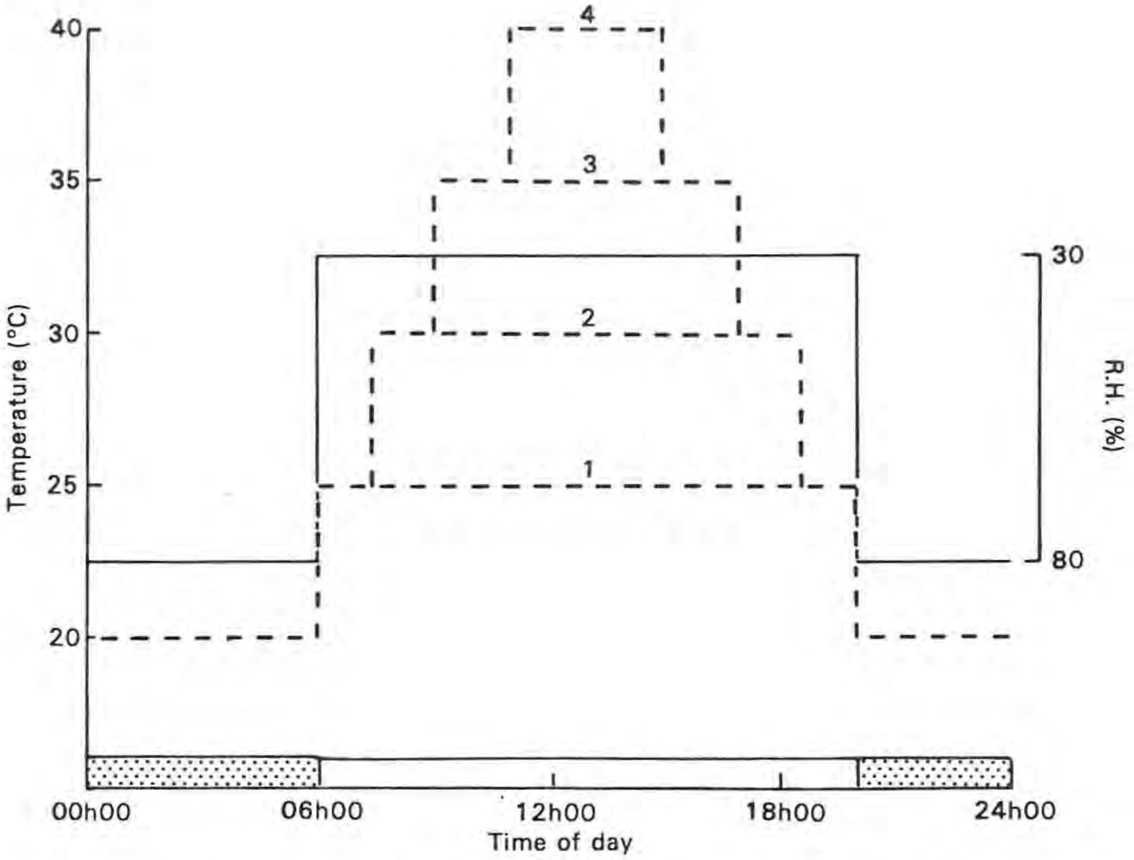


Fig. 24. Four fluctuating temperature regimes (maximum temperature of each regime numbered) used in a C.E. room in four separate experiments to simulate extremes of temperature found in the field. Broken lines - temperature(^{o}C); solid lines - relative humidity (R.H.%); stippled bars on time axis represent dark cycle.

Five batches of 100 crawlers 1 h old were placed in the C.E. room at the beginning of a light cycle and every 12 h (1 h after onset of light cycle and 1 h before onset of dark cycle) the numbers of dead crawlers were counted. Total immobility was used as the criterion for death. This procedure was repeated for all four temperature regimes (Fig. 24).

To compare survival of crawlers held at constant temperatures, five batches of 200 crawlers 1 h old were subjected to constant temperatures of 25°C, 30°C, 35°C and 40°C at 50% R.H. Larger batches of crawlers were used in each replicate to enable comparison of male and female crawler survival times. Counts of dead crawlers were taken every 24 h.

Figures 25 and 26 show that under fluctuating and constant temperature regimes the survival time of crawlers decreased as the maximum temperature in both regimes rose from 25°C to 40°C. Table 12 shows the LT50 (time to 50% crawler mortality) for the four fluctuating and four constant temperature regimes.

Table 12. LT50's (time to 50% crawler mortality) of D. austrinus crawlers held under four fluctuating temperature regimes (Fig. 25) and four constant temperature regimes (Fig. 26). The mean values of five replicates for each temperature regime are shown.

Maximum temperature (°C)	25	30	35	40
LT50 (h): Fluctuating temperature	172,2	121,2	103,8	79,4
LT50 (h): Constant temperature	169,2	124,8	88,8	54,2

Comparison of LT50's at 25°C and 30°C under both fluctuating and constant temperature regimes shows the survival times were very similar. At 35°C and 40°C there was a higher mortality under constant temperature regimes.

The crawlers held under constant temperatures of 25°C and 30°C were sexed on the basis of the pattern and development of filaments to enable comparison of the survival times of male and female crawlers. Figure 27 shows that the females were somewhat hardier than the males, but the difference is unlikely to be significant in terms of dispersal.

Comparison of survival times must be made with respect to fluctuating temperature regimes (Fig. 25), which are more similar to field conditions than constant temperature regimes. Under the harshest conditions (maximum temperature 40°C) there is little mortality for the first 48 h, but thereafter the number of survivors drops rapidly. As shown earlier (Section 4.3) crawlers congregate on spines once they are about 60 h old which suggests that few crawlers will survive to disperse if temperatures exceed 40°C on three consecutive days. However it is very unusual for temperatures to reach 40°C for several consecutive days.

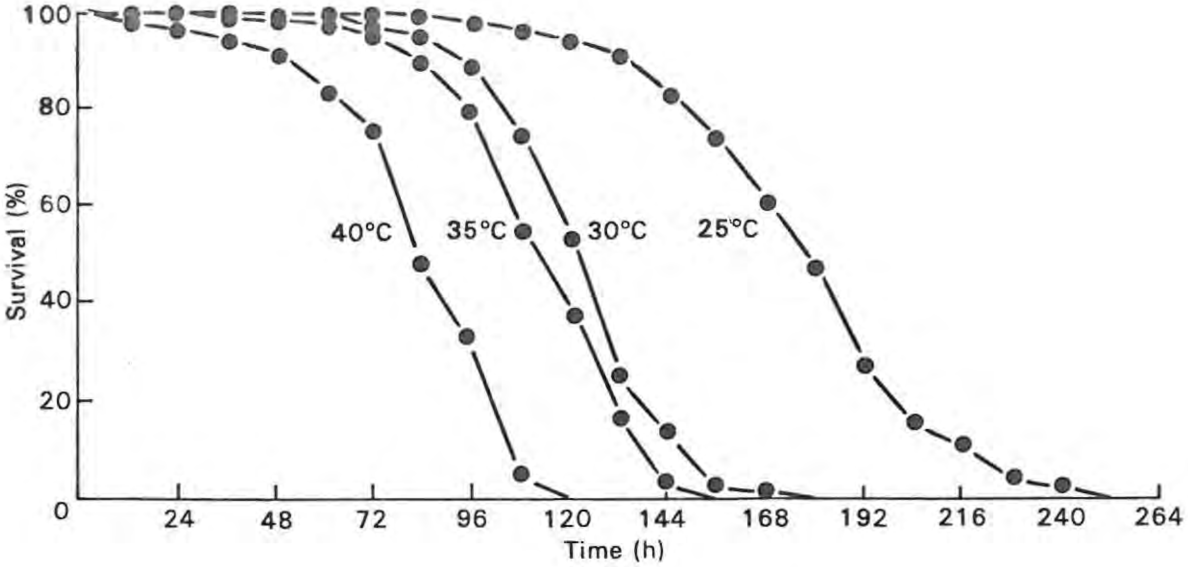


Fig. 25. Survival of D. austrinus crawlers at four fluctuating temperature regimes (see Fig. 24) maxima 25, 30, 35 and 40°C. Points represent the means for five replicates.

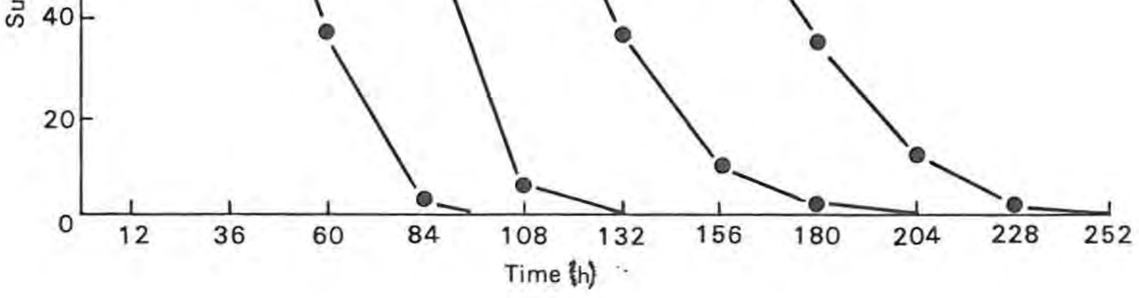


Fig. 26. Survival of D. austrinus crawlers at four constant temperature regimes. Points represent means for five replicates.

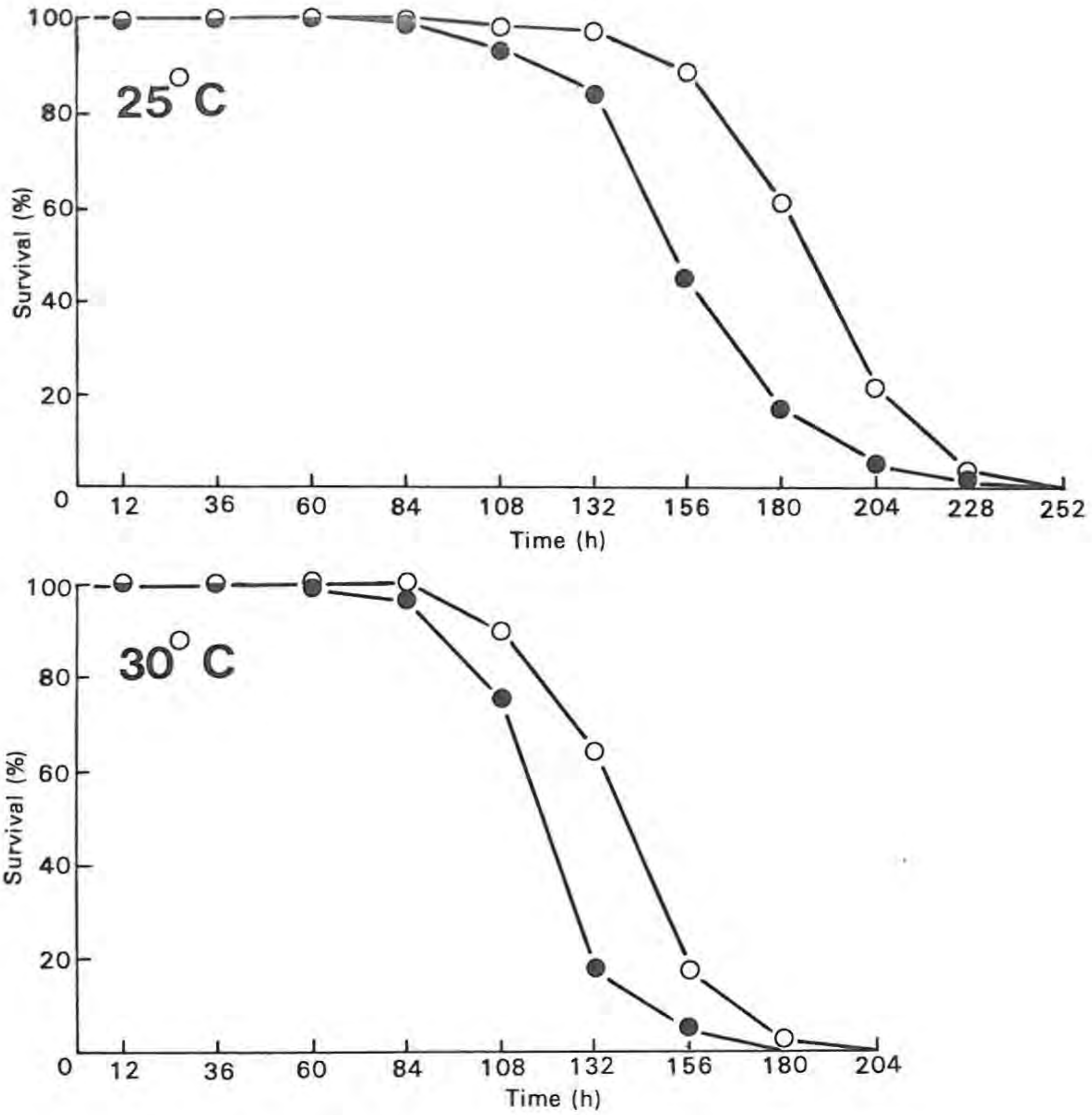


Fig 27. Survival of male (●) and female (○) *D.austrinus* crawlers held under constant temperatures of 25°C and 30°C at 50% R.H. Means for five replicates at each temperature are shown.

Mathis (1947) reported that the crawlers of *Chrysomphalus ficus* Ashm. survived 3 to 4 days on dry filter paper while Bedford (1968) reported that crawlers of *Gascardia sinoiae* (Hall) lived 5.2 days without food. Crawlers of the latter species remain beneath the parent female for over two days and the protection afforded possibly extends the survival time. Willard (1973b) studied the survival time of A.aurantii crawlers held in wire cages with a constant air flow through the cages, and found LT50 ranged from 5.7 h (temperature 35°C, 25% R.H. and air flow 35 cm sec^{-1}) to 17.1 h (temperature 15°C, 70% R.H. and air flow 35 cm sec^{-1}). It is difficult to compare the survival times of D.austrinus and A.aurantii, as the latter were held under conditions of a steady air flow and would have been subjected to a far higher rate of desiccation. Notwithstanding this feature, comparison of LT50 at 35°C shows the D.austrinus crawlers (LT50 of 88,8 h) are far hardier than A.aurantii crawlers (LT50 of 5.7 h). The small size(0,25 mm long) of A.aurantii crawlers, a large surface area to volume ratio, will increase the effect of desiccation on survival time.

The LT50 of A.tegalensis crawlers (temperature 30°C and 50% R.H.) was approximately 9 h (determined from Fig. 5; Greathead 1972) compared to 124,8 h for D.austrinus crawlers held under similar conditions of temperature and humidity. Both Greathead (1972) and Willard (1973b) made comment on the long range dispersal of crawlers in relation to survival.

Greathead (1972) calculated that A.tegalensis crawlers could possibly survive long range displacement up to 260 km which would account for infestation of sugar-cane in widely separated areas. Willard (1973b) pointed out that survival period of A.aurantii crawlers carried vertically upwards by turbulence or thermal convection would increase as temperatures decrease 6°C per km with increasing height. He stated, with reference to long range dispersal of A.aurantii crawlers, that "...there is little doubt that even during hot, dry summer weather the crawlers could withstand transport by wind over long distances.".

The hardiness of D.austrinus crawlers will mean that even crawlers 60 h or older (the apparent dispersal age) will survive long range dispersal. The pattern of hourly wind velocity in summer (Fig. 23) suggests crawlers swept up by turbulence or convection currents during the day would sink to the ground at night as wind velocities and temperatures drop. There was no mortality in 1 000 crawlers 60 h old held at 4°C for 24 h which means crawlers carried to high altitudes during long range displacement would survive.

The survival times of D.austrinus crawlers at high temperatures might suggest that wind dispersed crawlers deposited onto the ground could move considerable distances by walking which would also increase the chance of location of new host plants. However low ground temperatures at night would impede movement and the crawlers cannot survive the extremely high ground temperatures of about 65°C which have been recorded in the field during the day. Also the crawlers of D.austrinus are very small and move relatively slowly so that walking is unlikely to contribute significantly to dispersal in this species. Wind must be of paramount importance in dispersal of D.austrinus crawlers.

Beside morphological adaptation, behaviour and survival characteristics, reproduction must be an important facet in the success of this species with respect to dispersal and colonization.

4.5. Reproduction

The rate of increase in D.austrinus populations will depend on the number of reproducing individuals (female crawlers) produced by the parent generation. The fecundity of the adults and sex ratio of the offpsring will determine the number of female crawlers produced. The rapid build up of populations will ensure large numbers of crawlers enhancing the potential for dispersal and colonization. Mann (1969) reported that the cochineal insect D.opuntiae was parthenogenetic, with unfertilised females producing both males and females. This type of parthenogenesis (facultative deuterotoky) insures against the loss of males and a lowered reproductive potential due to unfertilised females failing to produce offspring (Nur 1971). However Mann (1969) based his observation on four individual females, two fertilised and two unfertilised, which casts doubt on the validity of his statement.

Two cultures of female crawlers were established to assess the status of parthenogenesis in D.austrinus reproduction. Two groups of 400 female crawlers 48 h old were released on loose cladodes, and once the crawlers had settled and begun feeding, one culture was isolated in a glass container covered with a perforated plastic sheet to prevent access by males. The second culture, in an open glass container accessible to adult males, was placed alongside potted jointed cactus plants with a large population of D.austrinus. Once the females in both cultures were mature, but prior to oviposition, they were removed from the cladodes and isolated in petri dishes. The number of females from both cultures producing crawlers were recorded.

D.austrinus females are not parthenogenetic. Only two of the females denied access by males produced offspring (Table 13). Two males, presumably included amongst the original crawlers released on the cladodes, probably fertilized the two productive females. In the control group, with access to males, 96% of the females produced crawlers.

Table 13. Number of fertilised and virgin D.austrinus females producing offspring.

Condition	No. female crawlers released in culture	No. of adult females reared	No. adult females with progeny
Virgin	400	145	2
Fertilised	400	223	214

A feature of the virgin females was the secretion of a second wax cover once they were removed from the cladodes and stripped of their original wax cover. The non-productive females were alive two months after their fertile counterparts had ceased oviposition and died. Cover renewal in virgin females has been noted for the white peach scale Pseudaulacaspis pentagona (Targ.) (Bennett & Brown 1958) and the olive scale Parlatia oleae Colvee (Ezzat 1957 in Beardsley & Gonzalez 1975).

The fecundities of two categories of females were determined. The first comprised females reared in large numbers on loose cladodes with between 15 and 25 females per cladode, and the second, females reared on potted jointed cactus plants with between 1 and 5 females per cladode. Thirty mature females of each category were removed from the cladodes and weighed. Each female was placed in a separate glass vial and when oviposition ceased the total progeny of each female was counted.

The fecundity of D.austrinus was variable. The females from the low density populations on plants produced a mean of 734 ± 44.9 crawlers (range: 375-1291) while females from the high density population on individual cladodes produced 443 ± 33.0 crawlers (range: 115-788). The females reared on plants were larger (mean mass: 0,0345 ± 0,0015g) than those reared on individual cladodes (mean mass: 0,0166 ± 0,0011g).

Figure 28 shows that there was a linear relationship between adult mass and crawler production. Regression analysis (Sokal & Rohlf 1973) shows that for both categories of females this relationship was significant at the 1% level (Table 14).

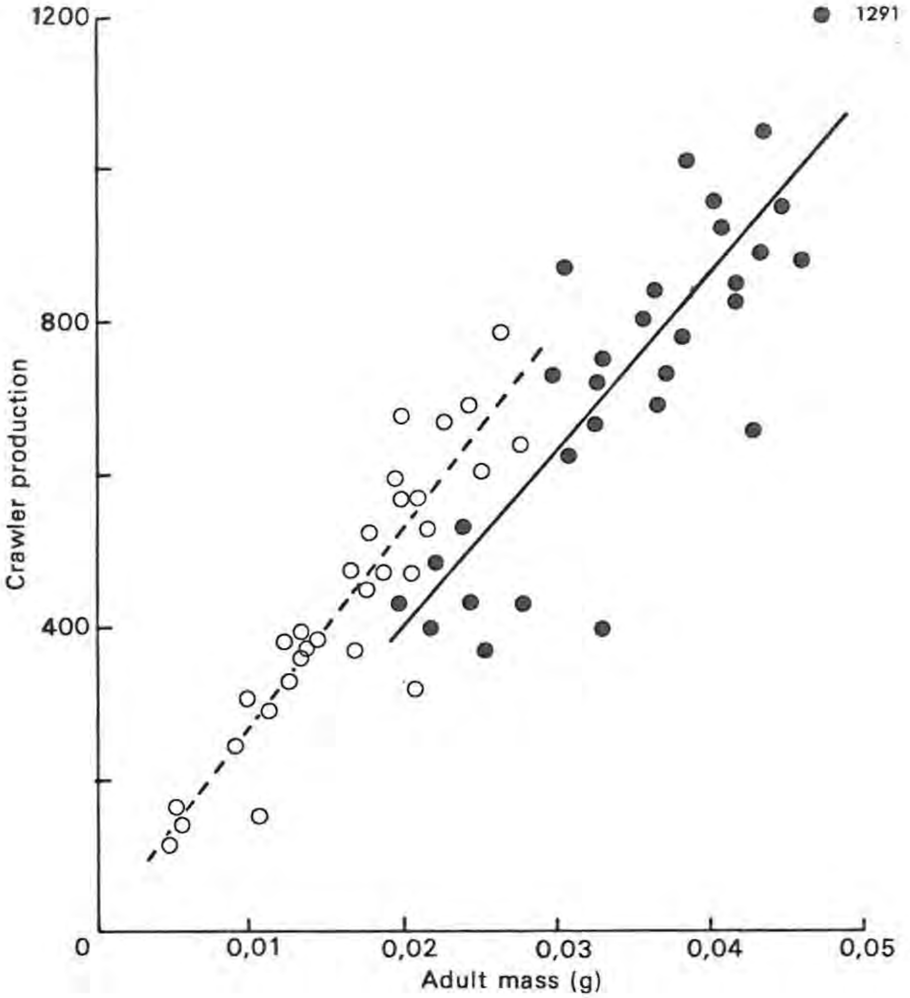


Fig. 28. Relationship between the mass of *D.austrinus* females reared on individual *O.aurantiaca* cladodes (o) and on *O.aurantiaca* plants (●) and crawler production. Regression values for the two categories shown in Table 14.

Table 14. Linear regression values on the productivity and mass of individual *D.austrinus* females reared on *O.aurantiaca* plants and loose cladodes of *O.aurantiaca*. Probability for 1/28 d.f.

	Intercept (a)	Slope (b)	SE (b)	"t" (b)	P
Whole plants	-67,04	23186,16	2860,69	8,11	<0,001
Loose cladodes	4,53	26413,34	74,69	353,64	<0,001

The adult females continue feeding after the onset of oviposition, and criticism may be levelled at the technique used to determine the fecundity. However, Moran and Cobby (1979) found no significant difference between the fecundity of females left on individual cladodes and those removed prior to the onset of oviposition. Females at low densities on whole plants (1 - 5 females per joint) did produce more crawlers if left in situ. Therefore the mean fecundity of females on the plants is probably an underestimate of the potential fecundity.

The major effect of removing the females was that the oviposition period was greatly reduced. Moran and Cobby (1979) found the oviposition period of females feeding on plants extended to 50 days, whereas those removed completed crawler production in 20 days (Fig. 29).

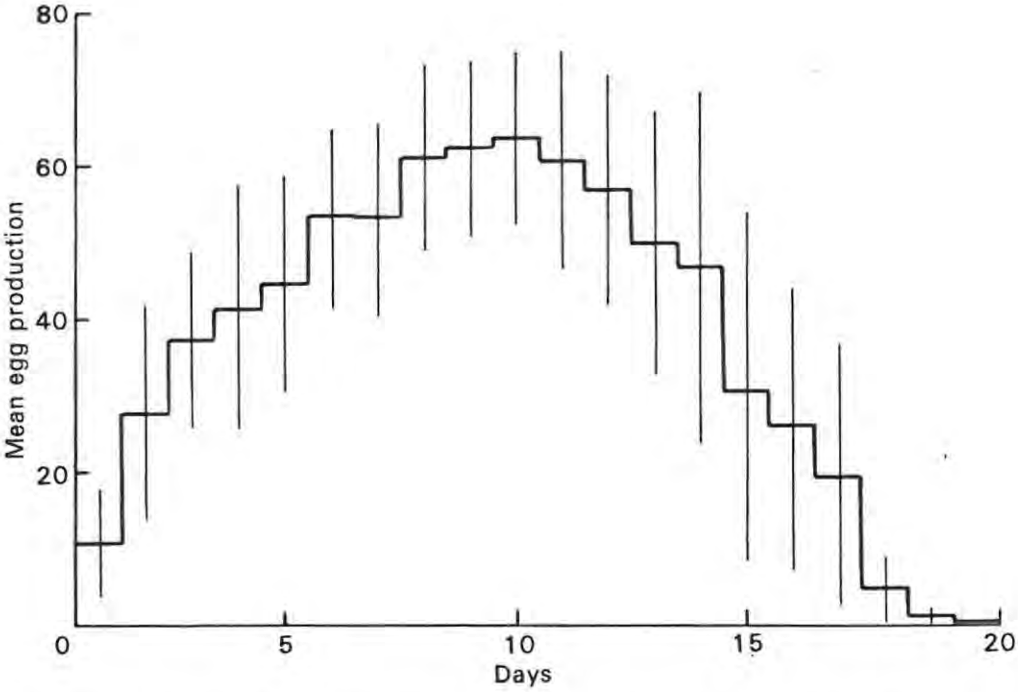


Fig. 29. Mean daily production (± 2 standard errors) of nine D. austrinus females. Data obtained during determination of sex ratios of offspring of the females.

The determined fecundities were comparable with the results obtained by Moran and Cobby (1979) but higher than those found by Karny (1972) and Dos Santos (1975) under similar environmental conditions (Table 15).

Table 15. Fecundity of D.austrinus females.

N	Mean Production (± standard error)	Host condition	Range	
30	734 ± 44,9	Plant	375-1291	(This study)
30	443 ± 30,0	Individual cladodes	115-788	(This study)
30	390 ± 21,3	Plant	37-599	(Dos Santos 1975)
20	124,3	Plant	?-288	(Karny 1972)

Moran and Cobby (1979) noted the importance of the density of adult females of D.austrinus in relation to the mass of plant material available in determining the fecundity of individual females. Karny (1972) and Dos Santos (1975) made no mention of female density in their results and this may explain the widely differing fecundities obtained by these authors.

Variations in the mass of females reared on loose cladodes had no effect on the size of the progeny of individual females. A correlation analysis on the mean length of 30 crawlers produced by each female and the weight of the parent showed no significant relationship ($r = 0{,}096$; $p > 0{,}05$ for 1/28 d.f.).

As D.austrinus females are not parthenogenetic the sex ratio of the progeny is important in determining the reproductive potential of this species i.e. the number of reproducing individuals in the next generation. The sex ratios of the progeny of ten females reared on loose cladodes and nine females reared on plants were determined. Individual females were isolated in glass vials and the progeny sexed on the basis of filament development (Tables 16 and 17).

The sex ratio (♂♂ per 100 ♀♀) of the progeny of females reared on whole plants was higher than that of females reared on loose cladodes. Examination of the individual sex ratios show they were variable but in all but one case there were more males than females produced. Hughes-Schrader (1948) cited in Nur (1971) has suggested the evolution of arrhenotokous and deuterotokous parthenogenesis in coccoid insects prevented complete loss of males, due to the fragility of males in relation to a high level of desiccation in the pupal stage, in any generation. The high male:female sex ratio in non-parthenogenetic D.austrinus females

Table 16. Sex ratio (♂♂ per 100 ♀♀) of the progeny of D. austrinus females reared on loose cladodes of O. aurantiaca.

Female No.	Total no. of crawlers produced	Males	Females	Sex ratio o o per 100 o o
1	437	230	207	111,1
2	221	123	98	125,5
3	345	183	162	113,0
4	422	236	186	126,9
5	335	187	148	126,4
6	262	147	115	127,8
7	219	76	143	53,2
8	279	175	104	168,3
9	356	211	145	145,6
10	180	113	67	168,7
			Mean sex ratio:	126,6 ± 10,38

Table 17. Sex ratio (♂♂ per 100 ♀♀) of the progeny of D. austrinus females reared on O. aurantiaca plants.

Female No.	Total no. of crawlers produced	Males	Females	Sex ratio o o per 100 o o
1	660	496	164	302,4
2	1184	753	431	174,7
3	610	469	141	332,6
4	698	529	169	313,0
5	900	558	342	163,2
6	743	438	305	143,6
7	662	446	216	206,5
8	353	229	124	184,7
9	441	240	201	119,4
			Mean sex ratio:	215,6 ± 26,52

may be to offset the potential loss of males in the pupal stage. There was no correlation between the fecundity of individual adults and the sex ratio of their progeny ($r = 0,4293$; $p > 0,05$ for 1/17 d.f.).

There was no sexual dichromism in crawler production as male and female crawlers were produced each day by individual adults. Bennett and Brown (1958) found the white peach scale P.pentagona showed sexual dichromism in that all the female crawlers were produced before male crawlers.

Greathead (1972) commenting on the high fecundity of A.tegalensis, the sugar-cane scale, said "It would be of great interest to compare fecundity and migration for other tree-infesting or grass-or herb-infesting Diaspididae to ascertain if migration and high reproductive rate are generally characteristic of scales occupying relatively temporary habitats.". Both D.austrinus and A.tegalensis show behaviour directed towards "take-off" characteristic of migrants (Kennedy 1961 and Southwood 1962), and comparison of the reproductive potential of these species with that of other coccoid species might, as suggested by Greathead (1972), provide further support for the migrant status of these two species.

Table 18 lists the fecundities of species of seven families of the Coccoidea in terms of their reproductive potential i.e. the number of reproducing individuals in the next generation. For parthenogenetic species the value for fecundity represents the reproductive potential as only females were recorded amongst the offspring. In bisexual species the reproductive potential has been expressed on the basis of the sex ratio and where this is not stated a sex ratio of 1:1 was assumed. Figure 30 summarises the reproductive potentials of species shown in Table 18 and enables comparison of the data. It is difficult to make direct comparisons of the reproductive potentials of the species of all the families as the data is often unreliable and there is a great deal of morphological variation between the families. However several general conclusions can be reached by examination of the data in Table 18 and Figure 30.

There is too little data for the families Asterolecaniidae, Eriococcidae and Margarodidae to justify positive comment, except to note that the recorded reproductive potentials are low. Members of the Coccidae have a large range of fecundities and reproductive potentials in comparison to other families but this must be related to the size of the adults which are large in comparison to other species. Morphological differences between the different species restricts comparison of the fecundity and reproductive potential of A.tegalensis and D.austrinus to the most closely related species, members of the Diaspididae and Pseudococcidae respectively.

Table 18. Fecundity, sex ratio, parthenogenetic status and mean reproductive potential of species of seven families of the Coccoidea. * Sex ratio assumed to be 100 ♂♂ per 100 ♀♀. ** Mean fecundity determined from the range.

Species	Fecundity		Parthenogenetic	Sex ratio ♂♂ per 100 ♀♀	Mean reproductive potential	Author
	Range	Mean				
Family Asterolecaniidae						
Asterolecanium coffeae Newst.	?-70	50	Yes	N/A	50	James 1933.
Asterolecanium pustulans (Ckll.)	50-60	55**	Yes	N/A	55	Avidov & Harpaz 1969.
Family Coccidae						
Ceroplastes floridensis (Comst.)	145-405	282	?	?	?	Sankaran 1959.
" " "		700	Yes	N/A	700	Avidov & Harpaz 1969.
Ceroplastes pseudoceriferus Green	1187-10 825	6 236	No	2475	252	Sankaran 1959.
Ceroplastes rusci L.	800-1 500	1 150**	Yes	N/A	1 150	Avidov & Harpaz 1969.
Coccus elongatus Sign.	250-703	475	Yes	N/A	475	El Minshawy & Moursi 1976.
Coccus hesperidum L.	?-201	73	Yes	N/A	73	Bodenheimer 1951.
Gascardia (=Ceroplastes) sinoiae Hall	88-10 625	3 726	Yes	N/A	3 726	Bedford 1968.
Lecanium kunoensis Kuwana	300-1 700	1 200	No	100	600	Husseiny & Madsen 1962.
Pulvinaria floccifera Westw.	766-1 002	857±26	Yes	N/A	857	El Minshawy & Moursi 1976.
Pulvinaria psidii Mask.	138-280	200±15	Yes	N/A	200	El Minshawy & Moursi 1976.
Saissetia nigra (Nietner)	453-1 632	628	Yes	N/A	628	Smith 1944.
Saissetia oleae (Bern.)	249-1 341	756	Yes	N/A	756	Bodenheimer 1951.
Toumeyella numismaticum (Pettit & McDaniel)	?	534±50	No	79-132	230-298	Rabkin & Lejeune 1954.
Family Dactylopiidae						
Dactylopius austrinus De Lotto	287-2 128	1 145	No	200	382	Moran & Cobby 1979.
Family Diaspididae						
Aonidiella aurantii (Mask.)	69-318	174	No	100*	87	Willard 1972a.
" " "		73	No	108	38	Jones 1936.
" " "	102-479	352	No	100*	176	Tashiro & Beavers 1968.
Aspidiotus hederae (Vallot)	60-100	80**	No	100*	40	Bodenheimer 1951.
Aulacaspis tegalensis (Zhnt.)	?-1 043	ca.750	No	100	ca.375	Williams 1970.
Chrysomphalus aonidium (L.)	?-525	224	No	100*	112	Avidov & Harpaz 1969.
Chrysomphalus ficus Ashm.	?-247	150	No	100*	75	Schweig & Grunberg 1936.
" " "	33-334	145	No	108-212	46-70	Avidov & Harpaz 1969.
Lepidosaphes beckii (Newm.)		250-300	No	100*	125-150	Avidov & Harpaz 1969.
" " "	?-286	172	No	153	69	Bodenheimer 1951.
Lepidosaphes ficus (Signoret)	0-51	30	No	100*	15	Stafford & Barnes 1948.
Lepidosaphes ulmi (L.)	?-96	59	Yes		69	Samarasinghe & le Roux

Species	Fecundity		Parthenogenetic	Sex ratio ♂♂ per 100 ♀♀	Mean reproductive potential	Author
	Range	Mean				
Lepidosaphes pinnaeformis (Bouche) Kirk.	50-100	75**	No	273	20	Stofberg 1937.
Melanaspis obscura (Comst.)		50	No	100*	25	Stoetzel & Davidson 1971.
Nuculaspis californica (Coleman)		ca. 40	No	100*	20	" " "
Parlatoria blanchardii (Targ.)		18-28		37-58	12-17	Salama 1972.
Parlatoria oleae (Colvee)	?-150	60	No	100*	30	Avidov & Harpaz 1969.
Parlatoria pergandii Comst.		88		100	44	Bodenheimer 1951.
Parlatoria pittospori Mask.	?-62	46	?		46	Timlin 1964.
Phenacaspis pinifoliae (Fitch)		47		116	22	Cumming 1953.
Pseudaulacaspis pentagona (Targ.)	13-95	47	No	100	23	Bobb *et al*. 1973.
" " "		100		100*	50	Oda 1963.
" " "	107-144	131		100*	63	Kuitert 1967.
Quadraspidiotus perniciosus (Comst.)	87-145	116**	No	100*	58	Gentile & Summers 1958.
Family Eriococcidae						
Eriococcus coriaceus Mask.	?-531	150-280	No	100*	75-140	Patel 1971.
Eriococcus orariensis Hoy	12-69	47±2	No	100	24	Hoy 1961.
Family Margarodidae						
Icerya aegyptica (Douglas)	15-247	143	Yes		143	Azab *et al*. 1968.
Icerya purchasi Mask.	?-830	170	Herm.	N/A	170	Avidov & Harpaz 1969.
Matsucoccus josephi (Bodenheimer & Harpaz)		340	No	100*	170	Avidov & Harpaz 1969.
Family Pseudococcidae						
Antonina graminis (Mask)	?-150		Yes		150	Brimblecombe 1968.
Ferrisia virgata Ckll.	?-955	657	No	20	526	Das *et al*. 1948.
" " "	93	93-335	No	20	74-268	Rawat & Modi 1969.
Maconellicoccus hirsutus (Green)	403-654	516	No	96-101	259-263	Ghose 1972.
Planococcus (=*Pseudococcus*) *citri* (Risso)	95-592	307	No	100	153	Myers 1932.
" " " "	38-404	239	No	101	119	James 1938.
Pseudococcus gahani Green	57-406	198	No	43	139	James 1938.
Pseudococcus longispinus Targ.	32-398	215	No	19	181	James 1938
Pseudococcus maritimus Ehr.	8-189	110	No	60	68	James 1938.
Pseudococcus njalensis Laing	6-90	36	Yes		36	Strickland 1951.
Puto sandini Washburn	19-67	30	No	100*	15	Washburn 1965.
Trionymus peregrinus Green	54-306	164	No	37	120	James 1938.

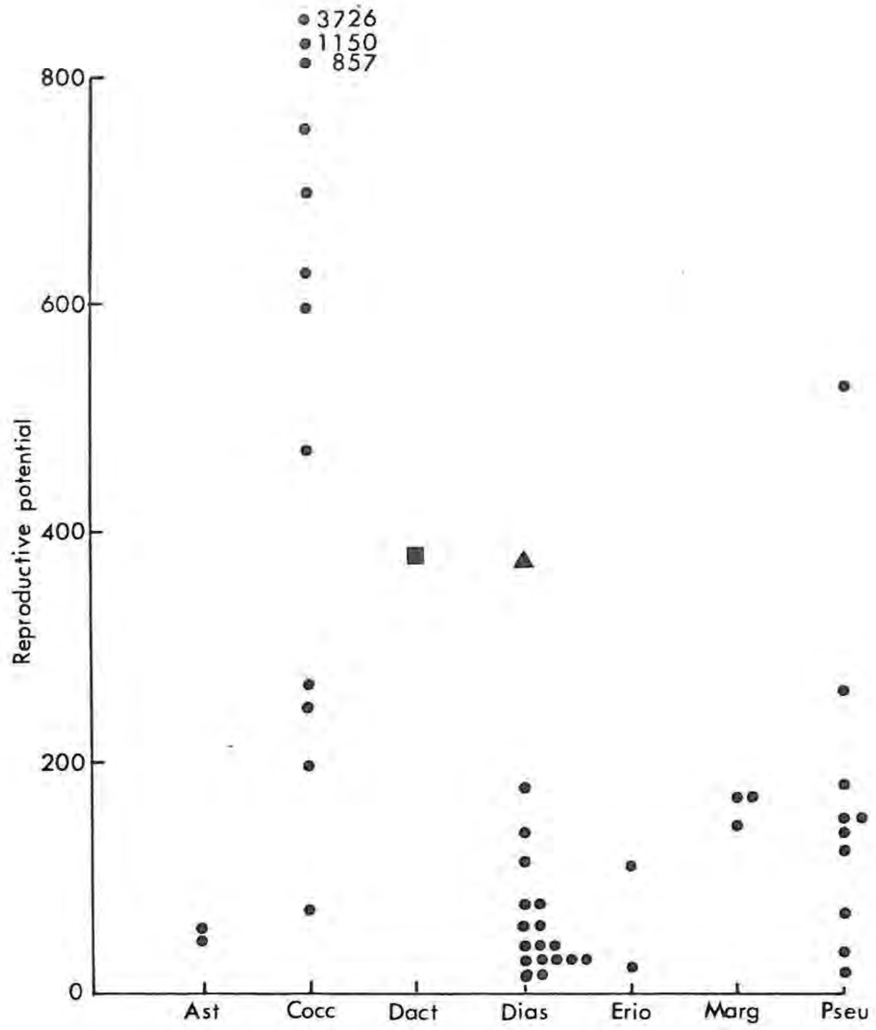


Fig. 30. Comparison of the reproductive potential of species of seven families of the Coccoidea. The reproductive potential of D. austrinus (■) and A. tegalensis (▲) recorded with different symbols to facilitate comparison. Ast - Asterolecaniidae; Cocc - Coccidae; Dact - Dactylopiidae: Dias - Diaspididae; Erio - Eriococcidae; Marg - Margarodidae; Pseu - Pseudococcidae.

A. tegalensis has a high reproductive potential (about 375) in comparison to that recorded for the other species which in all cases is below 200. The host plants of these species are all relatively permanent when compared to that of A. tegalensis which provides support for the idea of a high fecundity and reproductive potential amongst species of diaspidids infesting temporary habitats.

Similarly the reproductive potential of D. austrinus reared on whole plants (Moran & Cobby 1979) is high when compared to that recorded for pseudococcid species but the conclusions with regard to the permanence of the habitat and reproductive potential are not clear cut. Brimblecombe (1968) recorded the fecundity of the parthenogenetic females of A.graminis, which infest Rhodes grass, a relatively temporary habitat, at 150 crawlers per female which gives a reproductive potential lower than that calculated for a proportion of pseudococcids infesting trees (permanent habitats). Therefore no definite conclusions can be reached with regard to the reproductive potential of D.austrinus and migrant status of this species.

With the background of features of the biology of D.austrinus which influence the dispersal of this species it is now appropriate to examine the process of dispersal itself. The next section deals with laboratory studies of factors which determine the number of crawlers dispersed and timing of dispersal.

5. SOME FACTORS INFLUENCING DISPERSAL

Dispersal of coccoid crawlers is limited to the motile crawlers which have emerged from beneath the female and are moving on the host plant in search of a feeding site (Hulley 1962 and Willard 1973a). Once settled and feeding, the crawlers are anchored to the host plant by their mouthparts. In the case of crawlers which are short lived e.g. red scale (A.aurantii) crawlers, the wandering period is limited (about 186 min) and time and rhythm of emergence of crawlers from beneath the females is important in dispersal (Willard 1973a). Factors which affect the rhythm of emergence and the total wandering time will determine the number of crawlers dispersed and the timing of the dispersal.

Non-feeding D.austrinus crawlers are extremely hardy and will be available for dispersal over several days. In this case it is the number of crawlers rather than the rhythm of emergence or length of the wandering period that will determine the number dispersed and timing of dispersal. The small size of jointed cactus plants precludes destructive sampling for counts of motile crawlers. Observations during routine handling of cultures showed that many crawlers fell from cladodes in still air conditions. This suggested that "drop-off" of crawlers could be used as a measure of the number of crawlers moving on the host plant and hence available for dispersal.

Confirmation that drop-off could be used to estimate the density of motile crawlers was made by comparing drop-off and wind tunnel dispersal of crawlers. This enabled the influence of certain weather variables on motile crawler densities to be assessed in a series of laboratory experiments.

5.1. Estimation of motile crawler density

Two cladodes, heavily infested with D.austrinus, were clamped into position in the wind tunnel used in the earlier experiments (Section 4.2). Five infested cladodes were placed across a small metal frame, raised 20 cm above a sheet of perspex lightly coated with vaseline. C.E. room conditions were set with 14 h light, relative humidity 30 ± 3%; 10 h dark and 80 ± 3% R.H. The temperature in the dark cycle was constant at $15^{\circ} \pm 2^{\circ}C$ and from the onset of the light cycle (06h00) raised $5^{\circ}C$ every

2 h to 35°C and after 2 h at this level (14h00) lowered by 5°C every 2 h back to 15°C at 20h00 (Fig. 31).

With continual air flow in the wind tunnel and after a three day acclimation period, counts were made every 2 h (06h00 to 20h00) for five days of the number of crawlers wind dispersed and the number which dropped off cladodes in still air conditions (Fig. 31). A small percentage of the total number of crawlers were wind dispersed from and dropped off cladodes (2,2 and 5,5% respectively) during the dark cycle (20h00 to 06h00). With the onset of the light cycle there was an immediate increase in counts with increasing temperature.

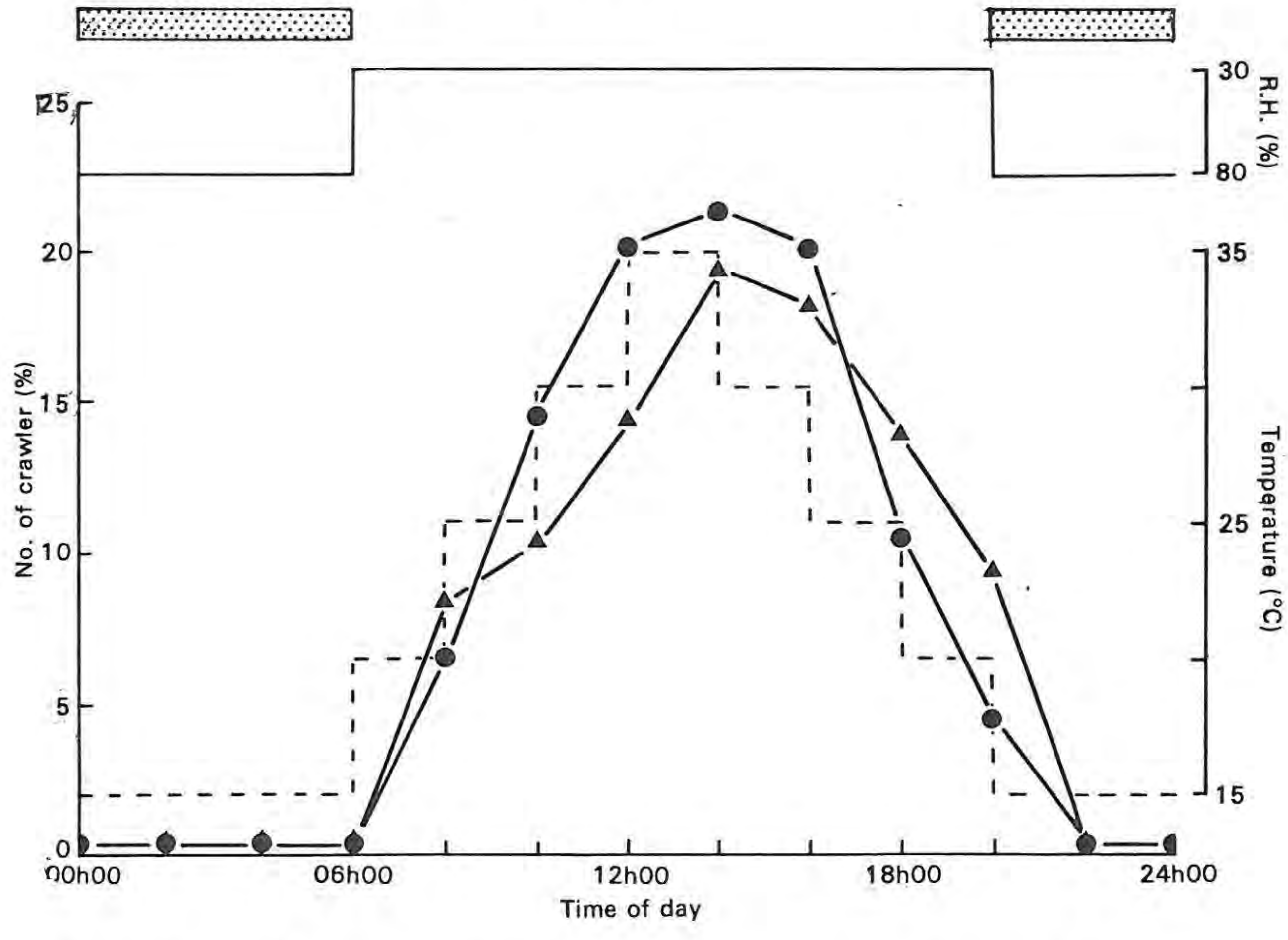


Fig. 31. Number (%) of D. austrinus crawlers wind dispersed (●) and dropping (▲) from O. aurantiaca cladodes at two hourly intervals over a five day period. Stippled area represents dark cycle. Temperature (----) and relative humidity (——) also shown. Counts between 20h00 and 06h00 are the mean two hourly values for the total catch between 20h00 and 06h00.

There was a linear increase and decrease in crawler counts which coincided with the increase and decrease in temperature. Regression analysis (Table 19) showed a significant relationship between crawler counts and temperature.

Table 19. Regression equations used to describe the number of D. austrinus crawlers dispersed from O. aurantiaca cladodes in a wind tunnel and dropping from cladodes in still air conditions with a) increasing temperatures and b) decreasing temperatures. Standard errors of slope values (S.E.(b)) and "t" values for slopes t(b) are shown.

	a	b	S.E.(b)	t(b)	P (for 3.d.f.)
a) Increasing temperature					
Wind dispersed	-494,70	36,10	4,61	-7,83	< 0,01
Drop-off	-291,10	22,82	2,68	-8,51	< 0,01
b) Decreasing temperature					
Wind dispersed	-565,90	37,3	4,13	-9,03	< 0,01
Drop-off	-287,00	24,44	4,21	-5,81	< 0,02

The regression equations were used to calculate the lower temperature thresholds for wind dispersal and drop-off of D. austrinus crawlers. The mean lower temperature threshold for the values obtained (13,7°C, 12,8°C, 15,2°C and 11,7°C) was 13,4°C. In later calculations I have therefore used 13°C as the lower temperature threshold for crawler movement.

Correlation analysis (Sokal & Rohlf 1973) showed a significant relationship between counts of wind dispersed and drop-off crawlers between 06h00 and 20h00 ($r = 0,89$; $p < 0,01$ for 1/6 d.f.). This confirmed that drop-off could be used as an estimate of the number of motile crawlers on the host plant which in turn determines the number of crawlers available for dispersal.

5.2. Effect of certain weather variables on motile crawler density.

The effect of temperature, light and humidity on the number of motile crawlers was investigated using crawler drop-off as an estimate of the number of moving crawlers. To obtain accurate hourly counts of drop-off over 24 h periods, a continuous recorder (Fig. 32) was assembled to trap crawlers falling from a group of cladodes. This comprised a side-mounted kymograph at one end of a wooden base with an additional kymograph drum

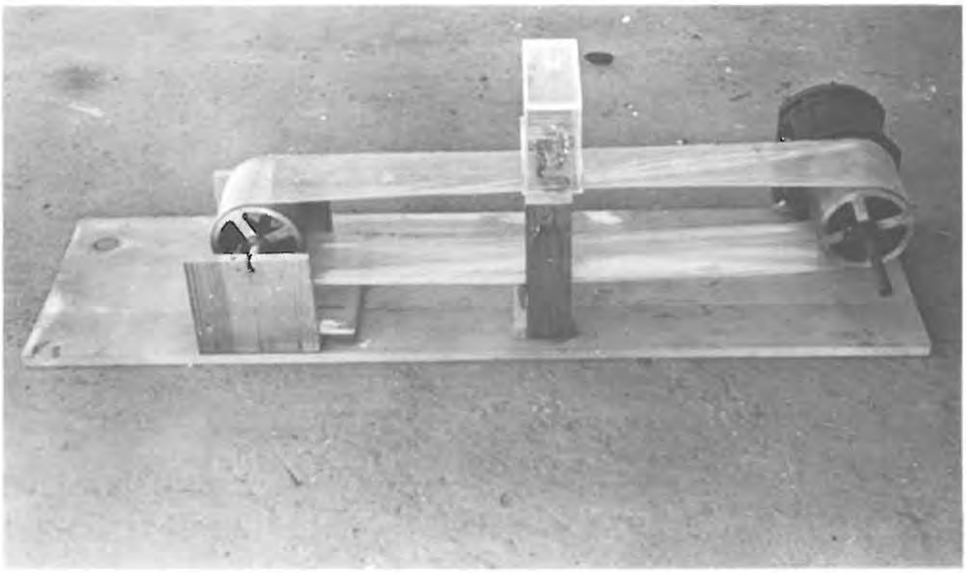


Fig. 32. Continuous recorder to measure the drop-off of D.austrinus crawlers from cladodes of the host plant O.aurantiaca over 24 h periods.

mounted on a sliding bracket at the other end. A 2,5 m long plastic belt (0,15 m wide), coated with a thin layer of vaseline, was placed over the drums. The belt was tensioned to prevent it slipping by adjusting the distance between the kymograph drums using the sliding bracket. Infested cladodes were placed in a perspex container on a stand above the belt and the kymograph switched on. After 24 h, the belt could be removed and placed on a separate set of rollers and the hourly catch (10 cm of the belt) recorded.

The absence of an endogenous rhythmicity in the number of motile crawlers during each 24 h period, which might otherwise obscure the effect of the three weather variables, was confirmed by monitoring drop-off under constant conditions of temperature, light and humidity. Five cladodes heavily infested with D.austrinus were removed from O.aurantiaca plants held under standard C.E. room conditions and placed in the perspex holder of the drop-off recorder in a C.E. room with constant conditions of temperature (25°C ± 2°C), relative humidity (50 ± 3%) and continuous light.

For the first 72 h there was an irregular pattern in the drop-off but thereafter the number of crawlers dropping from the cladodes levelled out to produce an even hourly drop-off showing no endogenous rhythmicity in the drop-off pattern (Fig. 33).

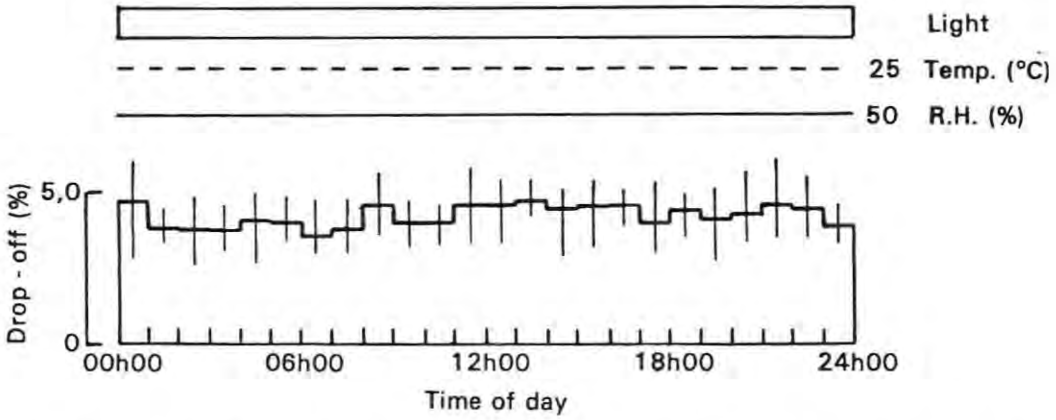


Fig. 33. Drop-off of D.austrinus crawlers from O.aurantiaca cladodes under constant conditions of light ( ), temperature (---) and relative humidity (——). Hourly means (%) and ranges (%) represent drop-off over a five day period.

The effect of light, temperature and relative humidity on crawler density was measured in a series of three experiments by changing one of the variables while the other two were held constant. A three day acclimation period preceded counts of crawler drop-off following transfer of infested cladodes maintained under standard C.E. room conditions to the drop-off recorder. Figure 34 shows the separate effects of light, temperature and relative humidity on the pattern of crawler drop-off.

The change from dark to light (Fig. 34A) and $20^{\circ}C$ to $25^{\circ}C$ (Fig. 34B) at 06h00 had a marked effect with a rapid increase in crawler drop-off to a peak between 07h00 and 09h00. Thereafter the drop-off decreased up to 20h00. Drop-off levels between 18h00 and 06h00 were much lower with a change in temperature from $25^{\circ}C$ to $20^{\circ}C$ than with a change from light to dark. Alternating relative humidity (Fig. 34C) had no effect on the rate of drop-off with an even hourly drop-off over the 24 h period.

Temperature and light are therefore important in determining the drop-off, a measure of the numbers of crawlers available for dispersal. Under field conditions, the transition between dark and light and the increase in temperature would be more gradual and the increase in the number of crawlers moving would be less abrupt. Willard (1972b) examined the effect of temperature, relative humidity, light intensity, length of photoperiod and shift in photoperiod on the rhythm of emergence of A.aurantii crawlers. He concluded that the rhythm of emergence was controlled by temperature and light with the lower thresholds for these variables at $12^{\circ}C$ and approximately 31 $lm\,ft^{-2}$ respectively. Emergence only occurred once both light intensity and temperature thresholds were reached, and therefore the effect of these environmental factors cannot be separated.

Cornwell (1958) showed the mean temperature at 9 a.m. and 3 p.m. was significantly correlated with the number of motile P.njalensis crawlers on cacao trees. The density of motile crawlers was also correlated with the number of sunlight hours. The lower threshold temperature for movement was $23{,}5^{\circ}C$, considerably higher than that for D.austrinus and A.aurantii crawlers. Cornwell (1958) considered that the high correlation between temperature and movement reflected crawler mobility and not adult reproduction i.e. the numbers of crawlers moving was not the result of increased reproduction.

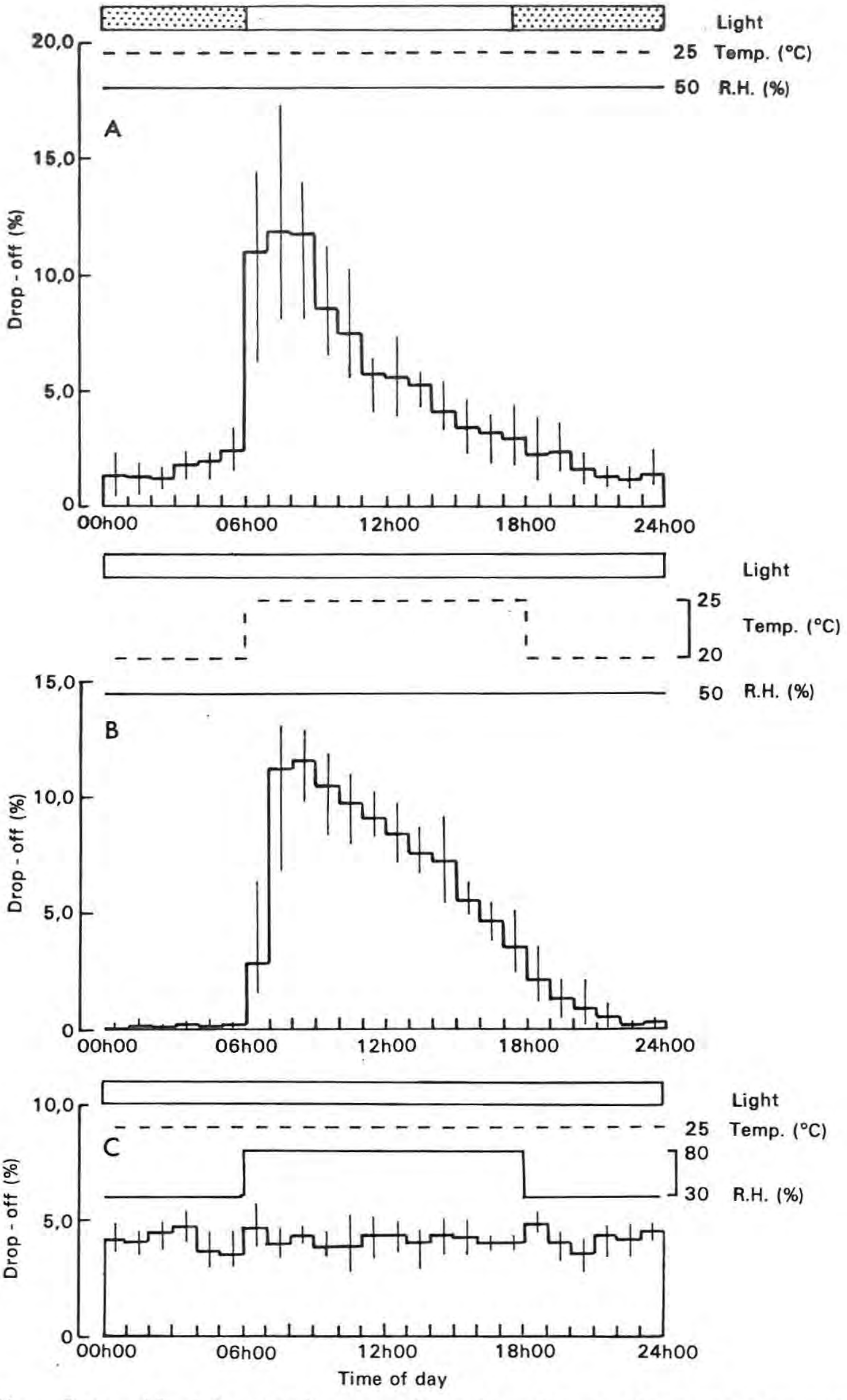


Fig. 34. Drop-off of D. austrinus crawlers from O. aurantiaca cladodes under three different C.E. room regimes. In each regime one of the weather variables (temperature (°C), humidity (R.H.%) and light) was varied while the other two were held constant. A. Variable light conditions. B. Variable temperature conditions. C. Variable humidity conditions.

Bliss et al (1935) found the time of emergence of crawlers of the camphor scale Pseudaonidea duplex Ckll. was dependant on temperature. They found little emergence below 20°C and considered that a temperature of 23°C would "not retard emergence.". However temperatures in excess of 30°C reduced the number of crawlers emerging from beneath the female.

Willard (1973a) commented on the synchronization of maximum crawler activity (09h00-11h00) with increasing wind velocities at this time, which would enhance the possibility of dispersal. Similarly, P.njalensis crawlers, which begin moving just before noon (Cornwell 1958) show maximum activity around 15h00 which coincides with the period of peak wind strength (Cornwell 1960).

The correlation between the number of D.austrinus crawlers dispersed in the wind tunnel and the drop-off of crawlers with increasing temperature and the increase mean daily wind velocities in the field (Section 4.3) suggests a similar synchronization for D.austrinus.

6. DISPERSAL FROM A SINGLE HOST PLANT

Wind dispersal of crawlers from a single host plant in the field was monitored to provide data on (6.2) the horizontal distribution of wind dispersed crawlers; (6.3) the effect of certain weather variables on the crawler dispersal; (6.4) correlation between wind velocity and direction and the pattern of crawler dispersal around the plant; and (6.5) the role of male and female crawlers in wind dispersal.

6.1. Materials and methods.

This part of the study was carried out on a vacant paddock in the grounds of the Tick Research Unit at Rhodes University during the 1977/78 summer season. The paddock provided a flat open area, free of obstructions which might otherwise have influenced wind dispersal of crawlers. The immediate area surrounding the Research Unit was free of jointed cactus and prickly pear which might otherwise have provided a reservoir of D.austrinus or D.opuntiae respectively; a source of crawlers which might have affected the results of this experiment.

Dispersal of crawlers from a single potted jointed cactus plant, heavily infested with D.austrinus, was monitored using horizontal sticky impact traps arranged in a compass pattern around the host plant (Fig. 35) placed in the centre of a 30 m square section of the paddock, mown to reduce grass cover to a minumum.

Monitoring dispersal in this way avoided problems associated with evaluating dispersal from artificially concentrated populations. Dispersal of crawlers in an area free from resident populations of D.austrinus obviated the development of marking techniques such as radioactive tracers.

The traps (Fig. 36) comprised a 29 x 21,5 cm section of hardboard to which a sheet of paper of the same dimensions was attached with paper-clips. The paper was coated with a thin film of paraffin-diluted Formex, a citrus banding material, to provide a tacky surface to trap the wind dispersed crawlers. The trap surface was raised above ground level which prevented crawlers which landed in the immediate vicinity of a trap wandering onto the sticky surface. The traps were anchored in place by driving a 15 cm nail through the leading edges.

Fig. 35. Arrangement of horizontal sticky impact traps to monitor wind dispersal of D. austrinus crawlers from a single potted jointed cactus (O. aurantiaca) plant.

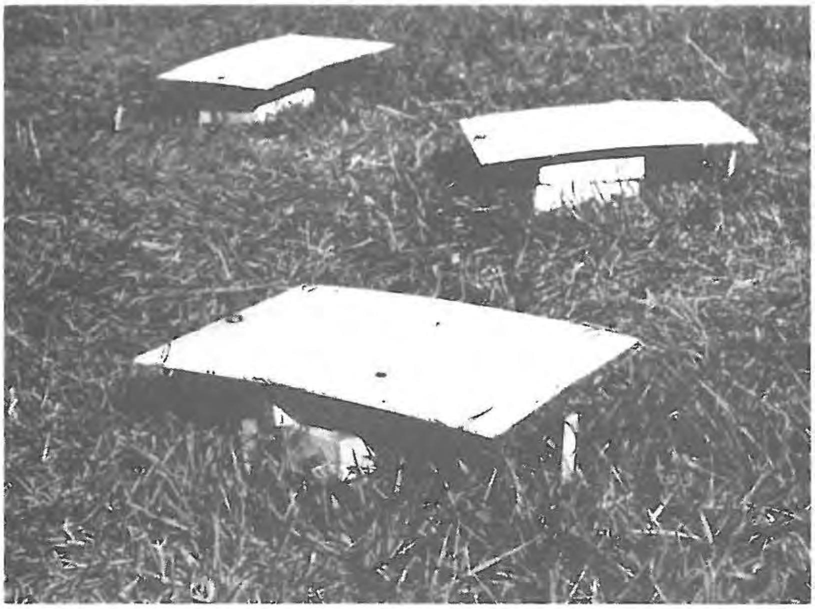


Fig. 36. Horizontal sticky impact traps (21,0 x 29,5 cm square) used to monitor dispersal of D. austrinus crawlers.

Six traps, placed a metre apart from 1 to 6 m from the 42 cm high potted plant, were set out on the four cardinal and four semi-cardinal directions, radiating from the plant (Fig. 37). This pattern provided 8 traps on each of six concentric rings, each a metre apart, around the host plant.

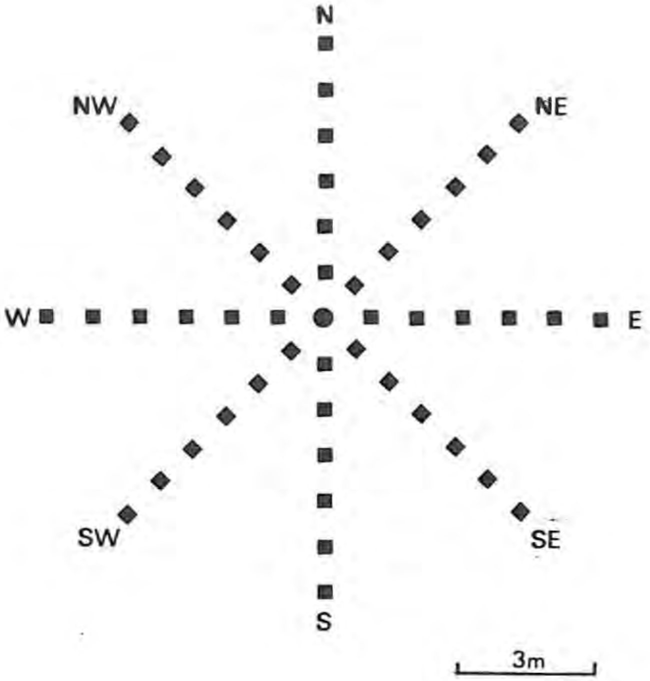


Fig. 37. Pattern of traps (■) used to monitor wind dispersal of D.austrinus crawlers from a single host plant O.aurantiaca (●).

The numbers of D.austrinus crawlers wind dispersed from the source plant were recorded over a 20 day period. For the first 10 days the traps on the 1 m ring around the host plant were changed every 2 h from 06h00 to 20h00. The remaining traps were changed at 06h00 each day. Thereafter all traps were changed at 06h00 on the fifteenth and twentieth days. The Formex covered paper on each trap was removed from the hardboard base, checked using a binocular microscope and the catch of crawlers on each trap recorded. Crawlers recovered from the outer margin of the sticky surface were not counted to ensure that crawlers which might have walked onto the traps were excluded.

Drop-off of crawlers was measured over the same period in a separate but nearby area. Ten infested cladodes were placed on a small metal frame over a vaseline-covered perspex sheet, sheltered from air currents in a large open topped perspex box. Counts of crawlers which dropped off the cladodes were taken every 2 h from 06h00 to 20h00 over the first ten days of the experiment.

A thermohygrograph, placed in a Stevenson screen sited near the experimental area, provided continuous recordings of temperature and humidity. Continuous recordings of wind velocity and direction were obtained using a Lambrecht (Type 1482) anemometer, mounted with the whirling cups 60 cm above ground level.

6.2. Horizontal distribution of *D.austrinus* crawlers.

Crawlers were wind dispersed in all four cardinal and four semi-cardinal directions during the 20 day experiment, with catches on all six traps in each direction. Table 20 shows the catches on each trap for the first and second 10 day periods of the experiment, together with total catches for each trap in all directions.

Highest catches were recorded on traps on the north axis with lowest recoveries from traps on the south-east axis. The number of wind dispersed crawlers decreased rapidly from 1 to 6 m in all directions. As all traps were of equal area the term "density" is used in the following test.
In analysing the data in Table 20 it is necessary to digress and consider how these sorts of data have been treated and analysed in the literature.

Several methods have been used to measure and describe the dispersal of a variety of actively and passively dispersing organisms (Southwood 1975a). The most common method of analysis is the examination of fall-off in the density of dispersed individuals with increasing distance from the point or area of origin. Generally, the relationship between density and increasing distance is graphically expressed as a decaying exponential curve, as the drop in density is at first steep and then levels off at greater distances (Wadley 1957). Where dispersal is monitored in an area where the species under study occurs naturally, the density may not reach zero but remains at "some low level characteristic of the region" (Wadley & Wolfenbarger 1944).

This pattern of dispersal has been shown for actively dispersing insects (Parker 1916 ; Dobzhansky & Wright 1943; Wadley & Wolfenbarger 1944; Kettle 1951; Yates *et al*. 1952; Baldwin *et al*. 1958; Gillies 1961; MacLeod & Donnelly 1963; Wallace 1966; Mowat & Coaker 1968; Hawkes 1972;

Table 20. Catches of wind dispersed *D.austrinus* crawlers recovered from horizontal sticky impact traps placed a metre apart from 1 - 6 m in the four cardinal and four semi-cardinal directions. around a single host plant (*O.aurantiaca*).

Direction	Distance (m)					
N	1	2	3	4	5	6
Days 1 - 10	317	50	69	40	20	8
Days 11 - 20	222	44	68	28	29	4
Total	539	94	137	68	49	12
NE						
Days 1 - 10	198	42	22	17	11	4
Days 11 - 20	163	23	17	26	4	5
Total	361	65	39	43	15	9
E						
Days 1 - 10	59	10	5	5	1	1
Days 11 - 20	61	10	9	8	3	3
Total	120	20	14	13	4	4
SE						
Days 1 - 10	44	10	2	4	1	1
Days 11 - 20	61	13	12	3	3	3
Total	105	23	14	7	4	4
S						
Days 1 - 10	153	23	6	4	1	1
Days 11 - 20	79	16	14	8	4	2
Total	232	39	20	12	5	3
SW						
Days 1 - 10	89	18	7	4	1	3
Days 11 - 20	59	27	7	3	1	1
Total	148	45	14	7	2	4
W						
Days 1 - 10	118	51	17	4	2	1
Days 11 - 20	74	36	6	8	6	1
Total	192	87	23	12	8	2
NW						
Days 1 - 10	189	40	26	22	10	5
Days 11 - 20	100	32	16	12	9	5
Total	289	72	42	34	19	10

Shepard et al. 1974; Wolfenbarger 1975; Wakid & Shoukry 1976 and Reissig 1977); passively dispersed insects, tick larvae and mites (Quayle 1916; Brown 1958; Cornwell 1960; Hoelscher 1967; Lewis 1970; Greathead 1972 and Willard 1974), isopods (Paris 1963), viruses (Frampton et al. 1942 and Gregory & Read 1949), pollen (Raynor & Ogden 1965), fungii (Wilson & Baker 1946a, b) and seeds (Watkinson 1978).

The drop in density with increasing distance from the point or area of origin or release can be attributed to two factors. Firstly, the density of the dispersed organism is "diluted" by the increasing area over which dispersal occurs as distance increases from the origin or release point (Wadley & Wolfenbarger 1944; Kettle 1951; Ito & Miyashita 1965 and Southwood 1975a). Secondly, there is a "loss" of individuals with increasing distance from the dispersal point or area attributable to various causes. For actively dispersing insects these include mortality, and the tendency to stop on locating a suitable site for feeding, shelter etc. (Wadley & Wolfenbarger 1944 and Southwood 1975a). For passively dispersed insects the "loss" factor is accounted for by individuals sinking to the ground during dispersal.

A number of mathematical functions have been derived to describe the exponential relationship between dispersal density and distance (Table 21). The normal practice in the analysis of dispersal is to fit one or more functions to dispersal data and the equation providing the smallest residual variance is selected as the best descriptor of the data.

In general these functions, regression equations relating density (N) at varying distances (X), serve only as an empirical description of the dispersal data. Wadley and Wolfenbarger (1944) included a third parameter "c" in their model ($N = a + b \log X + {}^{c}/X$) and Wadley (1957) suggested the terms "b log X" and "${}^{c}/X$" represented loss and dilution factors respectively. However as Taylor (1978) pointed out the use of the logarithm of distance (X) breaks "...the common sense boundary conditions of a finite density at zero distance and non negative densities at all distances.".

Willard (1974) used the equation $\log N = \log a - b X$ as the model to describe the horizontal distribution of wind dispersed crawlers, mature

Table 21. Mathematical functions used to describe the relationship between the dispersal density of a variety of insects, isopods, pollen, fungii and viruses and the dispersal distance. N is the number of individuals with dispersal distance X while a, b and c are constants. In cases where the authors have used different letters of the alphabet to denote number and distance these have been changed to N and X respectively for consistency.

Function	Organism	Authors
$N = a + bX$	Coleoptera	Wadley and Wolfenbarger (1944)
$N = a + b \log X$**	Coleoptera	Wadley and Wolfenbarger (1944)
	Isopoda	Paris (1963)
	Insecta	Wolfenbarger _et_ _al_. (1976)
$N = a + b \log X + {}^{c}/X$**	Coleoptera	Wadley and Wolfenbarger (1944)
	Hemiptera	Shepard _et_ _al_. (1974)
$N = a + {}^{c}/X$**	Isopoda	Paris (1963)
$N = aX^{b}$	Pollen	Raynor and Ogden (1965)
	Homoptera	Hoelscher (1967)
$N = aX^{-P}$*	Fungii	Wilson and Baker (1946b)
$\log N = a + bX$**	Viruses	Gregory and Read (1949)
	Diptera	Kettle (1951)
	Diptera	Gillies (1961)
	Isopoda	Paris (1963)
	Diptera	Mowat and Coaker (1968)
	Diptera	Riessig (1977)
$\log N = a + b \quad X$**	Diptera	Wallace (1966)
	Diptera	Hawkes (1972)
	Homoptera	Willard (1974)
$\log N = \log a + b \log X$**	Fungii	Wilson and Baker (1946a)
	Diptera	MacLeod and Donnelly (1963)
	Isopoda	Paris (1963)
	Pollen	Raynor and Ogden (1965)
$\log N = a + {}^{c}/X$**	Not tested	Taylor (1978)
$\log N = a + bX^{2}$**	Diptera	Cited by Taylor (1978) for Dobzansky and Wright (1943)

* a and P constants depending on wind velocity.

** Function used in a review by Taylor (1978).

females and adult males of the red scale A.aurantii. His study was limited to monitoring dispersal in a single direction and he concluded that "A repetition of the experiments for red scale or other organisms might allow the development of a more general equation in which the square root was replaced by a parameter, c, giving an equation $\log y = \log a - bX^c$, or $y = a.10 \exp(-bX^c)$ with more general application.". The difference in the horizontal distributions of D.austrinus crawlers (Table 20) in the eight directions for which dispersal was monitored, precluded the use of any single function (Table 21) as a general description for dispersal in all directions.

Taylor (1978) reviewed eight of the functions listed in Table 21 (marked with a double asterisk) and pointed out that these equations fall into two distinct groups: (also see Table 22).

(a) $N = a + bf(X)$

(b) $\log N = a + bf(X)$

He emphasised the distinction between the two groups in that in group (a) the rate of change of dispersal density with distance is independant of N while in group (b) it is proportional to N. Taylor (1978) listed the eight functions, with the group(b) functions rewritten to enable direct comparison with the group(a) functions (Table 22). Using a routine for minimising non-linear sums of squares, Taylor (1978) fitted all eight functions to the data obtained by eight workers for the dispersal of different species of actively dispersing insects and found that at least one of the group(b) functions provided a better description of the eight sets of dispersal data than any of the group(a) equations. He pointed out that the term f(X) in the general form of the group(b) equations (Table 22) was "...a special case of the form $f(X) = X^c$, providing a general model,

$$N = \exp(a + bX^c)$$

with the statistical form $N_i = \exp(a + bX_i^c) + \epsilon_i \quad \epsilon_i \sim N(0\ o)$.

Iterative fitting of this general model, using the method of Powell (1967) for minimising the non-linear residual deviations ($\sum\epsilon_i^z = \sum[N_i = \exp(a + bX_i^c)]^2$), provided Taylor (1978) with a better description of one of the eight sets of dispersal data than that provided by the best fitting function of group(b).

Table 22. Eight models relating dispersal density to distance fitted by Taylor (1978) to dispersal data of eight species of insects. The general form for the two groups into which the models fall are shown on the right hand side of the table (after Taylor 1978).

	General form
Group (a)	
$N = a + {}^{c}/X$	$N = a + bf(X)$
$N = a + b \ln X$	
$N = a + b \ln X + {}^{c}/X$	
Group (b)	
$N = \exp(a + {}^{c}/X)$	$N = \exp(a + bf(X))$
$N = \exp(a + b \ln X)$	
$N = \exp(a + b \quad X)$	
$N = \exp(a + bX^2)$	
$N = \exp(a + bX)$	

Taylor (1978) concluded that the inclusion of the parameter c in the general model provided a behavioural component in the function so that this model served as more than just an empirical description of dispersal data. The parameter c gave a measure of the degree of attraction or repulsion between dispersing individuals. With reference to Figure 38, if $c = 2$ (i.e. $N = \exp(a + bX^2)$) dispersal would be random as the resulting

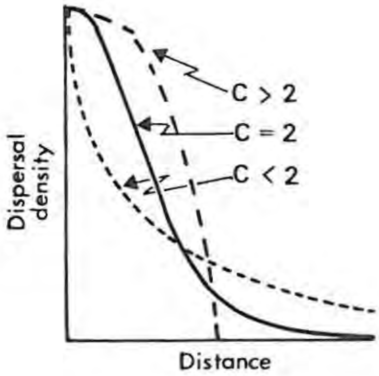


Fig. 38. Three curves relating dispersal density and distance to illustrate the suggested (Taylor 1978) function of the parameter c in the general equation $N = \exp(a + bX^c)$ in relation to attraction ($c \doteq > 2$) and repulsion ($c < 2$) between dispersing individuals.

dispersal curve would resemble a curve for normal distribution with its mode as the origin of dispersal (zero distance). In this case there would be neither attraction nor repulsion between individuals. Where c was greater than 2, the initial portion of the curve would be flattened suggesting attraction between dispersing individuals was limiting dispersal. A c value less than 2 would suggest repulsion between individuals, enhancing dispersal distances.

The general model developed by Taylor (1978) has provided a function with more general application than those used previously (Table 21) for the analysis of dispersal. D.austrinus crawlers, like other passively dispersed organisms, will not show a behavioural interaction during dispersal. Therefore the parameter c must reflect a component other than behaviour. Only air currents can affect the pattern of horizontal distribution of D.austrinus crawlers and will act as a repulsive force enhancing dispersal. This suggested that fitting the general model of Taylor (1978) to the dispersal data (Table 20) for D.austrinus crawlers should provide c values less than 2 and that these values might be correlated with the mean wind velocity.

Two computer programs were written to fit the general model of Taylor (1978) to the density-distance data for dispersal of D.austrinus crawlers. The first program (SINA, Appendix 2) provided a mechanical fit of the general equation by repeated linear regression, increasing the value of c from 0,01 to 2,00 in steps of 0,01. The regression which provided the smallest residual deviation (residual mean square) determined the value of a, b and c.

The second program (CTER, Appendix 3) provided an iterative fit of the general equation using two subroutines (Auxplex and Flexplex) for non-linear optimization, whose coding was developed by Dr P.D. Terry (Applied Mathematics Department, Rhodes University, Grahamstown) from a program in Himmelblau (1972) based on an algorithm of Nelder and Mead (1964). Both programs, with example data input and output formats, are shown in Appendices 2 and 3.

The data of Dobzhansky and Wright (1943) for dispersal of Drosophila pseudoobscura Frol. shown in Taylor (1978), were used to check the results obtained using both programs. The parameters a, b and c together with the regression sum of squares and residual mean squares obtained were compared with those obtained by Taylor (1978) who used the method of Powell (1964) for minimising the residual deviations (Table 23).

Table 23. Comparison of intercept (a), slope (b) and X eponent (c) together with the regression sum of squares (REG.SS.) and residual mean squares (RES.MS) obtained using three different computer programs to fit the function N = exp (a + bX^c) to the density distance data of Dobzhansky and Wright (1943) for Drosophila pseudoobscura Frol. dispersal.

Program	Method of fit	a	b	c	REG.SS	RES.MS
Taylor (1978)	Iterative	3,6953	-0,2433	0,4994	15,8117	0,9301
SINA	Mechanical	3,7327	-0,2747	0,4800	16,2902	0,9582
CTER	Iterative	3,6950	-0,2432	0,4996	15,8125	0,9301

The program CTER, which provided an iterative fit of the general equation, required estimated values of a, b and c to set up the initial approximations of the location of the minimum residual deviation of the function. The program SINA provided very good approximations of these values for the data of Dobzansky and Wright (1943). The estimation of these values often causes problems using non-linear optimising routines. The values obtained using CTER were very similar to those obtained by Taylor (1978) (Table 23).

Analysis of the dispersal data for D.austrinus crawlers (Table 20) was carried out by obtaining the values of a, b and c for the catch-distance data in each direction (N, NE, E, SE, S, SW, W and NW) for the two ten-day periods of the dispersal experiment using the program SINA. These values were then incorporated in the program CTER to obtain an iterative fit for the general model. Initially the true distance values (1 - 6 m) were used in the analysis so that the intercept value a, the estimation of crawler density at zero distance, was in fact an extrapolated value. The immense range (359 to 351^{85}) obtained for the intercept values, using the true distances clearly excluded extrapolation of the data to zero distance. Analysis was restricted over the distance 1 - 6 m by reducing all distances by 1 m and using distance values 0 - 5 m in the analysis.

Table 24 shows the values of the parameters a, b and c obtained using the computer programs SINA and CTER to fit the general equation (Taylor 1978) to the density-distance data for D.austrinus crawler dispersal (Table 20)

Table 24. Values for the intercept (a), slope (b) and distance exponent (c) obtained by fitting the general equation (Taylor 1978), $N = \exp (a + bX^c)$, to the density-distance data of D.austrinus crawler dispersal using a mechanical fit (Program SINA) and an iterative fitting (Program CTER). Results are shown for the first and second ten-day periods dispersal was monitored. Values of the significance test $Fs = s^2y*s^2y.X$ (Sokal & Rohlf 1973) are shown for 1/3 d.f. All Fs values are significant at the 1% level.

First ten-day period

Direction	Program	a	b	c	Fs
North	SINA	5,7911	-1,4408	0,50	125,8
	CTER	5,7586	-1,6110	0,3050	171,8
North-East	SINA	5,2921	-1,4528	0,56	1921,0
	CTER	5,2883	-1,5478	0,4768	4629,9
East	SINA	4,0799	-1,6421	0,57	1016,4
	CTER	4,0774	-1,7630	0,4552	1576,7
South-East	SINA	3,7795	-1,7121	0,51	376,1
	CTER	3,7846	-1,5381	0,6257	496,4
South	SINA	5,0321	-2,0110	0,60	6120,0
	CTER	5,0304	-1,9045	0,6865	16071,6
South-West	SINA	4,4890	-1,7648	0,52	1506,8
	CTER	4,4887	-1,6101	0,6158	3632,1
West	SINA	4,7704	-1,0005	1,00	493,4
	CTER	4,7707	-0,8384	1,2196	18222,7
North-West	SINA	5,2541	-1,3918	0,55	657,2
	CTER	5,2416	-1,5143	0,4294	1325,2

Second ten-day period

Direction	Program	a	b	c	Fs
North	SINA	5,4715	-1,1825	0,62	51,5
	CTER	5,4019	-1,3483	0,3427	69,7
North-East	SINA	5,1122	-1,7391	0,42	197,5
	CTER	5,0937	-1,8681	0,2676	238,4
East	SINA	4,1209	-1,6266	0,37	510,6
	CTER	4,1108	-1,7113	0,2871	624,0
South-East	SINA	4,1113	-1,4729	0,49	328,5
	CTER	4,1106	-1,4579	0,4634	336,2
South	SINA	4,3875	-1,3515	0,58	337,8
	CTER	4,3691	-1,4988	0,4251	599,7
South-West	SINA	4,0756	-1,0559	0,90	170,4
	CTER	4,0783	-0,7931	1,3394	2325,9
West	SINA	4,3148	-0,9970	0,84	93,1
	CTER	4,3076	-0,7767	1,2650	153,9
North-West	SINA	4,6092	-1,1740	0,56	3113,3
	CTER	4,6055	-1,1608	0,5704	3228,2

for the first and second ten-day periods of the dispersal experiment. The significance of the regression, the portion of the variance in N explained by regression on X, was tested using an Fs value (Sokal & Rohlf 1973), where Fs = regression mean square/residual mean square ($Fs = s^2y/s^2y.X$). The Fs values obtained for each regression were compared with the critical values of the F distribution (Rohlf & Sokal 1969) at the 1% and 5% levels for 1/3 d.f.

The regressions on all sets of density-distance data were significant at the 1% level and in all cases the iterative fit provided lowest residual deviations. The high Fs values clearly demonstrate that the general equation, $N = \exp (a + bX^c)$ (Taylor 1978), provides a good description of crawler dispersal in all directions around the host plant.

The curvilinear plot of the horizontal distribution of D. austrinus crawlers over the two ten-day periods are shown in Figures 39 and 40. The curves were fitted using the parameters a, b and c in the general equation obtained using the program CTER (Table 24) to calculate the estimated catch densities. It must be noted that the distance values shown in these figures are the true distances and not the X-1 values used in the analysis.

There is a clear exponential decrease in the density of dispersed crawlers with increasing distance from the host plant, as shown for many other dispersed organisms. Comparison of the curves and distance exponent values, parameter c, for the iterative fit (Table 24) show the curves become increasingly leptokurtic as the c values decrease. The average wind velocity in each direction (Table 25) obtained from analysis of the anemometer recordings (Section 6.3) are significantly correlated with the c values obtained using both the mechanical fit ($r = -0,691$; $p < 0,01$ for 1/14 d.f.) and the iterative fit ($r = -0,767$; $p < 0,01$ for 1/14 d.f.) of the general equation. From the negative correlation, an increase in the mean wind velocity decreases the c value.

This confirms that inclusion of the parameter c in the general equation incorporates a weather component (wind velocity) in the model describing the density-distance relationship for D. austrinus crawler dispersal. This work also provides confirmation of the suggestions of Taylor (1978) with regard to the functioning of the parameter c in his general model.

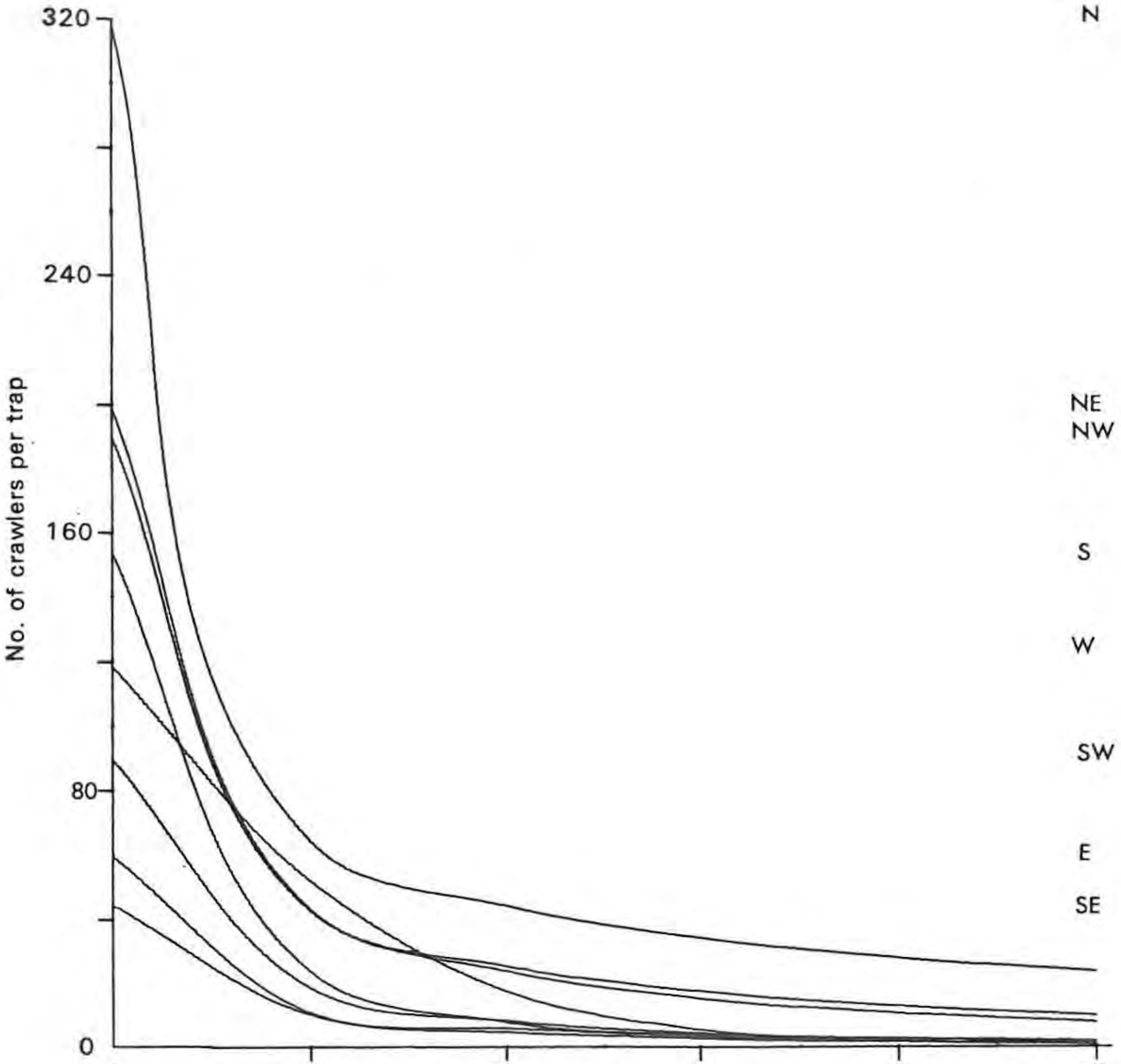


Fig. 39. Horizontal distribution of D.austrinus crawlers shown by curves obtained by using an iterative fit of the general function N = exp (a + bX^c) to the density-distance data for the first ten-day period of the dispersal experiment. Direction of dispersal is shown opposite the intercept point for each curve.

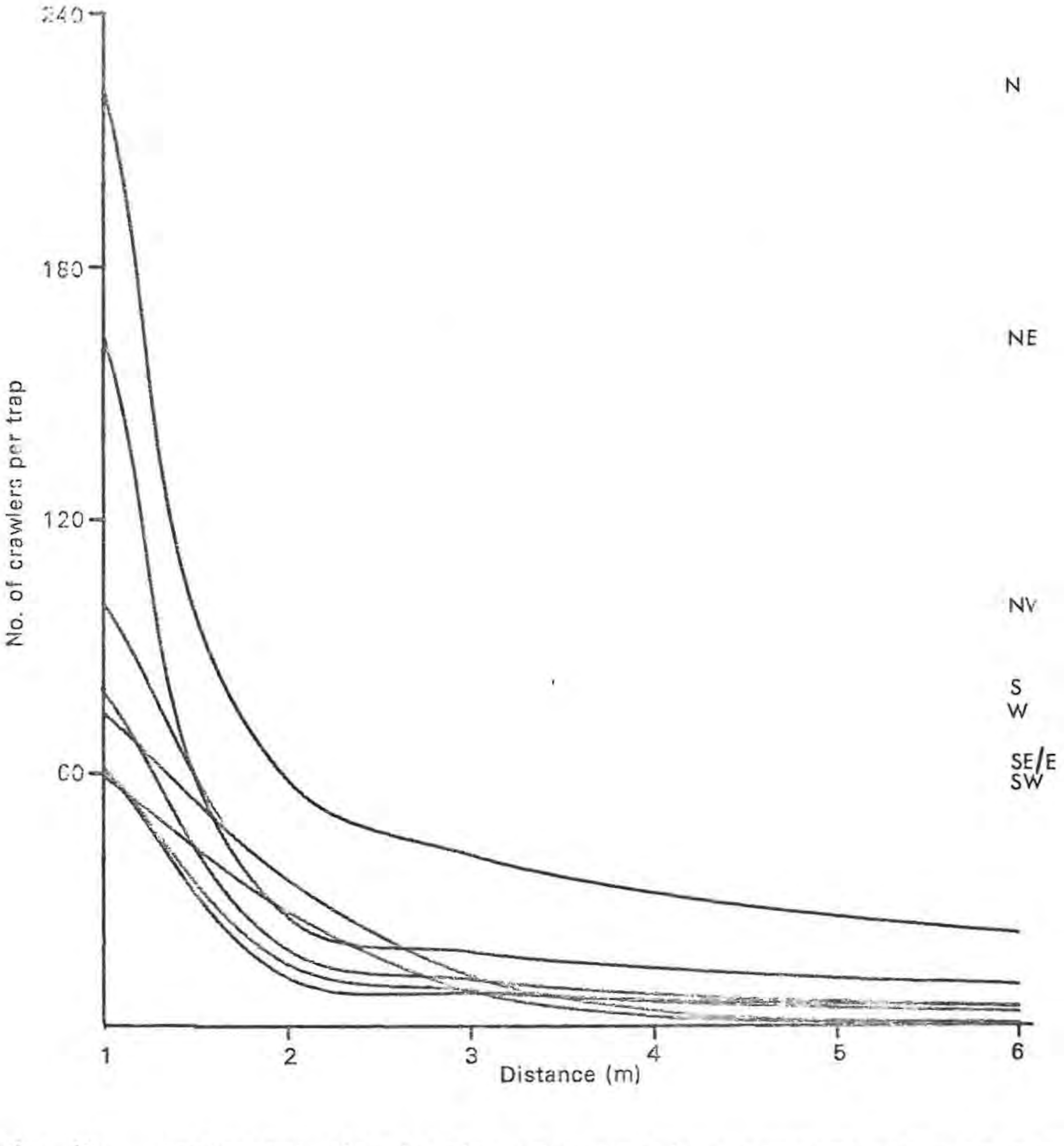


Fig. 40. Horizontal distribution of D. austrinus crawlers shown by curves obtained by using an iterative fit of the general function N = exp (a + bX^c) to the density-distance data for the second ten-day period of the dispersal experiment. Direction of dispersal is shown opposite the intercept point for each curve.

Willard (1974) provided linear plots of the dispersal data for A.aurantii crawlers and using analysis of variance for replicated regression was able to comment on proportions of the catch at varying distances from week to week i.e. changes in slope (parameter b). However the overall dispersal distances for D.austrinus are so small that significant differences between the proportion of catch in each direction are not important and the curvilinear plot is sufficient for descriptive purposes.

Table 25. Average wind velocities (m sec^{-1}) in four cardinal and four semi-cardinal directions in which dispersal of D.austrinus crawlers was monitored for two ten-day periods. Wind directions have been switched 180° for direct comparison with the catch data.

	N	NE	E	SE	S	SW	W	NW
1st 10 days	1,79	1,90	1,97	1,75	1,54	1,28	1,32	1,54
2nd 10 days	1,83	1,87	1,91	1,74	1,47	1,27	1,33	1,64

The plot of the horizontal distribution of D.austrinus crawlers (Figs 39 and 40) shows that there was a rapid drop in dispersal densities. A measure of the dispersal is provided by calculation of the mean dispersal distance in each direction. The calculation must include allowance for dilution, as the traps represent an increasingly smaller area of the circumference with increasing distance (X) from the host plant. From 2 - 6 m the circumference increases by factor of 2 - 6x the circumference at one metre. To convert catches (N) to numbers of crawlers (Nc) on the arc of the circumference represented by the traps in each direction the catches (N) are multiplied by the dilution factor. The mean dispersal distances $\bar{x}$ (Table 26) were calculated from the formula

$$\bar{x} = \Sigma(Nc_i \; X_i) / \Sigma Nc_i$$

Table 26. Mean dispersal distance (m) of D.austrinus crawlers in the four cardinal and four semi-cardinal directions for the two ten-day periods of the dispersal experiment

	N	NE	E	SE	S	SW	W	NW
1st 10 days	2,75	2,54	2,28	2,34	1,74	2,28	2,06	2,65
2nd 10 days	2,93	2,67	2,85	2,69	2,62	2,16	2,53	2,89

Although the values in directions where dispersal occurred beyond 6 m are an underestimate of the mean dispersal distance, these results emphasise the very limited dispersal from the low host plant *O.aurantiaca*.

The measured dispersal distances of crawlers of coccoid species infesting trees or high grass (Table 27) are many times greater than that measured for *D.austrinus* crawlers. The host plants of these species provide an "elevated platform" for dispersal thus enhancing the dispersal potential.

The measured dispersal distances of *D.austrinus* crawlers are an underestimate as the mean wind velocities which occurred during the experiment (Table 25) were low with the maximum hourly wind velocity only 4,17 m sec^{-1}. However even with wind velocities 2 - 3 times those measured, the dispersal distances would still be far less than that measured for other species.

Table 27. Measured dispersal distances of crawlers of coccoid species found on trees and high grass. The approximate height of the host plants is given.

Species	Dispersal distance	Host plant	Host plant height	Author
Saissetia oleae Bern.	150 m	Citrus	± 5 m	Quayle (1916)
Toumeyella numismaticum (Pettit and McDaniel)	ca.3400 m	Pine	± 20 m	Rabkin and Lejeune (1954)
Phenacaspis pinifoliae (Fitch)	ca.2400 m	Pine	± 20 m	Brown (1958)
Pseudococcus njalensis Laing	51 m	Cacao		Cornwell (1960)
Coccus hesperidum L.	55 m	Citrus	± 5 m	Hoelscher (1967)
Parlatoria pittospori Mask.	170 m	Apple	± 5 m	Timlin (1964)
Physokermes hemicryphus Dalm	500 m	Spruce	± 20 m	Pechhaker (1971)
Aulacaspis tegalensis (Zhnt.)	1000 m	Sugar cane	± 3 m	Greathead (1972)
Quadraspidiotus perniciosus Comst.	25 m	Apple	± 5 m	Maksimova (1973)
Aonidiella aurantii (Mask.)	312 m	Citrus	3.7-6.1	Willard (1974)

These results confirm that the dispersal potential of *D.austrinus* crawlers in comparison to other coccoid species is very poor and unlikely to extend much beyond 10 m from a plant in the open. This distance may be reduced under natural conditions because surrounding vegetation will reduce wind velocities and effective release height.

6.3. Dispersal in relation to weather variables and crawler movement.

The number of crawlers trapped on the 1 m ring of traps, which were changed at 2 h intervals from 06h00 to 20h00 for the first ten days of the experiment, provided an estimate of the total number of crawlers dispersed by wind from the host plant. The crawler drop-off, monitored separately but simultaneously (see section 6.1), reflected the number of motile crawlers on the host plant (crawler movement). These values, together with the two hourly temperature and relative humidity recordings and windrun, are represented graphically in Figure 41. Anemometer recordings of the windrun (km) for each hour were not converted to wind velocities expressed in m sec^{-1}, as the windrun values were adequate for purposes of analysis.

The catch and drop-off values at 06h00 each day represent the total for the preceding 10 h (20h00 to 06h00) as no counts were made at night.

A significant feature of these results is the very low number of crawlers dispersed at night with only 0,51% of crawlers dispersed between 20h00 and 06h00 over the 10 day period. 95,39% of the total number of crawlers were dispersed between 08h00 and 18h00 with peak dispersal (36,35%) between 14h00 and 16h00. The daily number of wind dispersed crawlers varied markedly from day to day, as did the pattern of crawler movement.

The importance of the recorded weather variables (temperature, relative humidity and wind) and crawler movement in relation to wind dispersal was determined using multiple regression analysis (Snedecor & Cochran 1967). This method of analysis demonstrates the linear dependance of a dependant variable on a number of independant variables. In this case the dependant variable was the catch on the ring of 1 m traps while the three weather variables and crawler movement formed the independant variables. A computer program for multiple regression, developed by Kim and Kohout (1975) was used to analyse the dispersal data. With virtually no dispersal at night, analysis was restricted to the period 06h00 to 20h00, and with trap counts every 2 h over the 10 day experimental period, 70 data cases were used in the analysis.

As the catches of wind dispersed crawlers and crawler drop-off were recorded every 2 h the hourly recordings of temperature and windrun were summated to give 2 h values. For more accurate statistical analysis temperature recordings were expressed as hour degrees above 13°C

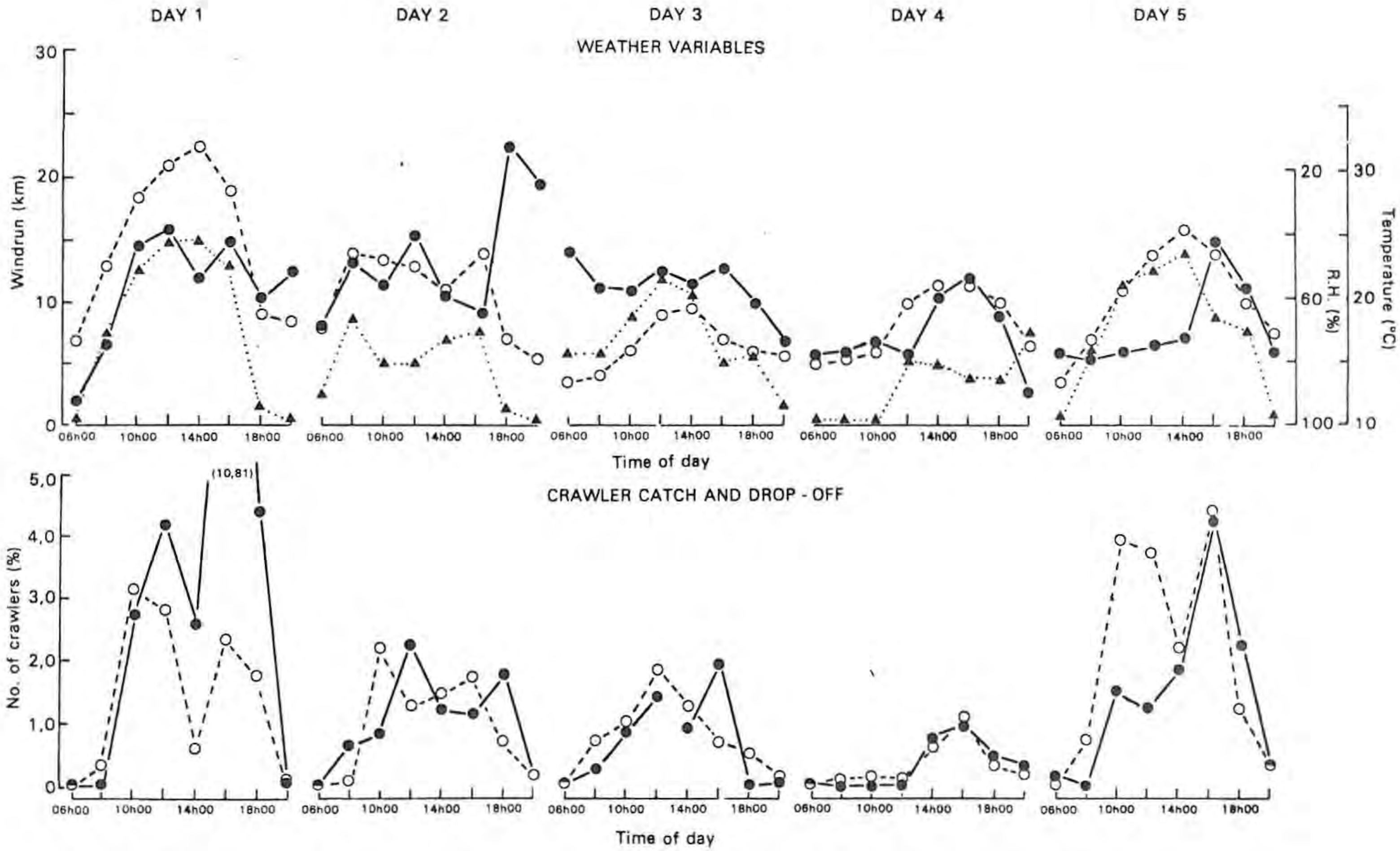


Fig. 41A. Weather variables (top figures); temperature (○---○); % relative humidity (▲·····▲) and windrun (●—●). Crawler catch (bottom figures); number of D. austrinus crawlers dropping from O. aurantiaca cladodes (○---○) and wind dispersed (●—●) over a five day period (25.01.78 - 30.01.78). See Fig. 45B for continuation of recordings for the following five day period.

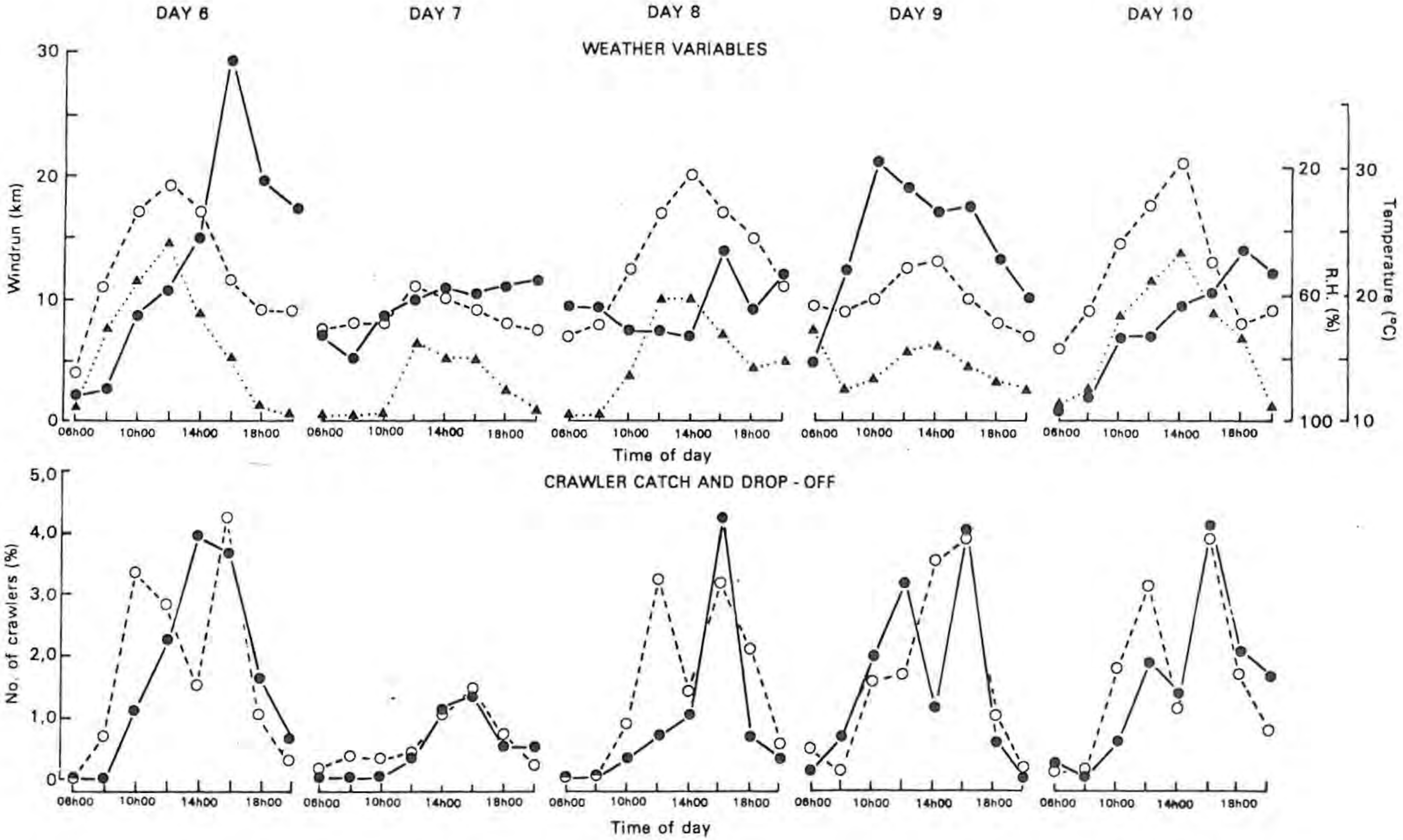


Fig. 41B. Weather variables (top figures); temperature (○---○), % relative humidity (▲·····▲) and windrun (●——●). Crawler catch (bottom figures); number of D. austrinus crawlers dropping from O. aurantiaca cladodes (○---○) and wind dispersed (●——●) over a five day period (31.01.78 - 04.02.78). See Fig. 45A for recordings for the preceding five day period.

($h^o > 13^oC$), the estimated lower temperature threshold for crawler movement. Relative humidity was expressed as the mean for each 2 h period. The two hour recording for the total crawler catch on the 1 m ring of traps, crawler drop off, temperature, relative humidity and windrun are shown in Appendix 6. Rain fell on two occasions during the analysis (06h00 - 12h00 on Day 4 and 06h00 to 10h00 on Day 7) but it was very light and these periods have been included in the analysis.

The relative importance of the individual weather variables and crawler movement in relation to wind dispersal of crawlers was assessed using a "forward (stepwise) inclusion" method (Kim & Kohout 1975) termed "step up" method by Snedecor and Cochran (1967), in the computer program. This is a method of ordering the sequence of variable entry in the regression equation on the amount of variance in the dependant variable (catch) explained by each of the independant variables (weather variables and crawler movement). The variable which accounted for the greatest amount of catch variance was the first variable entered in the equation. Thereafter the variable order was established by entry of the variable which accounted for the greatest amount of the catch variance unexplained by variables already in the regression equation.

The results of the multiple regression analysis on the dispersal data are shown in Table 28. At the top of the table there is a matrix of simple correlation coefficients for all the variables in the analysis. The catch is significantly correlated ($p < 0{,}01$ for 1/68 d.f.) with each of the weather variables and crawler movement, while temperature, humidity and movement are all significantly intercorrelated ($p < 0{,}01$ for 1/68 d.f.). This feature of multicollinearity between these three variables has an important bearing on the use of these variables in the multiple regression analysis.

The remaining portion of Table 28 shows the multiple regression coefficients and the analysis of variance (Anova) tables for the stepwise inclusion of variables in the multiple regression analysis. The central part of the table shows the partial regression coefficients of all the variables included in each step together with standard errors and the F ratios which provide a measure of the significance of the contribution of each variable to the regression. Standard partial regression coefficients (beta coefficients), in which the intercept = 0, are shown. The variable readings used in the calculation of these coefficients are standardised

Table 28. Simple correlation coefficients and multiple regression coefficients relating the two hourly catch of wind dispersed D.austrinus crawlers between 06h00 and 20h00 with three weather variables and the number of motile crawlers. ** Significant at 1% level; * significant at 5% level.

Simple correlation coefficients (n = 70)

	Catch	Temperature	Windrun	Humidity	Crawler movement
Catch	1,000	0,592**	0,445**	-0,520**	0,575**
Temperature		1,000	0,121	-0,774**	0,580**
Windrun			1,000	-0,018	0,276
Humidity				1,000	-0,603**

Multiple regression analysis (n = 70)

Dependant variable: Catch

Independant variable/s entered

		Intercept	Partial regression coefficient (b)	Standardised partial regression coefficient (beta)	S.E. (b)	F ratio	d.f.
Step (1)	Temperature	-6,073	1,357	0,592	0,224	36,75**	1/68
Step (2)	Temperature	-21,386	1,252	0,547	0,201	38,86**	2/67
	Windrun		1,525	0,379	0,353	18,69**	
Step (3)	Temperature	-19,328	0,938	0,409	0,237	15,59**	3/66
	Windrun		1,317	0,327	0,354	13,89**	
	Crawler movement		0,107	0,247	0,046	5,32**	
Step (4)	Temperature	-3,103	0,739	0,322	0,315	5,49**	4/65
	Windrun		1,392	0,346	0,362	14,78**	
	Crawler movement		0,091	0,209	0,049	3,37*	
	Humidity		-0,170	-0,138	0,176	0,93	

ANOVA table

		Sum of squares	Mean squares	r	r^2	r^2 change	F ratio
Step (1)	Regression	9246,590	9246,590	0,592	0,351	0,351	36,75**
	Residual	17107,181	251,576				
Step (2)	Regression	12977,296	6488,648	0,702	0,492	0,141	32,50**
	Residual	13376,475	199,649				
Step (3)	Regression	13974,587	4658,196	0,728	0,530	0,038	24,83**
	Residual	12379,185	187,563				
Step (4)	Regression	14148,942	3537,236	0,733	0,537	0,007	18,84**
	Residual	12204,829	187,767				

and measured on the same unit scale. This provides a direct comparison of partial regression coefficients to gauge the relative importance of each variable in relation to the catch. At the base of Table 28, the ANOVA tables for each step of the analysis are listed. The coefficient of determination (r^2), used as a percentage, is a measure of the variance in catch explained by all the variables in each step of the analysis. The change in r^2 in each successive step expresses the variance in catch explained by the variable added in each step. The multiple correlation coefficient (r) expressed the correlation between the observed catch and that predicted using the regression equation. Finally the F ratio tests the significance of the overall regression equation.

Temperature is the most important variable in relation to the dispersal of D. austrinus crawlers, accounting for 35,1% ($r^2 = 0{,}351$) of the variance in the catch. Together with windrun ($r^2 = 0{,}492$), these two factors account for 91,62% of the explained variance as the addition of crawler movement and relative humidity only increase r^2 to 0,537. The high intercorrelation between temperature, humidity and crawler movement (see correlation matrix - Table 28) casts doubt on the validity of including the latter two variables in the regression, as partial regression coefficients may not be uniquely determined (Kim & Kohout 1975) for each variable. Examination of the standard partial regression coefficients for the variables in each step shows that this does occur. The beta coefficients for windrun in steps 2, 3, 4 (0,379; 0,327; 0,346 respectively) are relatively stable showing little change with the inclusion of crawler movement and humidity. The successive beta coefficients for temperature, (0,592; 0,547; 0,409 and 0,322) show a rapid decrease with the inclusion of crawler movement and humidity to the extent that comparison of the beta coefficients for temperature and windrun in step 4 points to windrun as the most important variable in dispersal. Although the partial regression coefficient for crawler movement (step 3) is significant ($F = 5{,}32$; $p < 0{,}01$ for 3/66 d.f.) in relation to catch, the large reduction that inclusion of this variable causes to the beta coefficient for temperature suggests crawler movement, together with humidity, cannot be used in the regression analysis.

The laboratory experiments (Section 5.2) showed that temperature and light were the two factors controlling the movements of crawlers and that at constant windspeeds there was a close correlation between the number of moving crawlers and the number of crawlers dispersed. The results of the multiple regression analysis do not infer that crawler movement has no bearing on the number of crawlers dispersed, only that temperature estimates the catch more accurately than crawler movement in this analysis. This may be explained by the fact that crawler movement decreases once temperatures exceed ± $25^{\circ}C$ (Fig. 41 A, B). In terms of dispersal, although the number of crawlers moving on the plant decreases, they would not be anchored to the plant and could be blown from the plant by strong air currents.

The multiple regression analysis was repeated, excluding temperature as a variable (Table 29) and showed that crawler movement ($r^2 = 0{,}331$) together with windrun ($r^2 = 0{,}420$) were then the most important variables. The inclusion of humidity in step 3 causes a large decrease in the beta coefficient for crawler movement, with which it is intercorrelated ($r = -0{,}603$; $p < 0{,}01$ for 68 d.f.). Crawler movement and windrun account for 42,0% of the catch variance which is slightly less than that accounted for by temperature and windrun (49,2%). The greater part of the unexplained variance must be attributable to variables not included in the analysis. Part of the unexplained variance may be a result of the experimental design as the catch on the 1 m traps is not the total of crawlers dispersed, as a variable proportion of the crawlers would have been blown beyond or alighted before the 1 m ring of traps as the wind strength varied. However it was not possible to change all the traps at 2 h intervals and the use of a series of traps at differing heights close to the host plant would have affected the air currents around the small host plant. Snedecor and Cochran (1967) point out that it is not uncommon for explained variance to be in the order of 50%.

Willard (1977) found that only the density of red scale (A. aurantii crawlers on the host plant foliage was significantly correlated with catch ($r = 0{,}404$, $p < 0{,}01$ for 1/59 d.f.), although the inclusion of temperature, humidity and wind velocity together with crawler movement in a multiple regression analysis accounted for a significant proportion of the catch variance ($F = 3{,}93$; $p < 0{,}01$ for 4/57 d.f.). However the proportion accounted for was much lower (21,6%) that the amount of catch variance accounted for by the same variables in D. austrinus dispersal (53,7%).

As temperature and windrun account for a significant proportion of the catch variance for D. austrinus they can be used to predict the period dispersal is occurring. Both variables are simple to record and continuous recordings are easily obtained. The multiple regression coefficients obtained

Table 29. Simple correlation coefficients and multiple regression coefficients relating the two hourly catch of wind dispersed D. austrinus crawlers between 06h00 and 20h00 with three weather variables and the number of motile crawlers. ** Significant at 1% level; * significant at 5% level.

Simple correlation coefficients (n = 70)

	Catch	Windrun	Humidity	Crawler movement
Catch	1,000	0,445**	-0,520**	0,575**
Windrun		1,000	-0,018	0,276*
Humidity			1,000	-0,603**

Multiple regression analysis (n = 70)

Dependant variable: Catch

Independant variable/s entered

		Intercept	Partial regression coefficient (b)	Standardised regression coefficient (beta)	S.E. (b)	F ratio	d.f.
Step (1)	Crawler movement	3,746	0,250	0,575	0,043	33,570**	1/68
Step (2)	Crawler movement	-8,254	0,213	0,489	0,042	25,535**	2/67
	Windrun		1,247	0,310	0,390	10,249**	
Step (3)	Crawler movement	27,760	0,112	0,258	0,050	4,940**	3/66
	Windrun		1,479	0,368	0,372	15,794**	
	Humidity		-0,442	-0,358	0,138	10,310**	

ANOVA table

		Sum of squares	Mean squares	r	r^2	r^2 change	F ratio
Step (1)	Regression	8710,292	8710,292	0,575	0,331	0,331	33,570**
	Residual	17643,479	259,463				
Step (2)	Regression	11051,118	5525,559	0,648	0,420	0,089	24,193**
	Residual	15302,653	228,398				
Step (3)	Regression	13118,595	4372,865	0,705	0,497	0,078	21,806**
	Residual	13235,177	200,533				

in this analysis are applicable only to the crawler catch from the population monitored. In order to utilize these variables in the prediction of dispersal from other D.austrinus populations, regression analysis on catch and values for windrun multiplied by temperature was carried out. The combination of temperature and windrun in this manner accounted for 56,8% of the catch variance (Table 30) in the bivariate regression, a greater proportion of the variance than that accounted for when the two variables were used singly in the multiple regression.

Table 30. Simple correlation and bivariate regression coefficients between the 2 h catch (06h00 - 20h00) of wind dispersed D.austrinus crawlers on a ring of eight traps 1 m from the host plant O.aurantiaca and the 2 h value for windrun (km) x temperature ($h^{o} > 13^{o}C$) over a ten-day period. ** Significant at the 1% level for 1/68 d.f.

Regression analysis. N = 70

	Intercept(a)	Partial regression coefficient(b)	S.E.(b)	F.ratio	d.f.
Dependant variable: catch					
Independant variable: Windrun x Temperature	-5,071	0,113	0,012	89,56**	1,68

r = 0,754 r^2 = 0,568

The regression estimates of the daily catches using the 2 h values for windrun and temperature, and windrun x temperature in the respective regression equations were both significantly correlated with the daily catches on the 1 m traps at the 1% level (Table 31).

Table 31. Estimated daily catches on 1 m traps using (i) 2 h windrun (km) and temperature (h^{o} $13^{o}C$) values and (ii) 2 h values for windrun x temperatures in the equations N= -21,386 + 1,252 (temperature) + 1,525 (windrun) and N = -5,071 + 0,113 (windrun x temperature) respectively, and the daily catches on the 1 m traps. Correlation coefficients (r) for the comparisons of the estimated and observed catches are shown. ** Significant at 1% level for 1/8 d.f.

Day	1	2	3	4	5	6	7	8	9	10
(i)										
Catch	284	103	65	32	136	155	45	87	123	136
Estimated catch	208	148	38	46	90	189	61	150	143	130
							r = 0,8022**			
(ii)										
Estimated catch	231	136	35	45	83	199	60	135	148	111
							r = 0,8442**			

The effect of temperature on movement and dispersal of D.austrinus crawlers will ensure that the crawlers begin moving around the plant in the early morning as the temperature increases. This synchronises the movement with the increase in wind velocity (Fig. 23; Section 4.3) from 06h00 onwards and increases the chance of dispersal from the host plant.

Yeargan (1975), using stepwise multiple regression, found that temperature (difference between maximum and minimum temperature) explained 56,1% of the variance in the catch of ballooning spiders. The migrant ballooning spiders also move up to the tips of vegetation before extending a silk thread which enhances dispersal; a similar pattern of behaviour to that noted for D.austrinus.

6.4. Crawler dispersal pattern and wind.

The multiple regression analysis of the variables influencing the number of D.austrinus crawlers dispersed by air currents, provided a method to estimate the catch on the 1 m ring of traps. An extension of this analysis was to correlate the catch in each direction with the pattern of winds blowing during the experiment. This required analysis of the anemometer recordings to allocate the windrun in the different directions.

Air currents are characterised by horizontal and vertical eddies (Gregory 1945, Wilson & Baker 1946a and Raynor & Ogden 1965) and although the wind may blow in the same mean direction, particles will be spread either side of the mean line by the eddies. Wilson & Baker (1946a) found that the dispersion pattern of the spores of Sclerotinia laxa Ader and Ruh could be described by a horizontal cone, with the apex at the source of dispersal and the base perpendicular to the mean direction of the wind. The overall horizontal distribution of spores at any point down the length of the cone followed a normal distribution i.e. peak numbers at the centre and the numbers decreasing progressively to the right and left of the centre. The width of the conical pattern of dispersal is affected by windspeed with strong winds providing a narrower cone than weak winds (Raynor & Ogden 1965).

Anemometer wind direction records reflect the diluting effect of the horizontal eddies on dispersal of airborne particles. Figure 42A shows a portion of the wind direction and windrun recording from the Lambrecht anemometer used in this study. The wind direction trace is not a discrete line but runs either side of the mean direction. The band width of the

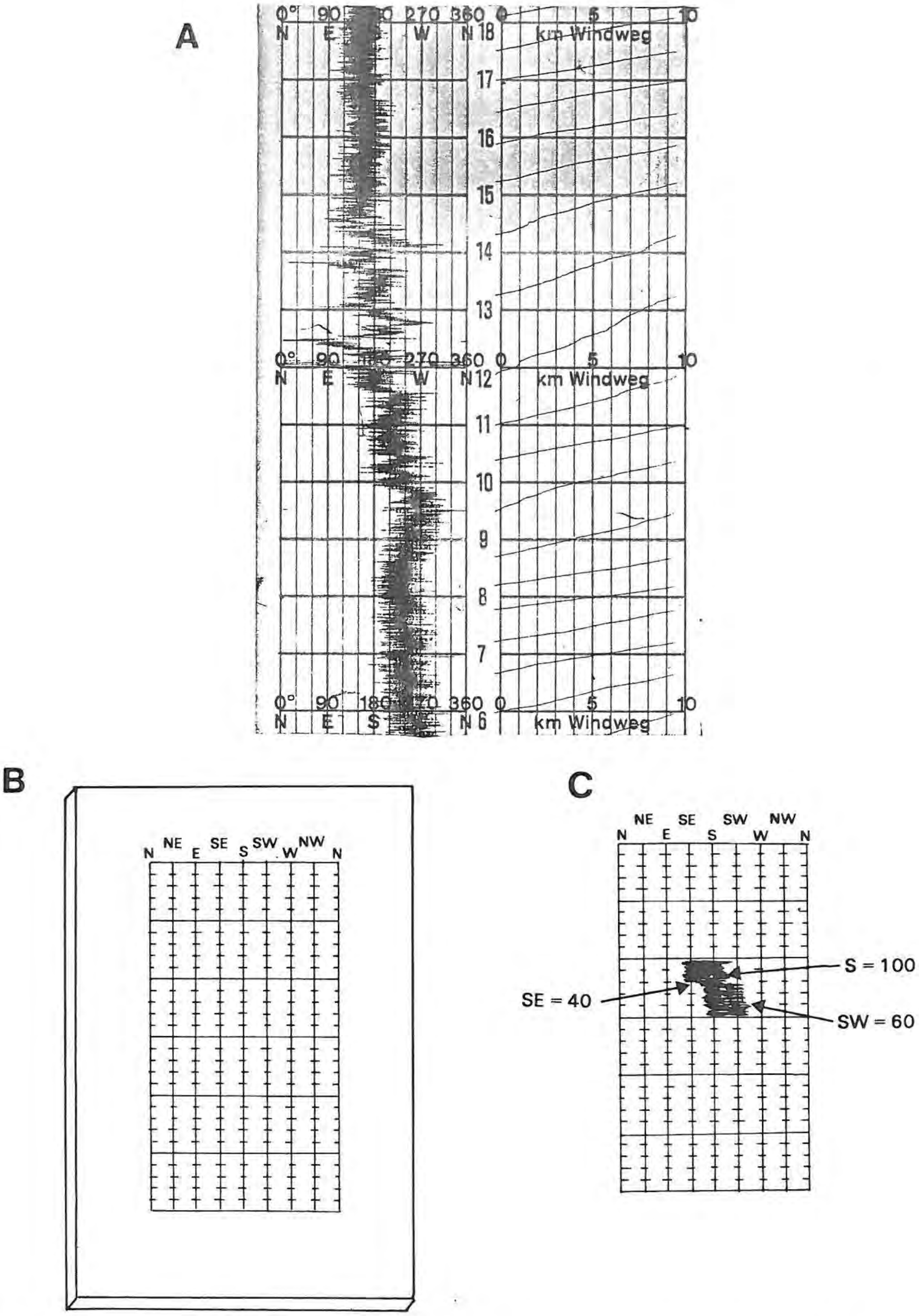


Fig. 42. A. Example of recording from Lambrecht anemometer showing the windrun and wind direction trace. B. Plastic overlay used to analyse wind direction recordings. C. Example scoring using the plastic overlay superimposed on the wind direction trace.

wind direction trace can extend to 60° either side of the mean direction although generally the width of the trace decreases as the windrun increases. As a result crawlers would be dispersed in more than one direction at the same time. Allocation of the windrun in different directions can account for the diluting effect of horizontal eddies by including the band width in the analysis.

The Lambrecht anemometer provided hourly recordings of the wind direction and windrun (Fig. 42A) during the dispersal experiment. A small plastic overlay (Fig. 42B) was used to analyse the wind direction trace. The vertical lines on the overlay represented the four cardinal and four semi-cardinal directions in which crawler dispersal was monitored. The horizontal lines on the overlay coincided with the hourly divisions on the anemometer recording; each hour was divided into five subdivisions by the small markings on the vertical lines. With the plastic overlay superimposed on the anemometer wind direction trace, scores out of 100 were assigned to each direction with which the trace coincided. An example of the scoring is given in Figure 42C where the directions S, SE and SW were allocated the scores 100, 40 and 60 respectively, based on the portion of the hourly trace coinciding with those directions. Snow (1976, 1977) used a similar but simpler scoring technique to correlate the flight direction of mosquitoes in relation to wind direction.

Estimates of the two-hourly catch of wind dispersed crawlers on the ring of 1 m traps could be obtained using the multiple regression equation (step 2, Table 28; Section 6.3) relating temperature ($h^{o} > 13^{o}C$) and windrun (km) to the catch and also using the bivariate regression equation (Table 30; Section 6.3) relating the value temperature x windrun to the catch. Two computer programs, EQUI and EQU2, were written to combine the multivariate and bivariate regression estimates of the catch respectively with wind direction scores and to allocate estimates of the total catch over the two ten-day periods to the four cardinal and four semi-cardinal directions. Both programs, together with example data input and output formats are shown in Appendix 4.

The temperature, windrun and wind direction scores were determined for each 2 h period between 06h00 and 20h00 for the twenty days dispersal was monitored. Table 32 shows the stepwise calculations carried out in the programs EQU1 and EQU2 in order to allocate the regression estimate of the catch in each direction for 2 h periods. The hourly wind direction scores are read from the data subfile (see example input format, Appendix 4). The wind direction score ratio is calculated for each hour, summated and halved to give the 2 h wind direction score ratio. The regression estimate of the two-hourly catch is determined from the two-hourly temperature and windrun values and allocated to each direction on the basis of the wind direction score ratio.

Table 32. Example of the stepwise calculations carried out using the programs EQU1 and EQU2 to allocate two hourly regression estimates of the catch of wind dispersed crawlers on the 1 m ring of traps to the four cardinal and four semi-cardinal directions.

Step 1. The temperature $(h^{o} \gtrsim 13^{o}C)$, windrun (km) and the wind direction score in each direction read from data subfile (See example data input format Appendix 4).

Time	Temperature	Windrun	Wind direction score								Total wind direction score
			N	NE	E	SE	S	SW	W	NW	
07h00	15,5	8,0				60	100	40			200
08h00	16,5	11,0					100				100

Step 2. The wind direction scores for each hour are converted to a ratio (wind direction score ratio = 1,0/Total wind direction score x wind direction score) and summated and halved to provide the ratio for a 2 h period.

	Wind direction score ratio							
	N	NE	E	SE	S	SW	W	NW
07h00 (1h)				0,3	0,5	0,2		
08h00 (1h)					1,0			
08h00 (2h)				0,15	0,75	0,10		

Step 3. Regression estimates of the 2 h catch (N) determined using temperature and windrun values.

EQU1: N = -21,386 + 1,252 (temperature) + 1,525 (windrun) = 10,22

EQU2: N = -5,071 + 0,113 (temperature x windrun) = 15,44

Step 4. The regression estimates of the catch are allocated to each direction on the basis of the 2 h wind direction score ratio.

Program	Time	Estimated catch								Total estimated catch
		N	NE	E	SE	S	SW	W	NW	
EQU1	08h00				3,07	5,11	2,04			10,22
EQU2	08h00					15,44				15,44

The two hourly catches were summated to provide daily totals (06h00 to 20h00) and total in each direction for the entire period of the analysis (See example output format in Appendix 4).

The estimated catches in each direction obtained using EQU1 and EQU2 for the first and second ten-day periods and the entire twenty-day period dispersal was monitored are shown in Table 33. The estimated catches in each direction and trap catches were compared using correlation analysis (Sokal & Rohlf 1973). The correlation coefficients for each set of data are shown in the table.

Table 33. Trap catches and estimated catches of wind dispersed *D.austrinus* crawlers 1 m from the host plant *O.aurantiaca* in the four cardinal and four semi-cardinal directions. Data for the first and second ten-day periods and all twenty days of the dispersal experiment are shown. The correlations between trap catches and estimated trap catches are shown. ** Significant at 1% level for 1/6 d.f. To enable direct comparison the estimated catches were switched 180^{o}.

First ten-day period.

	Program	N	NE	E	SE	S	SW	W	NW	Total catch
					Direction					
Trap catch		317	198	59	44	153	89	118	189	1167
Estimated catch	EQU1	283	249	110	100	120	81	93	168	1208
Correlation		r = 0,8914**								
Estimated catch	EQU2	281	252	113	103	119	73	82	161	1184
Correlation		r = 0,8650**								

Second ten-day period

	Program	N	NE	E	SE	S	SW	W	NW	Total catch
Trap catch		222	163	61	61	79	59	74	100	819
Estimated catch	EQU1	274	266	138	75	64	55	63	144	1079
Correlation		r = 0,9108**								
Estimated catch	EQU2	260	252	132	70	55	46	56	134	1005
Correlation		r = 0,9050**								

Total twenty-day period

	Program	N	NE	E	SE	S	SW	W	NW	Total catch
Trap catch		539	361	120	105	232	148	192	289	1986
Estimated catch	EQU1	558	514	248	175	184	136	156	312	2283
Correlation		r = 0,8937**								
Estimated catch	EQU2	541	504	245	173	174	119	138	295	2189
Correlation		r = 8793**								

In all cases the correlation between the estimated catches and traps catches are very highly significant, which suggests that the method of wind direction scores analysis, the basis for allocating the estimated catches in each direction was sound.

The use of regression equations in obtaining estimated catches is limited to the particular population studied and three alternative estimates of the catch were used. The windrun (km), windrun time (min) and a value for windrun (km) x temperature ($h^{o} > 13^{o}C$) were allocated to each direction on the basis of the hourly wind direction scores. Two computer programs, WIN1 and WIN2 (Appendix 5) were written to facilitate analysis of the data. These programs were similar to EQU1 and EQU2 only in that windrun and windrun time (WIN1) and windrun x temperature (WIN2) were used as an estimate of the catch rather than using regression estimates. The data input format are the same and the output formats (Appendix 5) are similar only in that the catch in each direction is shown as a ratio. The estimated catch ratios in each direction were reduced to frequency of 1 and then multiplied by the total trap catch to give an estimated catch in each direction (Table 34). This enabled comparison of the estimated catches and trap catches. In addition the program WINI provided the mean wind velocity (m sec^{-1}) in each direction.

Table 34. Examples of conversion of estimated catch ratio of wind dispersed D.austrinus in all directions to estimated catches to enable comparison with the observed trap catches.

	Direction								
	N	NE	E	SE	S	SW	W	NW	Total
Trap catches	100	50	50	20	100	100	50	20	490
Estimated catch ratio	400	100	150	80	380	420	130	60	1720
Frequency	0,2326	0,0551	0,0872	0,0465	0,2209	0,2442	0,0756	0,0349	1,0000
Estimated catch (Trap catch x frequency)	114	28	43	23	108	120	37	17	490

Estimated catch ratios, using programs WINI and WIN2, were obtained for the first and second ten-day periods and total twenty days of the dispersal experiment (Table 35). Analysis was restricted to the period 07h00 to 19h00 each day because of the prevalence of heavy dew between 06h00 and 07h00 and the onset of darkness soon after 19h00. Trap catches shown in this set of analyses were the total catches from 1 to 6 m, corrected for dilution

(Section 6.2), which provided a more realistic estimate of the number of crawlers dispersed.

Table 35. Trap catches (x dilution factor) and estimated catches of wind dispersed *D.austrinus* crawlers, using windrun (km) and windrun time (min) (program WINI) and a value for windrun (km) x temperature ($h^o > 13^oC$), (program WIN2) allocated in eight directions on the basis of the wind direction scores. Correlation value (r) for comparison of the trap catches (1 - 6 m) and estimated catches are shown for 1/6 d.f. ** Significant at 1% level; * significant at 5% level.

First ten-day period

	Direction								
	N	NE	E	SE	S	SW	W	NW	Total
Trap catches (1 - 6 m)	932	495	125	97	244	185	303	515	2896
Est. catch ratio (windrun)	161	146	63	47	48	32	40	88	625
Est. catch	746	676	293	218	222	148	185	408	2896
						r =	0,8645**		
Est. catch ratio (time)	1505	1281	535	452	526	414	508	959	6180
Est. catch	705	600	251	212	246	194	238	449	2896
						r =	0,9283**		
Est. catch ratio (Windrun x temp)	1436	1276	571	513	570	377	419	835	5997
Est. catch	693	616	276	248	275	182	202	403	2896
						r =	0,8792**		

Second ten-day period

	Direction								
	N	NE	E	SE	S	SW	W	NW	Total
Trap catches (1 - 6 m)	795	414	173	168	217	157	232	335	2491
Est. catch ratio (Windrun)	164	163	90	45	34	29	37	84	646
Est. catch	632	629	347	174	131	112	143	324	2491
						r =	0,8140*		
Est. catch ratio (time)	1449	1446	789	436	388	376	458	848	6240
Est. catch	598	577	315	174	155	150	183	339	2491
						r =	0,8464**		
Est. catch ratio (windrun x temp)	1313	1269	678	359	301	264	324	713	5221
Est. catch	626	605	323	171	144	126	155	340	2491
						r =	0,8392**		

Total Period

	Direction								
	N	NE	E	SE	S	SW	W	NW	Total
Trap catches (1 - 6 m)	1727	909	298	265	461	342	535	850	5387
Est. catch ratio (windrun)	326	308	153	93	83	60	77	172	1272
Est. catch	1381	1304	648	394	352	254	326	728	5387
						r	=	0,8428**	
Est. catch ratio (time)	3004	2727	1324	887	913	790	967	1807	12419
Est. catch	1303	1183	574	385	396	343	419	784	5387
						r	=	0,8912**	
Est. catch ratio (windrun x temp)	2749	2545	1249	872	871	641	744	1584	11219
Est. catch	1320	1222	600	419	418	308	357	743	5387
						r	=	0,8663**	

The time the wind blew in each direction provided a better estimate of the catch in each direction than using the windrun or windrun x temperature values. The correlation values were all significant at the 1% level (for 1/6 d.f.) with the exception of one set of data using windrun (significant at 5% level).

One would expect that using windrun x temperature would have provided the best estimate of the catch in each direction. The better values provided by using time might be explained by the very even mean wind velocities in each direction (Table 25).

Willard (1976) correlated the % time wind blew in each direction and the % catch for daily and weekly totals and found significant correlations for both sets of data. However he gave no details on the analysis of wind direction and only used time as the basis for the analysis.

6.5. The role of male and female crawlers in dispersal.

The earlier studies on the morphology and behaviour of the crawler stage suggested that female crawlers were adapted for dispersal. The long filaments on the female crawlers and the movement of females to the terminal points of the host plant would enhance the possibility of dispersal of females in relation to males.

Crawlers recovered from the 1 m circle of traps, between 08h00 and 20h00 on nine days and between 06h00 and 16h00 on one day, were sexed on the basis of the pattern and development of the filaments (Table 36). Of the 1 073 crawlers examined, 28,6% were either submerged in the sticky surface or too young to be positively sexed.

Of the remainder that were sexed (766), 81,2% were females and 18,8% males. Visual estimates of the filament length of the females pointed to the majority being 48 h or older. If it is assumed that the sex ratio of the crawlers which were submerged in the trap surface or too young to be sexed was the same as the others, these results emphasise the dominant role of the females in dispersal at the crawler stage.

Table 36. Numbers of male, female and unsexed wind dispersed crawlers of D. austrinus recovered over a ten day period from eight sticky traps placed around the host plant O. aurantiaca. Percentages shown in brackets.

	Male	Female	Unsexed	Total
Day 1	45 (19,3)	150 (64,7)	38 (16,3)	233
2	10 (10,3)	46 (47,4)	41 (42,3)	97
3	6 (9,4)	33 (51,6)	25 (39,0)	64
4	3 (10,7)	19 (67,9)	6 (21,4)	28
5	21 (15,4)	78 (57,4)	37 (27,2)	136
6	20 (13,6)	80 (54,4)	47 (32,0)	147
7	6 (13,3)	21 (46,7)	18 (40,0)	45
8	9 (10,8)	51 (61,5)	23 (27,7)	83
9	11 (8,9)	69 (56,1)	43 (35,0)	123
10	13 (11,1)	75 (64,1)	29 (24,8)	117
Total for ten days	144 (13,4)	622 (58,0)	307 (28,6)	1073

7. WIND DISPERSAL OF D.AUSTRINUS CRAWLERS FROM HOST PLANTS IN THE FIELD

Examination of the horizontal distribution of wind dispersed D.austrinus crawlers (Section 6.2) showed the dispersal range from the host plant was restricted compared to that of species of the Coccoidea infesting trees or tall grass. The importance of the height of the host plant in determining the release height, as shown by the formula of Brown (1958) suggests that the large O.aurantiaca plants will serve as the main source for wind dispersed D.austrinus crawlers in the field. The small plants, growing in amongst vegetation will be masked from the wind. Only the large plants, with the terminal cladodes level or above the surrounding vegetation are likely to serve as platforms for wind dispersal.

An experiment was carried out in the field to assess (7.2) the importance of the size of the host plant on the horizontal distribution of wind dispersed crawlers and to complete this dispersal study with (7.3) an examination of the vertical distribution of dispersed crawlers.

7.1. Materials and Methods

The study was conducted on the farm Maastricht near Carlisle Bridge in the Fish River Valley. The farm provided an ideal site for this study, as the area was flat and open (Fig. 43) and free from large bushes or trees.

Fig. 43. View of the farm Maastricht showing the flat open areas with low ground cover used in dispersal experiment.

The ground was covered by low growing ($\pm$ 25 cm) sweet karoo bush (Pentzia incana) in amongst which there was a high density of cochineal infested jointed cactus plants.

An area 35 m square was delimited and the position of each jointed cactus plant in the area marked. The height of each plant and presence or absence of cochineal was recorded. Nine horizontal sticky impact traps were set out on a 10 m grid with four sets of four cylindrical sticky impact traps mounted vertically at the corners of a 10 m square area at the centre of the delimited area (Fig. 44).

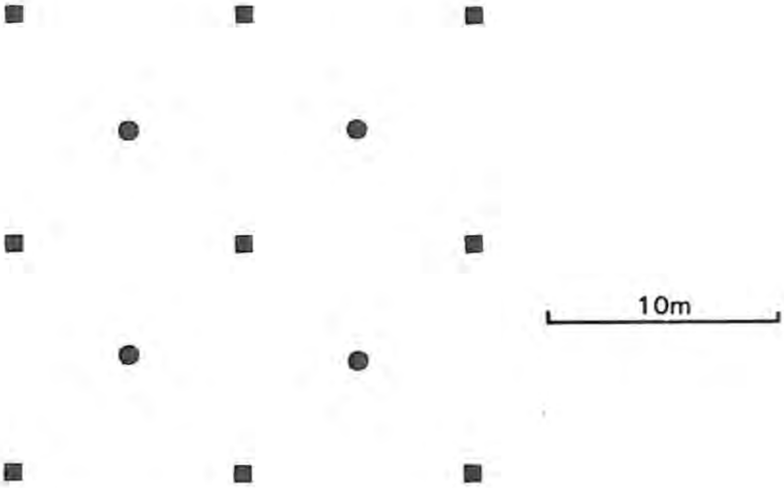


Fig. 44. Plan of the position of nine horizontal (■) and four sets of cylindrical sticky traps (●) used to monitor the horizontal and vertical distribution of wind dispersed D. austrinus crawlers.

Each horizontal impact trap (Fig. 45) comprised a square metal frame and a removable 41 cm square glass sheet. The metal frame of each trap was anchored in position by hammering the metal legs approximately 10 cms into the ground. The glass sheet was held horizontally in position by four aluminium brackets in the top corners of the frame. The trapping surface was then about 30 cm above ground level (Fig. 45).

The upper surface of the glass sheet was sandblasted to give a roughened surface which was coated with a thin film of Formex to provide a permanent sticky surface. Prior to application the Formex was warmed in a metal tray, heated by a 100 watt light bulb, to soften the mixture. A 1 cm wide margin around the edge of the glass sheet was left free of Formex for ease of handling and to enable the glass sheets to be loaded and

Fig. 45. Horizontal sticky impact trap used to monitor the dispersal of *D. austrinus* crawlers in the field.

Fig. 46. Carrying tray used to transport the removable glass sheets of the horizontal sticky impact traps.

unloaded easily from the carrying tray (Fig. 46).

Using glass sheets as trapping surfaces provided an efficient (see Section 8.1) and economical system of monitoring the crawler dispersal. The sheets could be changed rapidly and having recorded the number of crawlers trapped, the Formex could be removed with paraffin and the sheets recoated.

The cylindrical sticky traps (Fig. 47) were 20 cm lengths of plastic sanitation pipe fitted with wooden plugs, screwed in 10 cms from either end. The wooden plugs were drilled out allowing the cylinders to be slid onto a 2,5 m long metal pole. With the pole vertically in position, the cylinders were held in position by resting on a nail placed through the metal pole. Four traps were placed 0,5, 1,0, 1,5 and 2,0 m above ground level on each pole. Metal stakes driven into the ground provided the base to hold the pole and four traps vertically in position. Formex was applied in a thin layer over the surface of each cylinder, to give a permanent trapping surface.

Fig. 47. Set of four sticky cylindrical impact traps used to monitor the vertical distribution (0,5 to 2,0 m) of wind dispersed D. austrinus crawlers.

Crawler dispersal was monitored over a period of fourteen weeks from January 1976 to April 1976. For the first five weeks only the horizontal distribution was monitored but thereafter the vertical distribution was measured. The traps were changed at weekly intervals.

7.2. Horizontal distribution and host plant size.

Total trap catches ranged from 24 - 806 over the fourteen weeks dispersal of D.austrinus crawlers was monitored on the horizontal sticky traps (Table 37). The great range in total catches over the small area that dispersal was monitored, suggests wind dispersal of crawlers was very localised.

Table 37. Weekly catches of wind dispersed D.austrinus crawlers on nine horizontal sticky traps set out on a 10 x 10 m grid.

	Trap No.								
Week	1	2	3	4	5	6	7	8	9
1	13	4	3	9	183	8	8	1	6
2	17	5	0	17	49	2	4	3	3
3	12	8	5	43	85	10	1	2	1
4	6	1	5	6	111	5	2	0	3
5	25	7	21	33	129	2	0	2	3
6	34	5	23	14	121	0	4	1	6
7	6	20	19	17	35	9	3	11	6
8	1	6	4	11	20	6	1	3	5
9/10	12	5	7	6	37	4	1	0	0
11	2	0	2	0	10	1	0	0	0
12	0	0	1	1	18	1	0	0	1
13	0	0	1	0	5	0	0	0	0
14	0	0	0	0	3	0	0	1	0
Total	128	61	91	157	806	48	24	24	34

The consistent pattern of catches on each trap for each week pointed to dispersal of crawlers from a source close to each trap. Figure 48 is a plot of the trap positions and the position of all the infested jointed cactus plants in a 35 x 35 m area around the traps.

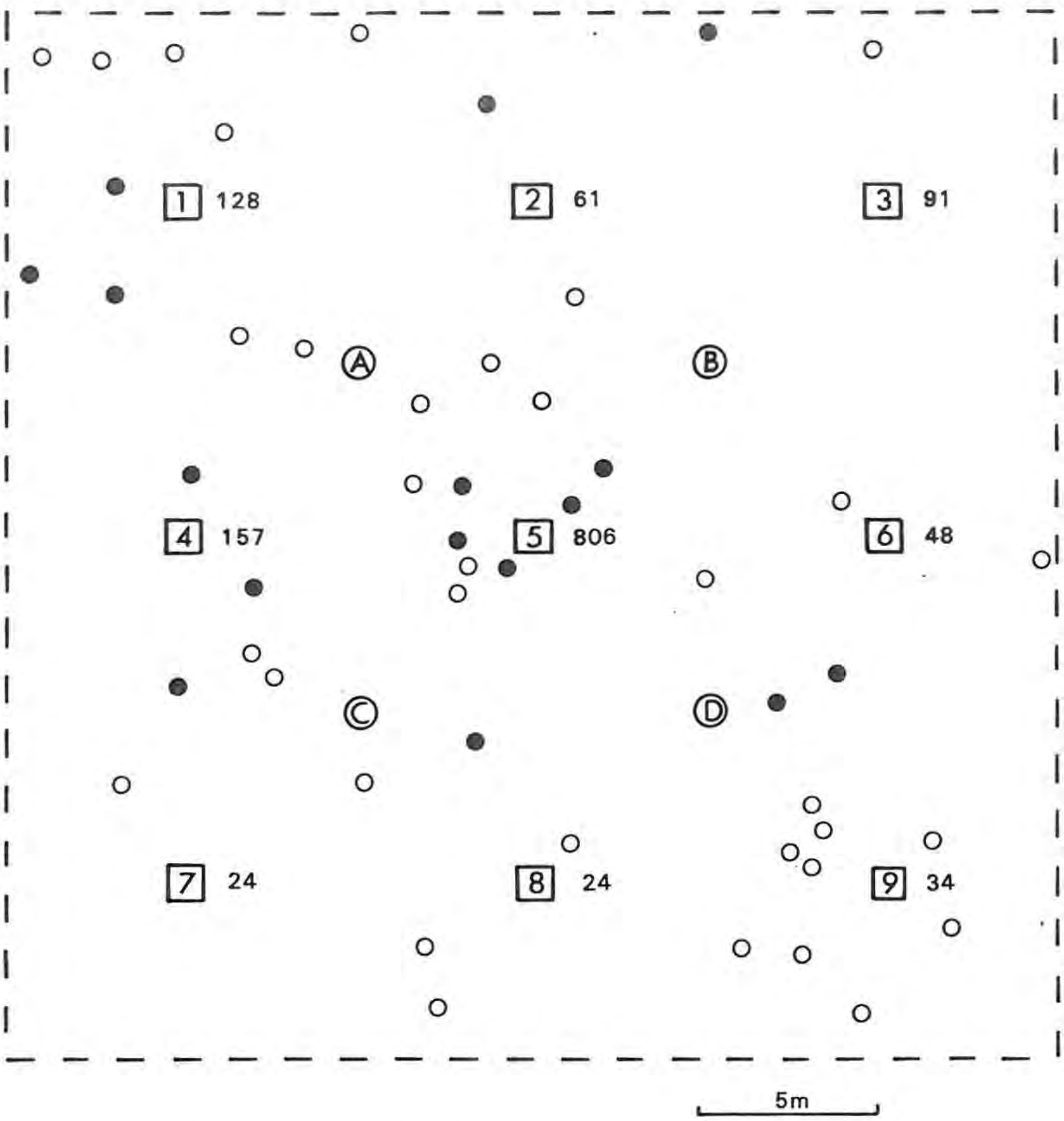


Fig. 48. Plan of the trap pattern used to monitor the horizontal and vertical distribution of wind dispersed D. austrinus crawlers from populations of cochineal in the field; numbered squares - horizontal sticky traps. Lettered circles - sets of 4 cylindrical sticky traps. Catches of dispersed crawlers on horizontal traps for a 14 week period shown alongside respective traps. The position of infested O. aurantiaca plants in relation to the traps are shown; closed circles - jointed cactus plants 20 - 40 cm high, open circles - jointed cactus plants 5 to 20 cm high.

The low growing vegetation covering the area was ± 25 cm in height. Only jointed cactus plants which grew above 20 cm were level or above the surrounding vegetation. These would serve as the dispersal platforms for crawlers dispersing to the level (30 cm) of the horizontal traps: the position of these plants (Fig. 48) in relation to the total catches on individual traps confirmed this prediction. Multiple regression analysis (Table 38) was used to assess the relative importance of the number and mean distance of infested jointed cactus plants, 20 to 40 cm high (represented by closed circles in Fig. 48) and within 8 m of each trap, in determining the catch.

The number of jointed cactus plants and the mean distance of these plants from each trap accounted for 76,5% of the total catch variance (r^2 expressed as a percentage). The inclusion of the mean distance of each group of plants made only a small change in the r^2 value (0,009) (step 2, Table 38), so that it is the number of large plants 20 cm or more in height which accounts for the greater proportion of the catch variance (75,6%). This confirms the very localised catches and therefore limited dispersal of D.austrinus crawlers from the host plant.

The high correlation between the number of plants within 8 m of the traps and the respective trap catches suggests horizontal dispersal will not be in excess of 8 m. Although the plants were surrounded by vegetation, which would have reduced the release height, the turbulence and vertical eddies set up by airflow over the vegetation (Slater 1945 and Monteith 1973) are likely to have increased horizontal dispersal distances offsetting the reduced release height. The effect of turbulence and convection currents was analysed by examining the vertical distribution of the crawlers.

7.3. Vertical distribution of D.austrinus crawlers

Table 39 gives the total numbers of crawlers recovered from the four sets of cylindrical sticky traps placed at 0,5, 1,0, 1,5 and 2,0 m above ground level for ten weeks during which the vertical distribution of crawlers was monitored.

Several significant points arise from examination of these data. Firstly there is a very rapid decrease in the mean catch for all sets of traps from 0,5 to 2,0 m. Figure 49 shows that the mean catch at 1,5 and 2,0 m was similar which may reflect the expected density above 2 m i.e. the proportion of crawlers carried vertically upwards by turbulence or convection currents.

Table 38. Simple correlation and multiple regression coefficients relating catch of wind dispersed D. austrinus crawlers to the number and distance of O. aurantiaca plants (20 cm or more in height) within 8 m of ten horizontal sticky impact traps. ** Significant at 1% level, * significant at 5% level.

Simple correlation coefficients n = 10	Catch	Number	Mean distance
Catch	1,000	0,869**	-0,670*
Number		1,000	-0,834**

Multiple regression analysis n = 10			Intercept	Partial regression coefficient (b)	S.E. (b)	F ratio	d.f.
Dependant variable: Catch							
Independant variables entered	Step (1)	Number of plants	-217,754	166,639	35,769	21,704**	1/7
	Step (2)	Number of plants	-397,846	193,512	68,762	7,920*	2/6
		Mean distance		25,733	54,912	0,220	

ANOVA table

		Sum of squares	Mean square	r	r^2	r^2 change	F ratio
Step (1)	Regression	376419,763	376419,763	0,869	0,756	0,756	21,704**
	Residual	121404,459	17343,494				
Step (2)	Regression	380706,524	190353,262	0,874	0,765	0,009	9,752*
	Residual	117117,698	19519,616				

Table 39. Catches of D. austrinus crawlers on four sets of cylindrical sticky impact traps at 0,5, 1,0, 1,5 and 2,0 m above ground level over a ten week period.

Trap	Height (m)			
	0,5	1,0	1,5	2,0
A	27	16	2	0
B	10	13	3	3
C	52	12	5	4
D	17	11	0	3

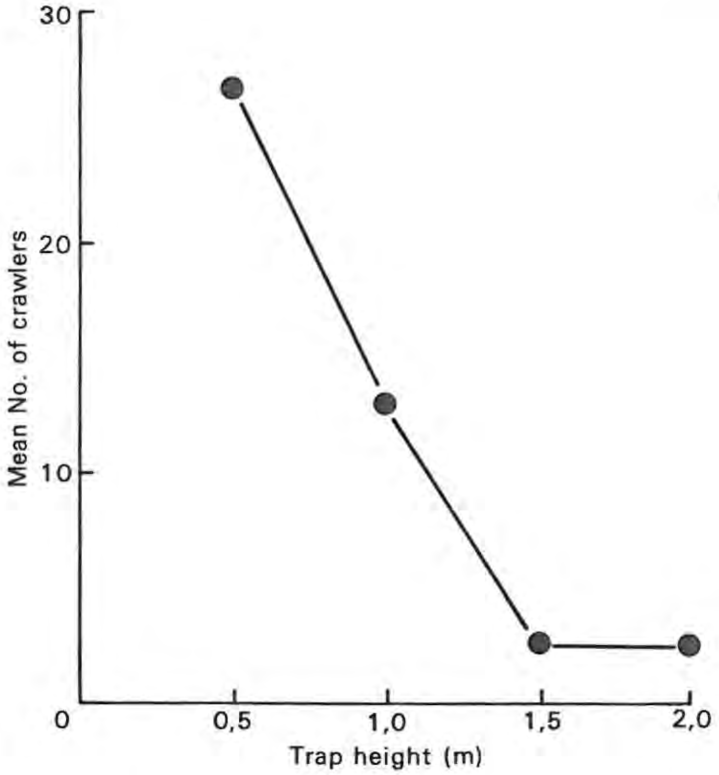


Fig. 49. Vertical distribution of wind dispersed D. austrinus crawlers on sticky impact traps.

Secondly, the range in catches at 0,5 m (10 to 52) with the traps only 10 m apart, must reflect the localised dispersal noted in the preceding section.

The height of the tallest jointed cactus plant in the area surveyed was 40 cm. Therefore the cylindrical sticky trap catch reflects the densities of crawlers carried vertically above the plants and do not include those crawlers which are dispersed horizontally below the height of the lowest trap. It is therefore difficult to compare the horizontal distribution densities and the vertical distribution densities i.e. short range and long range dispersal densities. However if it is assumed that the crawlers carried above 1 m are a proportion of dispersed crawlers carried to greater altitudes, and likely to be dispersed over distances measured in kilometres, and the remainder are dispersed short distances, 12,7% of the wind dispersed crawlers would be dispersed for long distances from the parent host plant. This percentage is likely to be far lower if the number dispersing below 0,5 m were included.

Seven percent of P.njalensis crawlers (Cornwell 1960) and 6.0% of A.aurantii crawlers (Willard 1976) were dispersed vertically above their respective host plants. Both authors emphasised that the crawlers dispersed vertically above the host provided for long-range dispersal as opposed to the horizontally distributed crawlers which only dispersed short distances.

The results of these dispersal studies have pointed to the importance of the host plant characteristics in determining the dispersal potential of D.austrinus. The large host plants (height up to 40 cm) provide the platform for short-range dispersal, which for the majority of the crawlers is measured in metres, although portion of the wind dispersed crawlers will be dispersed for greater distances.

The restriction on the dispersal range of D.austrinus set by the low height of the host plant suggested an alternative method of release; artificial enhancement of crawler dispersal. The dispersal of crawlers from cultures of D.austrinus reared on cladodes and placed on towers in the field to provide an elevated dispersal platform. The ease with which D.austrinus can be reared on loose cladodes, the high feculdity of the females and hardiness of the crawlers all suggested that this method would provide a simple method of dispersing large numbers of crawlers over long distances.

8. ARTIFICIAL ENHANCEMENT OF CRAWLER DISPERSAL

The necessity of augmenting or replacing chemical control methods, which have proved expensive and have failed to control the spread or reduce the densities of jointed cactus infestations (Neser & Annecke 1973 and Zimmermann _et al_. 1974), placed priority on evaluating a method of artificially enhancing crawler dispersal. Therefore the design and field trials of the system adopted was carried out in conjunction with studies on the biology and dispersal from the host plant over the period 1975 to 1978.

The method proposed to artificially enhance dispersal was simple. It comprised rearing cultures of _D.austrinus_ on cladodes which would be placed on elevated platforms in the field. This would provide a source for a large number of crawlers which would be wind dispersed from a height sufficient for the crawlers to be carried long distances before sinking to the ground. It was envisaged that the large number of crawlers that could be produced by a large culture would give a dense pattern of dispersed crawlers around the point of release, sufficient for all the plants to be infested. In this way populations of jointed cactus could be controlled before they reached damaging densities.

Field trials were carried out on two farms, the initial trials in an area in which cochineal occurred naturally and later trials in an area free of jointed cactus and cochineal.

The release system used in both trials was the same as was the trapping technique used to monitor the horizontal distribution of crawlers. The general methods used are described prior to describing the individual trials and results.

8.1. Materials and methods

Release towers

Each dispersal tower comprised a holding basket (Fig. 50), into which infested cladodes were placed and a metal bracket to hold the basket in place on top of a 5 m high metal pole. Each holding basket 1 m square and 25 cm high, was made of a frame of 6 mm mild steel rod with the base and sides covered with galvanised woven wire mesh (12 mm). The wire basket

Fig. 50. Ventral view of holding basket showing the metal bracket to anchor the basket on top of a 5 m high pole (Fig. 51), to enhance dispersal of D. austrinus crawlers from the culture in the holding basket.

Fig. 51. 5 m high tower used to enhance dispersal of D. austrinus crawlers.

was tied to the four corners of a metal bracket (Fig. 50), whose centre section fitted over the top of pole, held upright in the field by four guy-ropes (Fig. 51).

Infested material was obtained in two ways. Firstly cladodes from infested jointed cactus plants growing in the field were collected and placed in the holding basket. The disadvantage of this method was many of the cochineal insects were damaged on transfer and field populations of D.austrinus are not synchronised with respect to crawler production.

The second method involved rearing D.austrinus on fresh cladodes placed in the holding basket. Each basket could hold about 1500 cladodes which were inoculated with D.austrinus crawlers by placing infested cladodes on top of the fresh cladodes. The crawlers were reared to the adult stage under standard C.E. room conditions. Once the populations of cochineal on the cladodes began producing crawlers, the holding basket was transferred to the release tower in the field. The advantage of this method was that infested material for field use did not have to be transferred and there was synchronous production of crawlers.

The rearing procedure was simple although difficulty was encountered on one occasion with the early build-up of a population of an unidentified aphid in the group Aphis spp. (in lit; Eastop 1975). Copious honeydew secretion covered the developing crawlers, killing off a large part of the culture.

When setting up the release tower, the top of the holding basket was covered with a metre square section of fishing net to prevent the cladodes moving or falling from the basket. A double layer of nylon gauze was stretched over the top of the basket to prevent damage by heavy rain.

Traps

The dispersal of crawlers from the towers was monitored using the same horizontal sticky impact traps described in Section 7.1. The pattern of traps used in each field trial will be described in context. As mentioned earlier, the use of glass sheets provided an efficient and economical system of monitoring crawler dispersal.

A measure of the efficiency of this type of trap was obtained by marking the position of 524 crawlers recovered from the plates during tower dispersal. The leading edge of the glass sheets, the edge facing the dispersal tower, was marked and the position of crawlers recovered from the sticky surface was recorded in relation to the leading edge. The transparent 41 cm square glass sheets were placed on top of a sheet of paper divided into a grid of 4 cm squares. The number of crawlers in each of the ten 4 cm distance intervals from the leading edge to the trailing edge and the ten 4 cm distance intervals across the glass sheet at right angles to the leading edge were recorded (Table 40).

Table 40. Horizontal sticky impact trap catches of D.austrinus crawlers in 4 cm distance intervals from (a) the leading edge to the trailing edge of the glass sheet and (b) across the glass sheet at right angles to the leading edge.

a.	29	46	50	57	57	58	59	54	59	55
b.	41	52	54	51	68	52	42	52	56	56

There was a slight "edge effect" (Gregory & Stedman 1953) with lower catches 0 - 8 cm from the leading edge of the glass sheet. χ^2 analysis (Sokal & Rohlf 1973) of the observed catches from the leading to the trailing edge and across the sheet showed no significant deviation from the expected catches ($\chi^2 = 14{,}59$; $p > 0{,}1$ for 10 d.f. and $\chi^2 = 9{,}78$; $p > 0{,}1$ for 10 d.f.). Gregory and Stedman (1953) showed that the most efficient horizontal impact traps for fungal spores were improved by using horizontal glass slides that are thin on cross-section to reduce "edge shadow" effect caused by turbulence at the leading edge. The traps used in this study were thin in cross section and therefore efficient, and no correction factor was applied to the observed catches.

8.2. Maastricht Field Trial.

The initial evaluation of the system to artificially enhance crawler dispersal using elevated towers was carried out on the farm Maastricht from October 1975 to December 1975.

It was hoped that monitoring the number of crawlers dispersed from a tower in an area in which jointed cactus was present would serve to evaluate the dispersal range and density of dispersed crawlers as well as the impact of tower dispersal on the jointed cactus populations.

Two 200 m square (4 hectare) plots, 650 m apart, were marked off. The one plot served as a release site while the other served as a control plot to compare the levels of the cochineal population prior to and after release of crawlers from the tower. The two plots were surveyed for jointed cactus and *D.austrinus* using a method developed by Zimmermann (1977) based on randomly selected permanent transects. Forty transect lines, 50 m long, were marked off on each plot. The presence or absence of categories of jointed cactus plants in one metre square areas down the length of the transect (100 sq m) was recorded (Zimmermann 1977) and in addition the presence or absence of cochineal on the plants was noted. The four categories of plants were:

Category A:	loose joints without roots and	small plants
Category B:	rooted plants with 1 - 4 joints	
Category C:	plants with 5 - 10 joints	
Category D:	plants with 11 or more joints	large plants

The plots were surveyed one month prior to release and one and seven months post release.

The frames of the horizontal sticky traps were placed in a compass pattern around the central point of the release plot (Fig. 52). In the

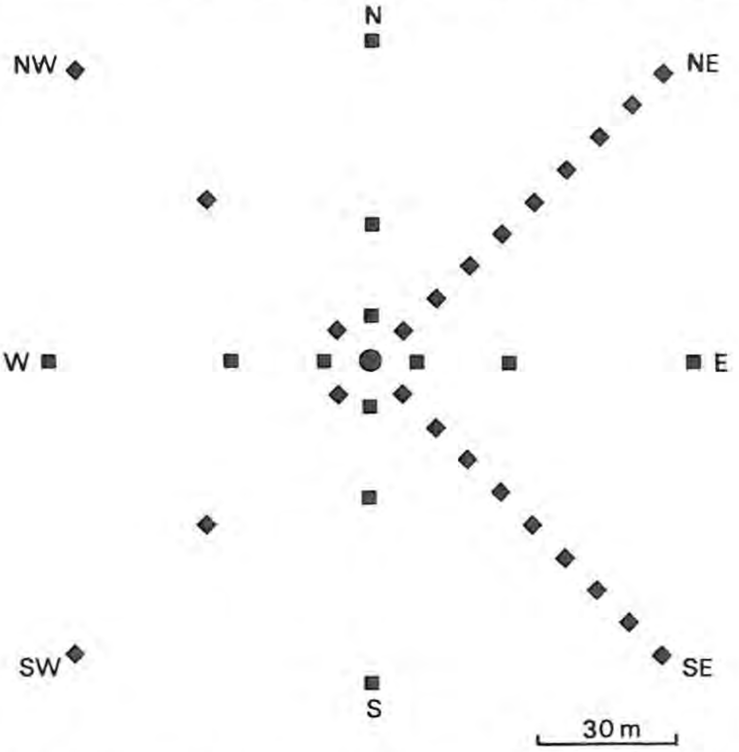


Fig. 52. Arrangement of horizontal sticky impact traps (■) around a tower (●) used to artificially enhance dispersal of *D.austrinus* crawlers.

NE and SE axes of the sampling pattern, traps were set out at 10 m intervals from 10 to 90 m. In the cardinal directions (N, S, E and W) traps were placed 10, 30 and 70 m from the central point and on the remaining two axes (NW and SW) at 10, 50 and 90 m.

The presence of a resident cochineal population necessitated monitoring wind dispersal of crawlers from the jointed cactus plants. For two weeks prior to dispersal from the tower, the glass sheets on the traps were set out on the metal frames and the number of crawlers found on the sheets recorded at weekly intervals. A culture of D.austrinus, collected from field infestations, was then set up on the tower at the central point of the plot. Glass sheets were then set out for the next seven weeks, and traps catches recorded at weekly intervals. The tower was then removed and dispersal from cochineal populations on plants monitored for a further two weeks.

The trap catches for the eleven weeks of the field trial are shown in Table 41. Very few crawlers were recovered from the traps in the two week pre-release period or during the two-week post-release period. Catches on the seven traps, from which crawlers dispersed from plants were recorded, were adjusted for the release period using the formula

Adjusted value = Trap catch in pre and post release period/4 x 7

The values 4 and 7 refer to the number of weeks in the pre-and post-release period and the release period respectively.

The catches on traps at similar distances were totalled and mean values obtained to show the average horizontal distribution of D.austrinus crawlers dispersed from the tower (Table 42). The graphical representation of these data (Fig. 53) was obtained using the programs SINA and CTER (Section 6.2) to fit the general equation of Taylor (1978) to the catch-distance data (Table 42).

Table 42. Mean trap catches of D.austrinus crawlers dispersed from a tower. The trap catches at similar distances in the four cardinal and four semi-cardinal directions were totalled and the mean values obtained to show the average horizontal distribution of D.austrinus crawlers.

Distance (m)	10	20	30	40	50	60	70	80	90
Mean catch	40,7	27,0	13,5	3,5	2,5	3,5	0,7	0,5	1,0

Table 41. Traps catches of *D.austrinus* crawlers recorded at weekly intervals during an evaluation of the crawler release system for enhancing dispersal of *D.austrinus* crawlers. The total catches for the pre- and post-release periods were used to correct for crawlers dispersed from plants during the seven week release period according to the formula:

Trap catches of crawlers dispersed from tower and trap catch in pre- and post-release/4 x 7 (see text).

	Week	N			NE									E			SE									S			SW			W			NW		
		10	30	70	10	20	30	40	50	60	70	80	90	10	30	70	10	20	30	40	50	60	70	80	90	10	30	70	10	50	90	10	30	70	10	50	90
Pre-release period	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Release period	1	2	0	0	1	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	4	0	1	1	2	2	0	2	0	0	0	0	2	2	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	1	0	1
	3	9	8	0	14	13	5	2	1	0	1	0	0	10	8	1	10	4	0	0	0	0	0	0	0	2	0	0	1	0	0	5	2	0	6	0	1
	4	26	9	1	18	18	4	0	0	2	1	4	1	21	4	0	23	8	5	1	0	0	0	0	0	5	0	0	23	0	0	14	6	0	23	2	1
	5	16	9	1	7	3	1	0	0	1	0	3	1	6	4	0	3	5	1	0	1	0	0	0	0	6	3	1	6	0	0	6	5	0	7	5	0
	6	4	1	0	1	2	0	0	0	2	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0
	7	5	0	0	5	1	4	3	0	0	0	1	0	2	2	2	9	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	5	0	0
Post-release period	1	0	0	0	0	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Total pre- and post-release		1	0	0	0	1	0	0	0	0	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Total for release period		62	27	2	50	37	14	6	3	7	2	14	2	41	18	3	49	19	6	1	1	0	1	0	1	16	3	1	30	0	0	29	13	0	45	7	3
Catch of tower dispersed crawlers		60	27	2	50	35	14	6	3	7	0	1	2	41	18	3	49	19	6	1	1	0	1	0	1	16	3	1	30	0	0	29	13	0	45	5	1

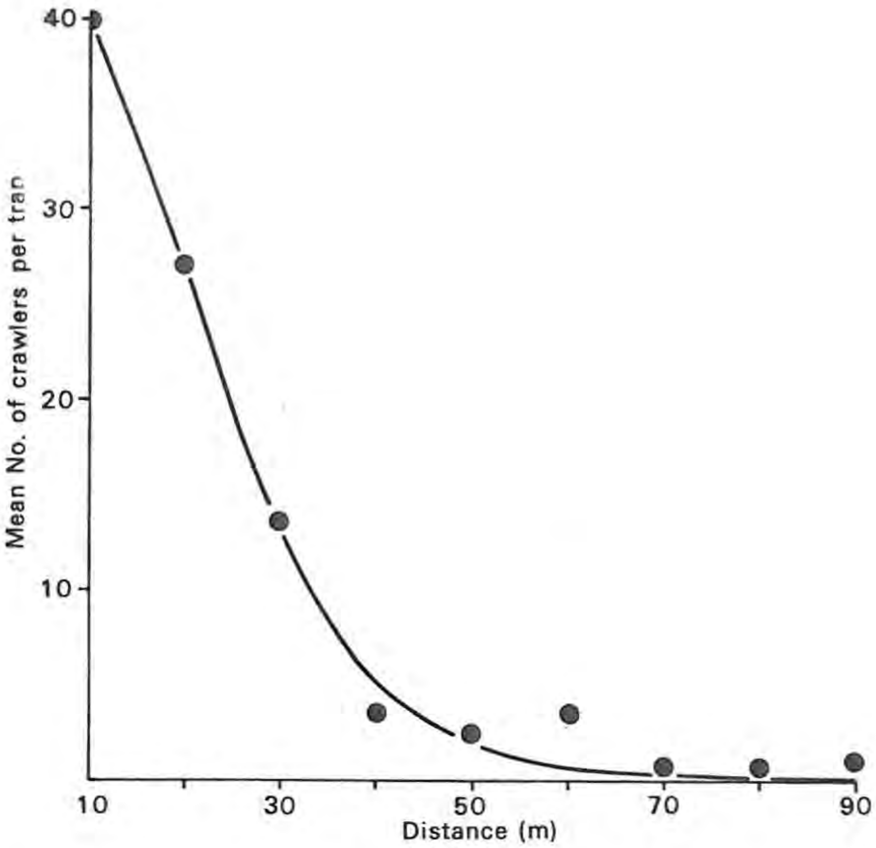


Fig. 53. Mean horizontal distribution of tower dispersed D. austrinus crawlers for the four cardinal and four semi-cardinal directions. Curve fitted using the function $N = \exp(3,6918 - 0,0139\ X^{1,464})$ obtained by an iterative fit (program CTER) of the general model (Taylor 1978) to the mean catch-distance data (Table 42). Mean catch (X). Significance of regression: $F = 715,50$; $p < 0,01$ for 1/6 d.f.

The graphical plot (Fig. 53) shows a rapid decrease in catches from 10 - 60 m, with very low catches thereafter, a similar exponential decrease in the catch with increasing distance as shown for dispersal of crawlers from a single host plant (Section 6.2).

No attempt was made to correlate the dispersal pattern of crawlers with the wind pattern as the staggered trap pattern (Fig. 52) prevented determination of catches equally in each direction.

The area of the glass sheet comprising each trap was 0,160 m^2 and multiplication of the mean catches by a factor of 6,25 provided the dispersal density in crawlers m^{-2} (Table 43).

Table 43. Mean dispersal density of D.austrinus crawlers from 10 to 90 m from the release tower. Trap catches (Table 42) multiplied by factor of 6,25 to provide the mean dispersal densities (crawlers m^{-2}).

Distance (m)	10	20	30	40	50	60	70	80	90
Crawler Density (m^2)	250	168,8	84,4	21,9	15,6	21,9	4,2	3,1	6,3

The mean crawler densities at increasing distances (10 - 90 m) from the tower, represented the mean densities on the circumferences of a series of circles with radii ranging from 10 - 90 m from the tower. An estimate of the total number of crawlers dispersed from the tower was obtained by calculating the number of crawlers in each concentric ring around the tower on the basis of the crawler density on the outer circumference i.e. mean crawler density at 30 m represented dispersal density in a ring 20 - 30 m around the tower. The areas of the nine concentric rings (0 - 90 m) around the tower were calculated and each area multiplied by the respective crawler density to give a value for the total number of crawlers wind dispersed (Table 44).

Table 44. Estimation of total number of D.austrinus crawlers dispersed from a 5 m high tower.

Distance (m)	Area (m^2)	Crawler density (m^2)	Number of dispersed crawlers
0 - 10	314,16	250	78540
10 - 20	942,48	168,8	159090
20 - 30	1570,79	84,4	132575
30 - 40	2199,12	21,9	48160
40 - 50	2827,43	15,6	44108
50 - 60	3455,75	21,9	75681
60 - 70	4084,07	4,2	17153
70 - 80	4712,39	3,1	14608
80 - 90	5340,71	6,3	33646
Total			603561

Population levels of the four categories of jointed cactus plants were expressed as the proportion of the 100 m^2 of each transect in which these categories occurred. With low numbers of crawlers dispersed beyond 60 m (Fig. 53), the overall frequency for the release and control plots was expressed as the mean proportion for the 16 transects within 60 m of the centre portion of each plot.

On both plots there were few large plants (categories C and D), with plants occurring in less than 3% of the surveyed area. This prevents positive comment on the cochineal levels on these plants but to note that this possibly explains the low catch of crawlers in the pre- and post-release periods. The population levels of A and B category plants was similar on the release and control plots and on both plots the frequency decreased over the successive surveys (Fig. 54).

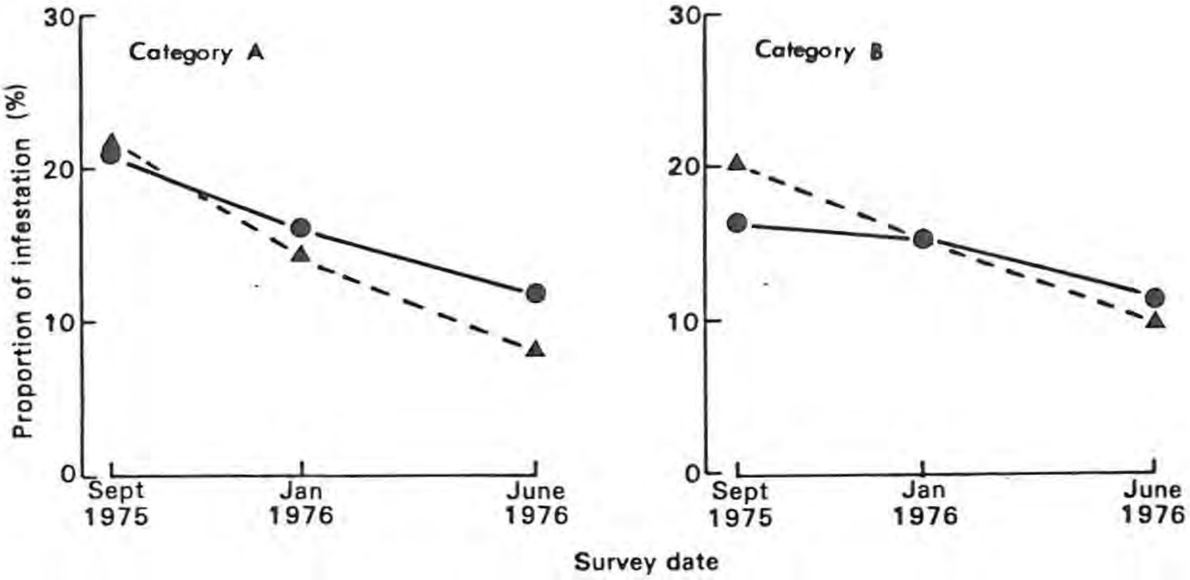


Fig. 54. Proportion (%) of 16 transects within 60 m of the centre points of the release (▲---▲) and control (●——●) plots in which two categories of jointed cactus (<u>O. aurantiaca</u>) occurred. Category A - loose joints, category B - jointed cactus plants with 1 - 4 joints.

Comparison of the cochineal levels on the two plots was made by determining the proportion of the area in which A and B category plants occurred and which also had cochineal (Fig. 55). There was a far higher level of cochineal on the A and B category plants on the control plot than the release plot prior to tower dispersal of crawlers. The level of cochineal on the plants on the control decreased thereafter while that on the release plot increased. These results clearly point to an increase in the amount of cochineal present on the jointed cactus plants after the dispersal of crawlers from the towers.

The drawback to these results was the use of frequency rather than density to estimate jointed cactus and cochineal population levels. The presence of a resident population of cochineal on the plants in the dispersal area tends to confuse the result and therefore it was decided to repeat the field trial in an area free from jointed cactus.

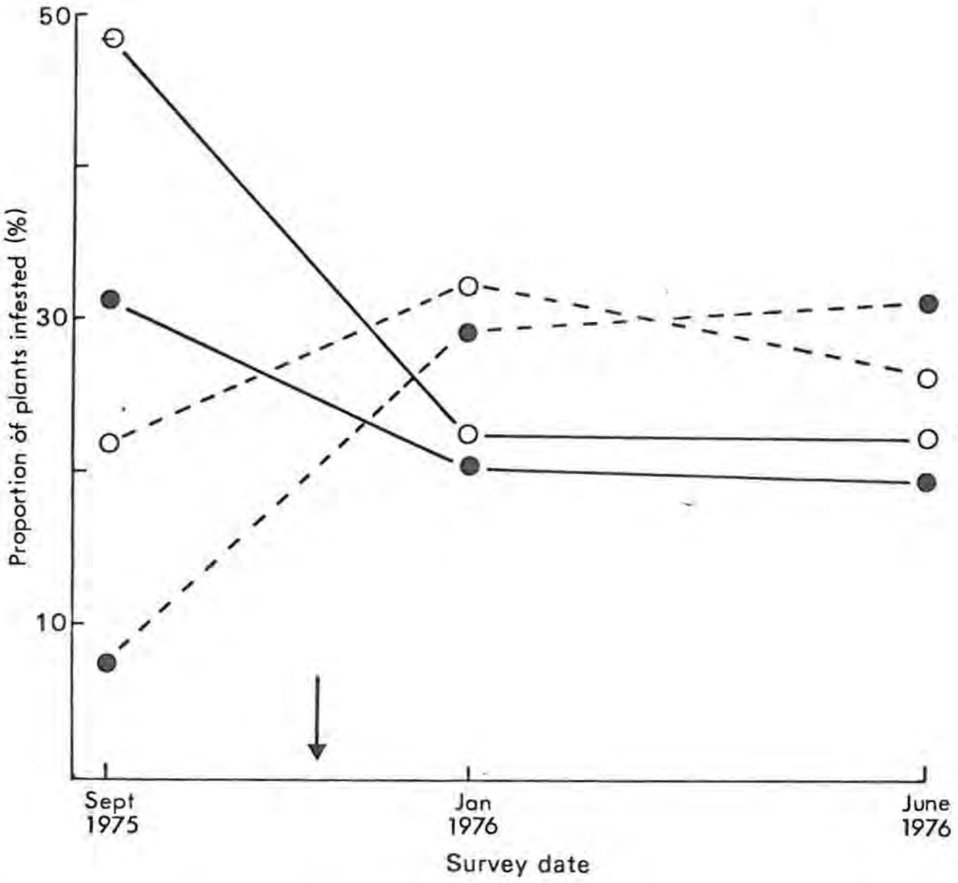


Fig. 55. Proportion (%) of 16 transects (within a 60 m radius of the centre of the release and control plots) in which D. austrinus was present on two categories of jointed cactus plants. Category A (o) - loose joints; category B (●) - rooted plants with 1 - 4 joints. Broken lines - release plot; solid lines - control plot. Vertical arrow indicates onset of seven week period of tower release.

8.3. Table Farm field trial

The second field trial was carried out on Table Farm, 12 km from Grahamstown on the road to Carlisle Bridge. The area was similar to Maastricht in that the plot chosen for dispersal was flat and open with uniform low growing vegetation.

A 2,25 hectare portion of a paddock was demarcated and fenced off to prevent sheep entering the dispersal area. This was necessary as in the absence of jointed cactus plants, potted jointed cactus plants were used to assess the impact of tower dispersal of crawlers, and fencing prevented the animals breaking the plants and spreading cladodes in an area otherwise free of jointed cactus.

On the basis of the horizontal distribution of tower dispersed crawlers in the first field trial (Fig. 53), further evaluation was limited to 60 m. A regular pattern of traps was set out, with six traps placed at 10 m intervals from 10 m to 60 m in each of the four cardinal and four semi-cardinal directions (Fig. 56).

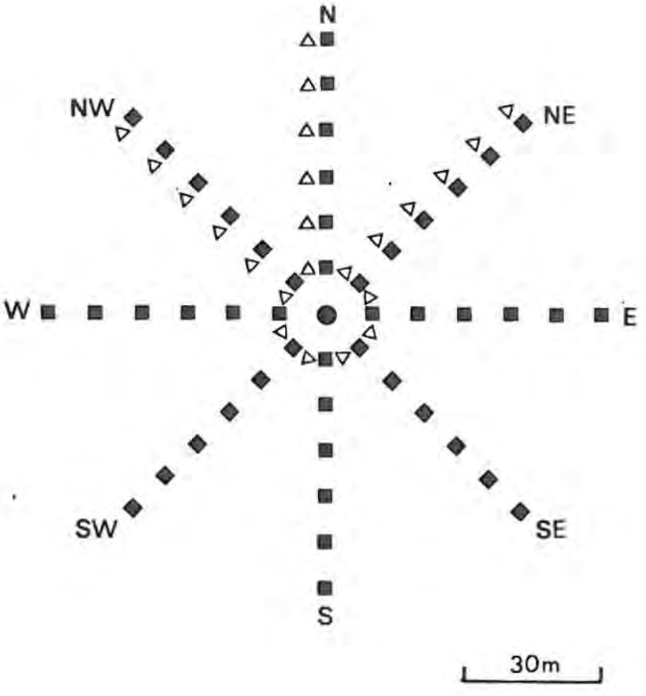


Fig. 56. Arrangement of horizontal sticky impact traps (■) around a tower (●) used to monitor dispersal of D. austrinus crawlers. The position of potted O. aurantiaca plants (△) set out 1 m from 23 of the traps are also shown.

Twenty three large potted jointed cactus plants were placed 1 m to the side of all eight traps in the 10 m circle around the centre point and the remaining traps on the N, NW and NE axes of the trap pattern (Fig. 56). The pots, holding the plants, were sunk into the ground and the soil around the base of the plant smoothed to create as natural conditions as possible.

Fig. 57. Position (arrowed) of potted jointed cactus plant (O.aurantiaca) in relation to horizontal sticky impact trap. Note that the pot has been sunk below ground level to create natural situation.

Figure 57 shows one of these jointed cactus plants in relation to the horizontal sticky impact trap. All plants had been sprayed with Ultracide, toxic to D.austrinus, six and three months prior to this field trial, to ensure there was no trace of cochineal on these plants. Prior to setting the plants in position, a close visual check of each cladode confirmed the absence of cochineal.

A culture of D.austrinus, reared in a holding basket in a C.E. room, was placed in position on top of the tower at the centre point of the trap pattern. For eight weeks from January to March 1977, the glass sheets on the traps were changed at weekly intervals and the number of crawlers on each glass sheet recorded. At the end of this period, the potted plants were returned to the laboratory where each cladode was individually inspected and the number of settled D.austrinus individuals were recorded.

Only three of the eight weeks provided catches that were sufficient to enable correlation of the pattern of crawler dispersal with the wind patterns. Therefore tower dispersal of crawlers, using a culture reared under C.E. room conditions of temperature and humidity, was monitored for a further four weeks from October to November 1977 to provide additional data. The culture was not placed in position on the tower until large numbers of crawlers were being produced.

The wind velocity and direction, temperature, humidity and rainfall were measured during the twelve weeks dispersal was monitored. The relative wind velocities would have increased from ground level to 5 m, the release height of the crawlers, but as it was the relative wind velocity in each direction that was important adequate measurements were obtained by a single anemometer placed on a metal stand 3 m above ground level.

Three features of the tower dispersal experiments are analysed and discussed. Firstly the horizontal distribution of crawlers; secondly the correlation between crawler dispersal and colonization of the jointed cactus plants set out on the plot; and finally comparison of the pattern of crawler dispersal with the wind velocity and direction.

Horizontal distribution

As dispersal of crawlers was only monitored to 60 m from the tower, no attempt has been made to describe the horizontal distribution of crawlers beyond detailing the total catches on each trap for the two periods that dispersal was monitored (Table 45).

The trap catches shown in Table 45 are far greater than those recorded during the Maastricht field trial. This reflects the higher densities of D.austrinus in laboratory reared cultures in the holding baskets in comparison to the density of females on material reared in the field, and the synchronous production of crawlers from laboratory reared cultures. The trap catches were converted to densities (crawler m^{-2}) and, using the mean density at each distance (10 - 60 m), the total number of crawlers dispersed from the towers was estimated using the method described for the Maastricht data (Table 44). Estimates of 1 201 419 and 1 727 144 were obtained for the total number of crawlers dispersed from the tower for the eight and four week dispersal periods respectively. These figures are well in excess of that obtained for the Maastricht field trial of seven weeks (603 561) which included the crawlers dispersed between 60 and 90 m from the tower.

Although the total number of crawlers dispersed during the four week trial exceeded that for the eight week trial it must be remembered that the majority of crawlers were dispersed in four of the eight weeks.

Table 45. Trap catches of D. austrinus crawlers dispersed from a tower for periods of (A) eight weeks (Jan-March 1977) and (B) four weeks (October-November 1977).

A. January-March 1977

	N	NE	E	SE	S	SW	W	NW
10	102	72	54	72	31	43	61	95
20	80	29	26	32	8	11	54	92
30	62	26	20	14	3	6	41	50
40	51	15	5	8	0	2	30	28
50	26	7	2	8	0	3	14	23
60	16	0	1	1	0	0	14	17

B. October-November 1977

	N	NE	E	SE	S	SW	W	NW
10	44	81	94	83	72	56	70	89
20	62	65	68	55	33	47	105	79
30	53	54	32	30	13	20	71	38
40	36	45	22	15	4	10	47	23
50	25	29	15	6	2	5	20	13
60	13	10	5	4	4	3	28	15

The individual trap catches (Table 45) show a general decrease from 10 to 60 m and this suggests that large scale tower release would involve setting up towers at 120 m apart. Overlapping dispersal would increase dispersal densities between 40 and 60 m from each tower. The catch recorded per trap for crawler dispersal from a high density population of jointed cactus heavily infested with cochineal (Section 7.2) ranged from 24 to 806 (mean 152.6) over a 14 week period. The mean catch on traps from 10 m to 30 m (24 traps) for the total 12 weeks of tower dispersal was 104.8. This figure suggests that with an increase in the size of the holding basket the tower system can provide long range dispersal of crawlers at densities equal to that for natural dispersal from high density jointed cactus populations. The overlapping dispersal, which would result with use of a pattern of towers would raise catches from 40 to 60 m but not to the levels recorded for traps from 10 to 30 m.

The analysis of the data on colonization of the potted plants by crawlers dispersed from the tower over eight weeks (January to March 1977) suggests that existing dispersal densities from towers (Table 45) would suffice to ensure inoculation of cochineal-free jointed cactus plants with D.austrinus crawlers.

Colonization of jointed cactus plants

Settled first and second instar D.austrinus nymphs were found on 22 of the 23 jointed cactus plants placed alongside the eight traps in the 10 m circle around the dispersal tower and alongside the remaining traps on the N, NE and NW axes of the trap pattern (Fig. 57). Each plant was broken up at the end of the experiment and the individual cladodes carefully scrutinised and the number, instar and sex of the settled crawlers recorded (Table 46).

The cladodes were categorised as shown in Figure 58. In certain cases there were more than one base cladode, where joints dislodged from the canopy had fallen alongside the plant and had rooted. The data obtained from the inspection of each cladode of the 23 plants is shown in Table 46.

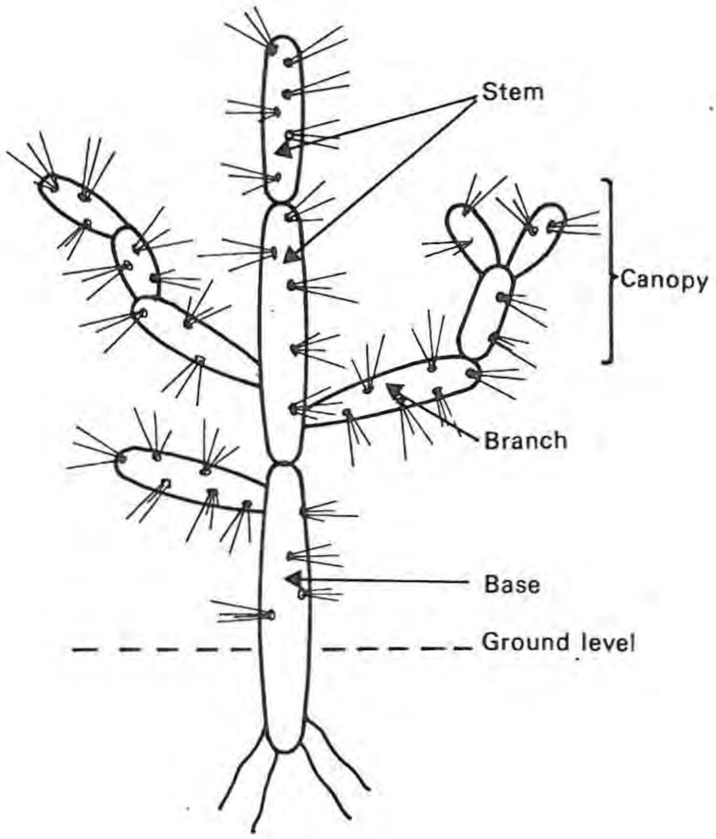


Fig. 58. Plan of the four categories of cladodes forming O.aurantiaca plants.

Table 46. Number, instar and sex of D.austrinus, wind dispersed from a 5 m high tower, colonizing and recovered from 23 jointed cactus plants (O.aurantiaca) (see Fig. 56). The direction and distance of each plant in relation to the tower is shown. The number of cladodes in each of four cladode categories (base, stem, branch and canopy) forming each plant are given. The number of D.austrinus individuals found on each of the four categories of cladode and the number found in the open or covered by soil is also recorded.

Plant		D.austrinus				No. of cladodes				Cladode position of D.austrinus				Position of D.austrinus	
Direction	Distance	Instar			Dead	Category									
		I	II	II		Base	Stem	Branch	Canopy	Base	Stem	Branch	Canopy	Open	Soil
N	10	2	1			1	3	12	26			3		3	
N	20	1				1	1	10	31			1		1	
N	30	7	3			1	1	8	10			10		3	7
N	40	1				1	1	11	13			1		1	
N	50	3	3			1	3	6	14		1	5		6	
N	60	2	6	1		2	6	13	57	2	5	2		7	2
NW	10	6	1		2	7	5	16	62	7		2		9	
NW	20	1	2			1	3	16	38		1	2		3	
NW	30		1	1		2	8	22	52			2		2	
NW	40	2	1		1	3	1	10	24			4		4	
NW	50	2	1			1	3	11	30		1	2		3	
NW	60	1			1	1	2	11	31		2			2	
NE	10	7				1	3	18	38		5	2		5	2
NE	20		1			1	1	12	18		1			1	
NE	30	6	4	1		1	7	13	29		10	1		7	4
NE	40	1				1	1	18	42			1		1	
NE	50		2			1	6	23	49		1	1		2	
NE	60														
E	10	9	3			2	8	9	20	4	8			5	7
SE	10	13			1	1	3	17	36	1		13		7	7
S	10	3				1	2	21	24		1	2		1	2
SW	10	6	3			1	6	8	10	2		7		6	3
W	10	13	2			1	7	21	15	3	1	11		11	4
		86	34	3	5					19	37	72		90	38

3,9% of the total number of 1st and 2nd instar D.austrinus recovered from the cladodes were dead. It is likely that the true mortality among the settled crawlers was higher as the remains of other dead crawlers were likely to have disappeared from the plants.

Crawlers, once settled and feeding, produce a different category of wax to that of the freeliving crawlers and it was not possible to sex the crawlers accurately on the basis of the filaments. Only the 2nd instar could be sexed positively and the number of male and female 2nd instar are shown in Table 46. Of the 2nd instar D.austrinus, 8,11% were males which must reflect the lower number of males dispersed from the tower. No adults were found but this was expected as the majority of crawlers were dispersed within 35 days of the inspection of individuals on the joints.

No crawlers were recovered from the canopy joints, while the proportions of crawlers recovered from the base, stem and branch cladodes were 14,8, 28,9 and 56,3% respectively. The branch and stem joints would be the most protected in terms of temperature as they would be shaded for certain times of the day by the outer canopy joints. The possible influence of direct sunlight on the settling position was shown by the fact that all the cochineal found on the branch joints had settled on the underside of the joints. This position would protect the newly settled crawlers from direct sunlight and the impact of rain drops. This settling pattern is a common feature of infested plants in the field. Three plants had crawlers which settled on the base cladodes, slightly below ground level, where the soil was loose. Crawlers were also recovered from dislodged cladodes which fell to the ground and rooted (categorised as base cladodes) alongside three other plants.

Rain, which fell during the eight weeks of dispersal, spattered soil onto the surface of cladodes close to the ground and formed a shallow crust on the vertical and ventral surfaces of the cladodes. Nearly one third (29.7%) of the settled individuals were found beneath this crust which would have provided additional protection.

There was no correlation between the density of dispersed crawlers (m^2), recovered from the traps 1 m from each plant, and the number of crawlers which settled on the plants (Fig. 59). The area of each plant was not measured, which may have accounted for part of the difference between dispersal and colonization levels. If it is assumed that only

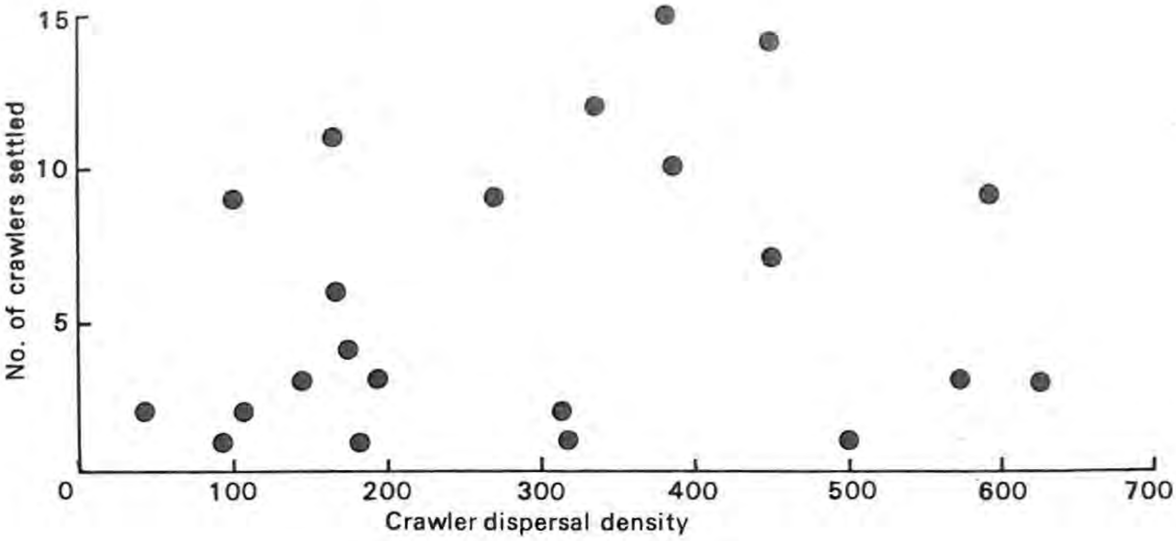


Fig. 59. Relationship between dispersal density of crawlers of D.austrinus and the number of crawlers colonizing O.aurantiaca plants.

crawlers landing in the metre area containing the jointed cactus plants had access to the plants, i.e. allowing for ground movement up to 50 cm, the percentage colonization by dispersed crawlers can be calculated for each plant (Table 47).

Table 47. Calculated percentage colonization of O.aurantiaca plants by wind dispersed crawlers landing in a metre square area around each plant. Percentage colonization = number of D.austrinus settled on the plant/number of crawlers dispersed into metre square area around plant.

Plant	% colonization	Plant	% colonization	Plant	% colonization	Plant	% colonization
N 10	0,5	NW 10	1,5	NE 10	1,6	E 10	3,6
N 20	0,2	NW 20	0,6	NE 20	0,6	SE 10	3,1
N 30	2,6	NW 30	0,6	NE 30	6,8	S 10	1,6
N 40	0,3	NW 40	2,3	NE 40	1,2	SW 10	3,4
N 50	4,0	NW 50	2,1	NE 50	4,6	W 10	3,9
N 60	9,0	NW 60	1,9	NE 60	N.A.		

The pots in which the jointed cactus plants were reared were 20 cm in diameter, a cross-sectional area of 0,031 m^2. In all cases the canopy area of the plants was never less than the cross-sectional area of the pot. Therefore using the cross-sectional area of the pot as the minimum for the jointed cactus plants, each plant would have occupied 3,1% of the metre square around the plant. The mean colonization percentage was 2,5% and when compared with the minimum area of the plants canopy (3,1%), this suggests that only crawlers which land within the canopy are capable of colonizing the plant. This in turn emphasises the importance of the large clumps of jointed cactus plants as colonization sites for dispersed crawlers.

The most important feature of these results is that all the plants, which were within the dispersal range of crawlers blown from the tower, were "inoculated" with D. austrinus. Although the plants were large, they were isolated and this confirms that the dispersal densities obtained by tower release for the eight-week trial would be sufficient to introduce D. austrinus into areas previously free of cochineal.

The implementation of tower dispersal of D. austrinus on a large scale to augment or introduce cochineal on jointed cactus infestations would involve monitoring dispersal densities over wide areas. The high correlation between the pattern of crawler dispersal from the host plant and the pattern and strength of winds (Section 6.4) could provide a simple method of monitoring the dispersal patterns of tower dispersed crawlers.

The two computer programs (WINI and WIN2) developed to estimate catches of crawlers in eight directions around the host plant on the basis of (i) the windrun in each direction, (ii) the time the wind blew in each direction and (iii) the value for windrun x temperature in each direction were used to obtain estimates of tower dispersed crawlers (see Section 6.4).

Anemometer and thermohygrograph recordings for three weeks of the first field trial (January to March 1977) and all four weeks of the second field trial (October to November 1977) were analysed to provide hourly temperatures and the hourly wind direction scores (Section 6.4). The analysis was restricted to daylight hours between 07h00 and 19h00. The period 06h00 - 07h00 was not included due to the prevalence of heavy dews in the early morning which saturated the cladodes in the cultures and prevented movement and dispersal of crawlers. In addition, the hours during which rain fell and periods of high winds were not included in the analysis. It has been shown that the majority of dispersed crawlers comprise female crawler 48 h and older (Section 6.5). On the basis of the terminal velocity of 48 h old crawlers and the release height of the tower it was calculated, using the formula of Brown (1958), that hourly windrun in excess of 16 km would carry crawlers beyond the 60 m mark. Therefore periods with windrun exceeding 16 km per hour were omitted from the analysis. Table 48 shows the estimated catches for the seven weeks made on the basis of the ratios of windrun, time and windrun x temperature in each direction. The catches in each direction, the total for the six traps from 10 - 60 m, are corrected for dilution.

Table 48. Trap catches (x dilution factor) and estimated catches of D.austrinus crawlers dispersed from a 5 m high tower using windrun (km) windrun time (mins) and value for windrun (km) x temperature ($h^{o} > 13^{o}C$) allocated in the four cardinal and four semi-cardinal directions on the basis of wind direction scores. The correlation values for observed and estimated catches are shown for 1/6 d.f.** Significant at the 1% level; * significant at 5% level.

Week 1. (10.02.77 - 17.02.77)

Direction	N	NE	E	SE	S	SW	W	NW
Catch	214	44	22	19	11	6	65	89
Est. catch ratio (windrun)	141	73	19	13	7	3	18	73
Est. catch	192	99	26	17	9	4	24	99
Correlation					r = 0,9175**			
Est. catch ratio (windrun time)	737	492	153	151	98	36	104	389
Est. catch	160	107	33	33	21	8	23	85
Correlation					r = 0,8563**			
Est. catch ratio (windrun x temp)	2415	1125	346	290	155	94	457	1388
Est. catch	181	84	26	22	12	7	34	104
Correlation					r = 0,9418**			

Week 2. (17.02.77 - 23.02.77)

Direction	N	NE	E	SE	S	SW	W	NW
Catch	346	78	21	30	8	5	129	328
Est. catch ratio (windrun)	139	51	15	11	6	1	32	180
Est. catch	302	111	33	24	13	2	70	391
Correlation					r = 0,9640**			
Est. catch ratio (windrun time)	766	357	143	118	63	19	191	922
Est. catch	281	131	52	43	23	7	70	337
Correlation					r = 0,9596**			
Est. catch ratio (windrun x temp)	1350	414	132	107	57	18	286	1761
Est. catch	309	95	30	24	13	4	66	403
Correlation					r = 0,9647**			

Week 3. (24.02.77 - 03.03.77)

Direction	N	NE	E	SE	S	SW	W	NW
Catch	122	23	85	149	16	40	211	107
Est. catch ratio (windrun)	69	16	42	50	11	32	150	73
Est. catch	117	27	71	85	19	54	254	124
Correlation					r = 0,9113**			
Est. catch ratio (windrun time)	405	93	210	286	109	175	744	438
Est. catch	124	28	64	88	33	54	228	134
Correlation					r = 0,9095**			
Est. catch ratio (windrun x temp)	473	292	791	746	134	355	1328	465
Est. catch	78	48	129	123	22	58	218	76
Correlation					r = 0,8915**			

Week 4. (25.10.77 - 31.10.77)

Direction	N	NE	E	SE	S	SW	W	NW
Catch	194	232	77	33	39	94	259	314
Est. catch ratio (windrun)	83	56	27	10	15	36	91	105
Est. catch	244	165	79	29	44	106	268	309
Correlation					r = 0,9552**			
Est. catch ratio (windrun time)	485	333	194	105	140	270	597	636
Est. catch	218	150	87	47	63	123	269	286
Correlation					r = 0,9413**			

Est. catch ratio (windrun x temp)	830	398	184	106	140	303	798	1010
Est. catch	274	131	61	35	46	100	263	333
Correlation					r = 9057**			

Week 5. (31.10.77 - 07.11.77)

Direction	N	NE	E	SE	S	SW	W	NW
Catch	82	77	107	154	87	59	584	172
Est. catch ratio (windrun)	63	15	12	19	22	57	151	102
Est. catch	189	45	36	57	66	171	453	306
Correlation					r = 0,8047*			
Est. catch ratio (windrun time)	301	84	88	140	170	296	717	485
Est. catch	174	49	51	81	99	172	416	281
Correlation					r = 0,8196*			
Est. catch ratio (Windrun x temp)	400	76	143	193	160	387	971	633
Est. catch	178	34	64	86	72	173	433	282
Correlation					r = 0,8317*			

Week 6. (07.11.77 - 14.11.77)

Direction	N	NE	E	SE	S	SW	W	NW
Catch	180	202	212	73	26	12	15	40
Est. catch ratio (windrun)	131	152	61	36	17	15	37	82
Est. catch	188	217	87	52	24	21	53	117
Correlation					r = 0,7526*			
Est. catch ratio (windrun time)	712	788	355	257	117	81	182	450
Est. catch	184	204	92	66	30	21	47	116
Correlation					r = 0,7770 *			
Est. catch ratio (windrun x temp)	678	745	339	179	82	110	270	449
Est. catch	181	198	90	48	22	29	72	120
Correlation					r = 0,7270 *			

Week 7. (14.11.77 - 22.11.77)

Direction	N	NE	E	SE	S	SW	W	NW
Catch	215	214	123	137	75	128	111	83
Est. catch ratio (windrun)	89	104	54	28	39	45	77	103
Est. catch	179	210	109	56	78	91	155	133
Correlation					r = 0,6637			
Est. catch ratio (windrun time)	427	525	338	213	284	345	463	466
Est. catch	151	186	120	76	101	122	164	165
Correlation					r = 0,3806			
Est. catch ratio (windrun x temp)	619	979	526	328	448	425	657	425
Est. catch	153	241	130	81	110	105	162	65
Correlation					r = 0,6639			

With the exception of week 7, the estimated catches determined on the basis of wind direction score were significantly correlated with the observed catches corrected for dilution. Where significant correlations were obtained there was little difference between using windrun as opposed to windrun x temperature in catch allocation.

The programs WIN1 and WIN2 provide an estimated catch ratio in each direction. The estimated catches in each direction were obtained by converting the estimated catch ratio to a frequency of 1 and allocating the total trap catch in each direction of the basis of the frequency (see Table 33, section 6.4). It is not necessary to know the total catch in all directions as the catch in one direction could be used with the estimated catch ratio (converted to a frequency of 1) to estimate the catches in the remaining directions. As the catches from 10 m to 60 m show a virtually linear decrease in numbers (Table 45), the single catch could be used to estimate the catch out to 60 m. Therefore a single trap and analysis of either the windrun, windrun time or a value for windrun x temperature in each direction could provide an estimate of the dispersal pattern around the tower. This would enable estimates of dispersal densities over large areas using multiple tower release.

9. DISCUSSION

The diversity of information obtained during this study necessitates a summary of this work and discussion of the relevance of these findings in relation to the potential of *D.austrinus* to control jointed cactus populations. The importance of the habitat in determining the strategies insects evolve in order to survive and reproduce (Southwood 1977) emphasises the necessity of evaluating dispersal in relation to characteristics of the host plant. Comparison of features of *D.austrinus* biology which influence the dispersal potential of this species with those of other coccoid species will enable an assessment of the migratory status of this insect.

Southwood (1977) stated that "In the course of evolution the members of a species will evolve those strategies that maximise the numbers of their descendants in their habitat which must be viewed from two dimensions... namely time and space.". The stability of a habitat will depend on the time the habitat (H) remains favourable for the insect in relation to the generation time of the insect (τ). The ratio ($\frac{\tau}{H}$) provides a measure of this relationship (Southwood 1975b). Where the ratio is close to unity the habitat is unstable or temporary while low ratio values point to a permanent habitat. The association of a high level of migratory movement in species inhabiting temporary habitats was emphasised in the introduction to this study. Jointed cactus plants are rapidly destroyed by the toxic feeding action of *D.austrinus* and must rate as temporary habitats.

The terms "*r*" and "*K*" (MacArthur & Wilson 1967) have been used to describe the ecological strategies evolved by species utilizing temporary and permanent habitats respectively (Dingle 1972; Southwood *et al.* 1974 and Southwood 1977). Conway (1976) summarises the features of "*r*" strategists as a high potential increase, strong dispersal and host finding ability and of small size compared to "*K*" strategists which have low rates of potential increase, greater competitive ability and more specialised food preference.

Species living in temporary habitats will require to move and locate new habitats (Southwood 1962) which in the initial stages of colonization are "ecological vacuums" with no density or crowding effects (Pianka 1967). The optimal strategy of a colonizing insect will be high productivity

(MacArthur & Wilson 1967; Pianka 1967; Dingle 1972; Southwood et al. 1974 and Southwood 1977) and rapid population growth at low densities (Southwood et al. 1974). The latter is achieved by rapid development, decreased generation time and reproduction early in adult life (Pianka 1967; Dingle 1972 and Southwood et al. 1974). The result of this strategy is the rapid increase in numbers utilizing short term resources leading to "scramble type" competition with populations overshooting equilibrium levels (Southwood 1977), a characteristic feature of "r" strategists.

Southwood (1977) stated "Evolution will...favour all traits that serve to maximise the expectancy of arriving and surviving to breed...i.e. the ability to migrate, the ability to survive the dangers of migration or dispersal and the ability to find (or arrive in) the new habitats.". Although actively dispersing insects may not have control over the direction of displacement during migration (Kennedy 1961 and Rainey 1962), they have the ability to search, locate and select new habitats at the end of the migratory flight. Passively dispersed organisms may have the ability to disperse from the parent habitat and behavioural patterns to enhance dispersal, but are restricted in the location of new habitats as deposition in suitable areas of the environment is purely fortuitous. For a passively dispersed organism like D. austrinus this emphasises the necessity to assess the ability of the species in question to (i) leave the parent habitat; the migrant status of the species, and (ii) the importance of the spatial distribution of new habitats with regard to the chance of "location" of new resources for feeding and reproduction.

Active dispersal requires the utilization of energy which might otherwise have gone into reproduction (Roff 1977). The energy expended is not limited to fuel for movement but also that directed into the formation of locomotor organs. The redirection of energy is shown in migrant forms of species which have reduced fecundities in comparison to their more sedentary counterparts (Dingle 1972). Many species are capable of histolysis of flight muscle but it is questionable whether or not this material is reinvested in reproduction (Johnson 1969).

Johnson (1969) described the 'oogenesis-flight syndrome'; relating the differential development of the flight apparatus and ovaries in response to environmental factors to "produce" a variety of morphs that range from sexually immature but flight-worthy females (characteristic of the migrant state) through sexually mature flight-worthy non-migrants, and brachypterous adults, to parthenogenetic and paedogenetic flightless forms.". He stated that the syndrome was a characteristic of the Insecta and central to the lives of the insects. Johnson (1969) noted that early larval stages of sessile non-migratory adults were adapted to "disperse in an inert manner.".

The "oogenesis-flight syndrome" does infer a lack of migrant status in sessile paedogenetic species, which further suggests the restriction of these species to permanent habitats which require a low level of migratory potential.

Miller and Denno (1977) see the evolution of a sessile paedogenetic female in the Coccoidea as a strategy to increase feeding efficiency and reproduction potential. The sessile life style along with the development of specialised mouthparts provides coccoid females with access to a continuous food supply through the phloem vessels of the host plant. Englemann (1970) states; "It is apparent from the many reports on insect reproduction that a variety of factors, both external and internal to the animal, influences total egg production. Nutrition which has been shown to affect the total egg output in several ways, is probably the most important single factor in the majority of insect species.". Both the quality and quantity of food are important in determining fecundity (Johannson 1964). In coccoid insects, the sessile mode of life, high feeding efficiency and the absence of functional locomotor organs all provide for the redirection of energy into reproduction.

The advantage of this life style must be balanced against the disadvantage of the dispersal of an apterous immature sector of the population which will result in a great loss amongst the crawlers which fail to locate new host plants. However the status of the Coccoidea as a major problem in agriculture and forestry points to the success of this strategy, which can be described by a general statement made by Pianka (1967) "as putting all possible matter and energy, into reproduction with the smallest predictable amount into each individual offspring, and to produce as many total progeny as possible.". The restriction of the "oogenesis-flight syndrome" is the allocation of migrant status to the young adult, which is a common feature of this process in actively dispersing insects. I suggest that the evolution of the paedogenetic sessile female in D.austrinus has shifted the migratory phase to the developmentally immature stage and in no way detracts from the migrant status of this species. Evaluation of the results of this study will help to confirm this hypothesis.

The recognition of sexual dimorphism in filament development of D.austrinus crawlers (Gunn 1978) has enabled differentiation of the role of male and female crawlers in dispersal. Since the adult female is paedogenetic and sessile, dispersal of females is limited to the free-living crawler stage between emergence from beneath the adult and the time the crawlers settle and begin feeding. The importance of this wandering period with respect to dispersal, has been emphasised by Hulley (1962) and Willard (1974). The males on the other hand may disperse in the crawler stage and as winged adults. Differences in morphology, terminal velocities and behaviour reflect the importance of dispersal of female crawlers as opposed to male crawlers.

After hatching, male crawlers settle and feed beneath or in the immediate vicinity of the adult, while female crawlers move away from the adult in search of a suitable feeding position. Avidov and Harpaz (1969) state "The phenomenon of male and female insects concentrating separately is fairly common among the armoured scale family Diaspididae." This separation in feeding sites can result from limited movement by males in relation to females or by the selection of different feeding sites on the host plants.

The male crawlers of Pseudaulacaspis pentagona Targ. settle close to the adult while the female crawlers wander for several hours (Bennett & Brown 1958), and as a result the males are clustered on the older and lower portions of the tree while the females move out over the whole plant including new growth (Kiutert 1967). Cumming (1953) found 70% of female crawlers of the pine needle scale Phenacaspis pinifoliae (Fitch) on new growth of white spruce twigs while 99% of the males remained on old growth. The female crawlers moved four times as far as the males (Brown 1958).

Bliss et al (1935) recorded that the crawlers of the camphor scale Pseudaonidia duplex Ckll. were found predominately on the leaf blades while the majority of the female crawlers settled on the leaf stem. Morgan and Angle (1969) found a similar pattern in the feeding positions of the crawlers of the San Jose scale Aspidiotus perniciosus Comst. Their observation that the females which settled on the leaf blades failed to mature, suggests that the short-lived males require less nutrient than the developing females.

Mathis (1947) and Bodenheimer (1951) have shown preferences by the male crawlers of *Chrysomphalus aonidium* (L.) for the upper sides of leaves as opposed to the females which settle on the lower sides. Schweig and Grunberg (1936) made a similar observation for crawlers of the black scale *Chrsomphalus ficus* Ashm.. The undersides of the leaves are more protected and the females with the longer life cycle will benefit from protection by the leaf blade; in addition Avidov and Harpaz (1969) suggest higher temperatures on the upper side of the leaves will accelerate growth of the males.

Le Baron (1871) and Riley (1873) (cited in Brown 1958) suggested movement of the female crawlers of the pine needle scale *P.pinifoliae* to new growth provided access to the most suitable feeding sites and sufficient time to complete their development before the needles senesced and fell from the plant. The males, they reasoned, fed for only a short time and the feeding site was of little importance.

D.austrinus males, which form cocoons at the end of the second instar, feed for approximately 26 days in comparison to the female which feeds for the entire life cycle (ca. 116-196 days). The separation of feeding positions ensures that the female, which requires a large volume of nutrient for the production of offspring and continuous access to food during her life, has access to the most suitable feeding sites.

The behaviour of the male crawlers is also important in the context of dispersal. Since the male crawlers feed and pupate in close proximity to the parent, they emerge as adults at the point from which female crawlers of the same generation had previously set out in search of a settling sites. Therefore, movement of the adult males away from the parent is then likely to bring the males into contact with settled virgin females on the plant. Furthermore, Rice and Moreno (1970) have shown adult males of the red scale *A.aurantii* are blown downwind and Willard (1974) has shown that the horizontal distribution of these adult males is similar to that in the crawler stage. This suggests that *D.austrinus* males, which remain in the vicinity of the parent during development, may be blown to areas to which females of the same generation were dispersed as crawlers. This will ensure fertilization of virgin females dispersed as crawlers.

The behaviour of newly emerged female crawlers differs totally from that of males. The movement of female crawlers to the spines of the terminal cladodes of the plants is obviously behaviour orientated towards "take-off", which enhances the possibility of dispersal. The advanced age of females (ca. 60 h)which display this behaviour pattern suggests a sequence of events to enhance firstly the location of feeding sites on the parent host plant and then dispersal and the chance location of new host plants.

On emergence from beneath the parent, the females move around the plant, probing the plant with their mouthparts to select a suitable site to begin feeding. At this stage filament development is minimal in comparison to the full potential development and there is less chance of removal by air currents. After two to three days, the crawlers which fail to settle switch their behaviour from trivial movements around the plant (appetative movements) to a behaviour pattern which enhances removal from the parent host plant, and move to the terminal points of the plant. At this stage the filaments are sufficiently developed to increase the chance of dispersal and removal from the parent host plant.

Taylor and Taylor (1977) stated "In an environment changing through time and space, the most probable strategy for a new individual to adopt to survive and reproduce is not necessarily to stay and compete with its parents or congeners but may be to go elsewhere, to find an empty environmental hole to inhabit. Its ability to do this depends on its malleable migrant status.". A further statement by these authors was that "...all spatial dispositions can legitimately be regarded as resulting from the balance between two fundamental antithetical sets of behaviour always present between individuals. These are, repulsion behaviour, which results from the selection pressure for individuals to maximise their resources and hence to separate, and attraction behaviour, which results from the selection pressure to make maximum use of available resources and hence to congregate wherever these resources are currently most abundant. The balance between these two conflicting behavioural tendencies operating on each individual determines its movements and hence the resulting spatial pattern of the population at any instant in time. It is the response of this balance to changing internal and external environmental conditions that, we suggest, constitutes the dynamic element in populations.".

I suggest the behaviour and filament development of D.austrinus female crawlers provide a labile system which enhances firstly, the chance of utilization of current resources and then secondly, the chance of location of resources elsewhere. It is possible that the physiological status of the host plant (current resource) is signalled to the crawlers by the feeding action of the parent generation. On heavily infested plants, this prevents the crawlers settling and enhances dispersal thereby preventing competition for a limited and temporary resource.

The behaviour of A.tegalensis crawlers, the movement of newly emerged crawlers to the tips of leaves ("take-off") led Greathead (1972) to suggest that photokinesis and upward movement of crawlers of other species, suggested by different authors as movement to new growth, might be reassessed as migratory movement.

Movement of crawlers to new growth in deciduous trees and conifers is well documented in several families of the Coccoidea. In the Asterolecaniidae, James (1933) commented for crawlers of the coffee scale Asterolecanium coffeae Newst. in Kenya: "The heavy flow of sap induced by the 'rains' results in great reproductivity among the surviving scales, and there is a noticeable migration of larvae from the older parts of the tree to the rapidly developing shoots.". There are numerous similar comments for members of the Coccidae (Smith 1944; Bodenheimer 1951; Rabkin and Lejeune 1954; Husseiny and Madsen 1962; Phillips 1962; Bedford 1968; Avidov & Harpaz 1969 and Chatterji & Datta 1974), Diaspididae (Bliss et al. 1935; Jones 1936; Stafford & Barnes 1948; Cumming 1953; Brown 1958; Gentile & Summers 1958; Samarasinghe & Le Roux 1966 and Avidov & Harpaz 1969); Eriococcidae (Hoy 1961), Margarodidae (Avidov & Harpaz 1969) and Pseudococcidae (Strickland 1951b; Highland 1956; Browning 1958; Washburn 1965 and Ghose 1972).

The non-lignified growing points of the host plant provide the crawlers with easy access to nutrients flowing to the developing tissues. Podsialdo (1976) showed that the crawlers of Asterodiaspis variolosa (Ratzeburg) moved greater distances from the adults on older bark than from those on younger bark. Hoy (1961) and Willard (1974) have shown that the crawlers of E.orariensis and A.aurantii respectively display no behaviour to enhance dispersal. From this literature I conclude that movement to new growth in species living on deciduous trees and conifers is appetative and not behaviour directed to enhance dispersal.

However movement to new flush will place the crawlers in the outer portion of the canopy where air currents are strong (Cornwell 1960) and this, together with the jarring movement of leaves and branches in the wind, will dislodge many crawlers prior to their settling. Cornwell (1960) and Willard (1974, 1976) showed large numbers of cacao mealy bug (P.njalensis) and red scale (A.aurantii) crawlers respectively are dispersed from the host plant in this manner. Dispersal of these species is "accidental" in comparison to the directed movements of A.tegalensis and D.austrinus crawlers which removes them from protected areas of the habitat to points where the possibility of dispersal increases.

The assessment of the dispersal potential of D.austrinus has shown that this insect, which inhabits a temporary host plant, is well adapted for dispersal from a low growing host plant. Therefore if dispersal is the limiting factor in the biocontrol potential of D.austrinus, as suggested by Zimmermann et al. (1974), it is possibly characteristics of the host plant rather than the insect which limit dispersal and subsequent colonization of new host plants.

Southwood (1977) states that the habitat may be characterised by favourable areas and unfavourable areas, quantified as "patch size" and "interpatch size" respectively. Kitching (1971) pointed out that in any ecosystem there are major habitats "and their faunas are spatially limited only by the limits of the ecosystem itself.". He drew attention to the minor habitat components scattered throughout the major habitat units, which are strictly delimited and are restricted areas for their fauna e.g. carrion, dung, water-filled tree holes and fallen logs. Kitching (1971) emphasised the separateness of these minor habitat units by describing them as "discrete" habitats.

Although ground movement by D.austrinus crawlers has not been fully quantified, the small size of the crawlers and high ground temperatures will severely limit this mode of dispersal. Therefore jointed cactus plants or clumps of plants will be discrete habitats for D.austrinus and the "patch size" and "interpatch size" will be of paramount importance with respect to crawler dispersal.

The dispersal range of horizontally dispersed D.austrinus crawlers is limited with the majority of crawlers deposited a few metres from the parent host plant. Once the distances between "patches" or rather jointed cactus plants, exceed the dispersal range the majority of crawlers will fail to locate new host plants. However it has been shown that a small percentage of crawlers are carried vertically upwards and are sufficiently hardy to survive long distance dispersal. The success or failure of these individuals to "locate" new host plants will depend on the proportion of ground covered by jointed cactus; the "target size" of the host plant for crawlers dropping to the ground.

Zimmermann (1977) has recorded the clumped distribution of jointed cactus plants, caused by joints falling and rooting in the immediate vicinity of the parent plants. Thus the older, larger plants would form the larger "patches" or "targets" for the wind dispersed D.austrinus crawlers. This has been confirmed by Zimmermann (1978) who noted the positive association of D.austrinus with large clumps of plants. In addition, I have shown that only the large plants serve as dispersal platforms for crawlers. Therefore the dispersal and rapid spread of cochineal populations will depend on the presence of large plants at densities where the horizontal dispersal range of D.austrinus crawlers exceeds the inter-patch distances.

The continued presence of D.austrinus on infestations of jointed cactus in South Africa, despite an intensive chemical control program designed to reduce infestations of the host plant, confirm that crawler dispersal suffices to maintain viable populations.

Doutt and De Bach (1964), in defining the attributes of a natural enemy, state "The prime requisite would seem to be a high searching capacity, that is, the ability to find its host when the host is scarce." Dispersal of D.austrinus will depend on the presence of tall jointed cactus plants and the rapid spread of cochineal populations will only occur when large clumps of the host are present at densities which enable colonization by horizontally dispersed crawlers, i.e. dispersal and effective control will only occur at jointed cactus densities which are above the sub-economic threshold point, which may be at damaging levels for stock farmers.

The importance of the spatial distribution of the habitat in relation to dispersal of coccoid insects is highlighted in a recent publication by Miller and Denno (1977). These authors described three arboreal pseudococcid species, Plotococcus eugeniae Miller and Denno, Leptococcus metroxyli Reyne and Macrocepicoccus lorantii Morrison, which have adult females with exceptionally long legs in relation to body size. They have suggested that convergent evolution of this feature in the three unrelated species is connected with dispersal, the habitat is sufficiently abundant to enable dispersal of the adult females. The advantages would include a greater tolerance to desiccation than crawlers, and the ability to reproduce immediately and colonise the new host plant.

Pettey (1948) commented on the rapid destruction of jointed cactus populations following the release of *D.austrinus* in 1936 and the subsequent failure of *D.austrinus* to control regrowth. Pettey (1948) gave no details as to the density of jointed cactus populations prior to and after release of *D.austrinus*. I suggest that the presence of dense populations of large jointed plants enabled the build up and dispersal of cochineal populations which rapidly destroyed the host plants. Destruction of the large plants removed the source and points for dispersal, reduced the patch size of the habitat increasing interpatch distances which prevented subsequent dispersal.

These suggestions have two important implications with regard to the control of jointed cactus populations in South Africa. Firstly the present control measures, the use of herbicides, are totally antagonistic to the existing biological control methods using *D.austrinus*. Zimmermann (1978) has shown that the searching efficiency of spray gangs is correlated with the aggregation of jointed cactus plants; the clumps of large plants are most efficiently eliminated leaving the small plants to reinfest the sprayed areas. As a result the large reservoirs of cochineal are destroyed by either the herbicide or paraffin solvent used in spraying and the dispersal points destroyed.

Secondly biological control of jointed cactus by *D.austrinus* will only occur once large plants are present at densities which are of pest proportion. Although long-range wind dispersal of crawlers is likely to introduce cochineal into areas once the jointed cactus populations have built up, the delay in the build up of populations of cochineal may be too long for farmers to tolerate high density populations of jointed cactus.

The alternative to dismissing *D.austrinus* as a biological control agent is the augmentation of populations of the insect by periodic release of cochineal as suggested by Huffacker *et al.* (1976) for entomophagous biological control agents. Release of *D.austrinus* can be either inundative to destroy high density jointed cactus populations or else inoculative to establish cochineal on lower density cactus populations to ensure rapid build-up of cochineal populations once the plant density reaches levels where effective dispersal of *D.austrinus* can occur. The normal practice when releasing *D.austrinus* is to place infested cladodes in amongst the jointed stems of large plants. This system is labour intensive and the proportion of the plants infested using this system is small.

Tower dispersal of *D.austrinus* does provide a simple and efficient method to augment field populations of cochineal. This system is an alternative to hand release of infested cladodes and with further evaluation may offer a practical alternative to present chemical control methods.

10. SUMMARY

1. Dispersal of first instar nymphs (crawlers) of the cochineal insect *Dactylopius austrinus* De Lotto, a biological control agent against jointed cactus *Opuntia aurantiaca* was investigated.

2. There is a clear sexual dimorphism in the pattern and development of the wax filaments on the dorsal and dorsolateral surface of the crawlers. Female crawlers have long filaments on the head, thorax and abdomen while the males have long filaments restricted to the abdomen.

3. The greater number of long filaments on female crawlers reduces the terminal velocities (sinking speed) of females in comparison to that of male crawlers and increases the possibility of removal of female crawlers from the host plant by air currents.

4. Male crawlers are more sedentary than female crawlers, settling, feeding and pupating in close proximity to the sessile parent. Female crawlers move away from the parent prior to settling. A feature of female crawler behaviour is the aggregation of female crawlers, about 60 h old, on the spines of the terminal cladodes of the host plant. This behavioural pattern, together with growth of long filaments, serves to enhance the possibility of dispersal. The movement towards "take-off" from the host plant is similar to that noted for the sugar-cane scale *Aulacaspis tegalensis* (Greathead 1972) and migrant ballooning spiders and mites.

5. The crawlers are exceptionally hardy in comparison to other coccoid species and non-feeding crawlers survive up to 252 h at 25°C (R.H. 50%). An increase in temperature from 25°C to 40°C reduces survival time to 90 h.

6. The non-parthenogenetic females reared on loose cladodes produced fewer crawlers (mean; 443) than those reared on whole plants (mean; 734). For both categories of females there was a linear relationship between fecundity and female mass. The sex ratios of the offspring ranged from 126,6 ♂♂ per 100 ♀♀ (adults reared on loose cladodes) to 215,6 ♂♂ per 100 ♀♀ (adults reared on whole plants).

7. Drop-off of crawlers from cladodes was used as a measure of the number of motile crawlers available for dispersal. Monitoring drop-off under different environment room conditions showed that temperature and light determined the number of motile crawlers.

8. Dispersal of crawlers from a single host plant was monitored in the four cardinal and four semi-cardinal directions. The horizontal distributions, described using an iterative fit of the general equation ($N = \exp(a + bX^{c})$) of Taylor (1978), was limited (generally less than 6 m). Multiple regression analysis showed temperature and windrun were the most important factors influencing the number of crawlers dispersed. Allocation of windrun, (on the basis of anemometer wind direction traces) in each of the eight directions in which dispersal was monitored enabled allocation of the multiple regression estimates of catch in each direction.

9. Of the dispersed crawlers recovered from sticky traps that were used to monitor dispersal, 82,2% were females which confirms that the behaviour towards "take-off" and long filaments increases the possibility of dispersal of female crawlers in relation to males.

10. Dispersal of field populations of cochineal was monitored and pointed to the importance of large plants (20 - 40 cm) in height) in dispersal of D. austrinus. Data from these studies showed that about 12% of wind dispersed crawlers were dispersed vertically and were likely to be dispersed long distances.

11. The importance of the height of the host plant in crawler dispersal suggested a system of elevated towers to enhance crawler dispersal in the field. Two separate field trials were carried out to evaluate this system as a method of augmenting field populations of cochineal. Wind dispersal of crawlers from cultures of D. austrinus placed on the tower was increased as crawlers were dispersed in excess of 90 m. Surveys of jointed cactus densities and levels of cochineal infestation and the use of catch plants (cochineal free jointed cactus plants) showed the system is more practical than hand augmentation of cochineal and may offer an alternative to the costly and inefficient herbicidal control program.

11. APPENDICES

APPENDIX 1: Preparative technique for slide mounting cochineal insects (after De Lotto pers.comm.).

1. Place several newly mounted 3rd instar females in 8% KOH and boil until the carmine coloured body has cleared.

2. Puncture the dorsum and gently squeeze out the body contents. If necessary tease out the trachae to ensure the test is empty.

3. Reboil in 8% KOH and repeat step 2 if necessary.

4. Pass through pure acetic acid for 10 - 15 min.

5. Leave in acid fuchsin overnight.

6. Pass through lactophenol to remove excess stain (10 - 15 min.)

7. Dehydrate in acetic acid for 10 - 15 min.

8. Place in oil of cloves for 5 - 10 min.

9. Mount the test on slide using Canada Balsam or synthetic mountant such as Emexel.

APPENDICES 2 - 5: Computer programs.

All programs were written in standard Fortran IV.

Six programs are shown in these appendices together with the relevant input and output formats. The programs described are:

APPENDIX 2:	SINA -	provides a mechanical fit of the general function of Taylor (1978) to catch-distance data.
APPENDIX 3:	CTER -	provides an iterative fit of the general function using partial regression coefficients obtained using SINA.
APPENDIX 4:	EQUI and EQU2 -	combines regression estimates of catch with wind direction scores to allocate the catch in four cardinal and four semi-cardinal directions.
APPENDIX 5:	WINI and WIN2 -	allocates catch in eight directions on the basis of windrun, windrun time, and a value for windrun x temperature in each direction.

APPENDIX 2

```
PROGRAM: SINA.
==============

C  THIS PROGRAM PROVIDES A MECHANICAL FIT OF THE GENERAL
C  EQUATION (N = EXP(A-BX**C)), DEVELOPED BY TAYLOR (1978),
C  TO DESCRIBE THE RELATIONSHIP BETWEEN DENSITY (CATCH) OF
C  DACTYLOPIUS AUSTRINUS DE LOTTO CRAWLERS AND INCREASING
C  DISTANCE FROM THE HOST PLANT OPUNTIA AURANTIACA LINDLEY.
C  BY REPEATED REGRESSION, THE VALUE OF THE DISTANCE
C  EXPONENT (C) IS RAISED FROM 0,01 TO 4,0 IN STEPS OF 0,01.
C  THE REGRESSION EQUATION PROVIDING THE SMALLEST RESIDUAL
C  DEVIATION (RESIDUAL MEAN SQUARE) DETERMINES THE VALUE
C  OF THE PARAMETERS A, B AND C USED IN THE FUNCTION TO
C  PROVIDE A DESCRIPTION OF THE RELATIONSHIP BETWEEN DENSITY
C  AND DISTANCE. THE VALUES OF THE INTERCEPT (A), REGRESSION
C  COEFFICIENT (B) AND THE DISTANCE EXPONENT (C) OBTAINED
C  ARE USED IN THE SUBROUTINE AUXPLEX IN THE PROGRAM CTER
C  WHICH PROVIDES AN ITERATIVE FIT OF THE GENERAL EQUATION
C  TO THE DISPERSAL DATA.

      MASTER ZOLR
      REAL XX(20),X(20),Y(20),ZZ(20)
      LOGICAL HFOUND
      HFOUND = .FALSE.

C  THE NUMBER OF CATCH-DISTANCE DATA ENTRIES TO BE USED
C  IN THE ANALYSIS ARE SET. THE MAXIMUM NUMBER THAT CAN
C  BE USED IS 20 AS SET BY THE ARRAY DECLARATION.

      READ (5,500) NO
500   FORMAT (I2)
      WRITE (6,600)
600   FORMAT (1H1, 4X, 8HDISTANCE, 6X, 5HCATCH / 1X, 2(4X,
     18(1H-)))
      TOTYP=0
      DO 10 I = 1,NO

C  THE CATCHES (YY) AT THE DIFFERENT DISTANCES (XX) ARE READ.

      READ (5,501) XX(I),YY
501   FORMAT (2F0.0)

C  THE VALUES OF CATCH AND DISTANCE ARE PRINTED.

      WRITE (6,601) XX(I),YY
601   FORMAT (1X,2F12.4)

C  CATCH VALUES ARE TRANSFORMED TO LOGS TO ALLOW LINEAR REGRESSION
C  ANALYSIS OF THE DATA.

      Y(I) = ALOG(YY)
      ZZ(I)=YY
10    TOTYP=TOTYP+ZZ(I)

C  THE INITIAL VALUE FOR C IS SET AT 0.01
```

```
      C = 0.01
C  COMPUTATION FOR LINEAR REGRESSION AFTER SOKAL & ROHLF (1973).
1     DO 15 I = 1,NO
15    X(I) = XX(I)**C
      XSUM = 0.0
      YSUM = 0.0
      XSUM2 = 0.0
      YSUM2 = 0.0
      XY = 0.0
      XMEAN=0
      YMEAN=0
      XRSUM2 = 0.0
      YRSUM2 = 0.0
      XRYR = 0.0
      DO 20 I = 1,NO
      XSUM = XSUM + X(I)
      YSUM = YSUM + Y(I)
      XSUM2 = XSUM2 + X(I)**2
      YSUM2 = YSUM2 + Y(I)**2
20    XY = XY + X(I)*Y(I)
      XMEAN = XSUM / NO
      YMEAN = YSUM / NO
      DO 30 I = 1,NO
      XRSUM2 = XRSUM2 + (X(I) - XMEAN)**2
      YRSUM2 = YRSUM2 + (Y(I) - YMEAN)**2
30    XRYR = XRYR + (X(I) - XMEAN)*(Y(I) - YMEAN)
      RCOEF = XRYR / XRSUM2
      YINTER = YMEAN - RCOEF * XMEAN
      REGMS=0
      RESSS=0
C  CALCULATION OF REGRESSION DEVIATIONS FOR CURVILINEAR PLOT.
      DO 40 I=1,NO
      YHAT=EXP(YINTER + RCOEF*(XX(I)**C))
      YT=YHAT-TOTYP/NO
      G=YHAT-ZZ(I)
      REGMS=REGMS+YT*YT
40    RESSS=RESSS+G*G
      RESMS=RESSS/(NO-3)
      FRAT=REGMS/RESMS
      IF (HFOUND) GO TO 3
C  SELECTION OF THE REGRESSION WHICH PROVIDES THE LOWEST RESIDUAL
C  DEVIATIONS.
      IF (FRAT .LE. HRAT) GO TO 4
      HC = C
      HRAT = FRAT
4     IF (C.GT.4.0) GO TO 2
      C = C + 0.01
      GO TO 1
2     HFOUND = .TRUE.
      C = HC
      GO TO 1
3     WRITE (6,602)
602   FORMAT (1H ,//,4X,8HDISTANCE,3X,10HEST. CATCH,/,1X,
     *2(4X,8(1H-)))
      DO 50 I=1,NO
```

```
      YHAT=EXP(YINTER+RCOEF*(XX(I)**C))

C  THE ESTIMATED CATCH VALUES USING THE GENERAL EQUATION OF
C  TAYLOR (1978) OBTAINED FROM THE REGRESSION FOR WHICH THE
C  PARAMETER C PROVIDED THE SMALLEST RESIDUAL DEVIATIONS ARE
C  CALCULATED AND PRINTED..

50    WRITE (6,603) XX(I),YHAT
603   FORMAT(1X,2F12.4)
      WRITE (6,604)

C  THE VALUES FFOR THE INTERCEPT (A), REGRESSION COEFFICIENT (B)
C  WHICH PROVIDE THE SMALLEST RESIDUAL DEVIATION TOGETHER WITH
C  SUMS OF SQUARES AND MEAN SQUARES AND THE F RATIO (FS RATIO OF
C  SOKAL AND ROHLF 1973) ARE PRINTED.

604   FORMAT (1H ,//,1X,18HFINAL RESULTS ARE /1X, 18(1H=))
      WRITE (6,605) RCOEF
605   FORMAT (1X, 9HRCOEF  = ,F12.4)
      WRITE (6,606) YINTER
606   FORMAT (1X, 9HYINTER = ,F12.4)
      WRITE (6,607) REGMS
607   FORMAT (1X, 9HREG MS = ,F12.4)
      WRITE (6,608) RESSS
608   FORMAT (1X, 9HRES SS = ,F12.4)
      WRITE (6,609) RESMS
609   FORMAT (1X, 9HRES MS = ,F12.4)
      WRITE (6,610) C
610   FORMAT (1X, 9HC      = ,F12.4)
      WRITE (6,611) FRAT
611   FORMAT (1X, 9HFRATIO = ,F12.4)
      STOP
      END
      FINISH
```

DATA INPUT FORMAT FOR PROGRAM SINA.

THE DATA USED TO ILLUSTRATE THE INPUT/OUTPUT FORMATS FOR PROGRAM SINA ARE THE CATCH-DISTANCE DATA FOR DISPERSAL OF DROSOPHILA PSEUDOOBSCURA FROL. (DOBZHANSKY & WRIGHT (1943) QUOTED BY TAYLOR (1978).

THE INITIAL VALUE ENTERED SETS THE NUMBER OF CATCH-DISTANCE DATA ENTRIES TO BE USED IN THE ANALYSIS

```
20
```

THE CATCH-DISTANCE VALUES ARE LISTED.

```
1.0  31.65
20.0  12.11
40.0  11.66
60.0  4.96
80.0  5.52
100.0  2.74
120.0  1.94
140.0  1.76
160.0  1.40
180.0  2.06
200.0  1.49
220.0  1.30
240.0  1.12
260.0  0.69
280.0  0.72
300.0  0.64
320.0  0.60
340.0  0.72
360.0  0.44
380.0  0.17
```

```
OUTPUT FORMAT FOR PROGRAM SINA.
===============================


THE CATCH-DISTANCE DATA IS PRINTED.

     DISTANCE         CATCH
     --------       --------
       1.0000       31,6500
      20.0000       12,1100
      40.0000       11,6600
      60.0000        4,9600
      80.0000        5,5200
     100.0000        2,7400
     120.0000        1,9400
     140.0000        1,7600
     160.0000        1,4000
     180.0000        2,0600
     200.0000        1,4900
     220.0000        1,3000
     240.0000        1,1200
     260.0000        0,6900
     280.0000        0,7200
     300.0000        0,6400
     320.0000        0,6000
     340.0000        0,7200
     360.0000        0,4400
     380.0000        0,1700


THE DENSITY (CATCH) VALUES ESTIMATED USING THE
REGRESSION EQUATION GIVING THE LOWEST RESIDUAL
DEVIATION ARE PRINTED.

    DISTANCE    EST. CATCH
    --------     --------
       1.0000       31,7550
      20.0000       13,1423
      40.0000        8,3242
      60.0000        5,8855
      80.0000        4,4027
     100.0000        3,4137
     120.0000        2,7148
     140.0000        2,2006
     160.0000        1,8110
     180.0000        1,5088
     200.0000        1,2700
     220.0000        1,0784
     240.0000        0,9226
     260.0000        0,7946
     280.0000        0,6884
     300.0000        0,5995
     320.0000        0,5246
     340.0000        0,4610
     360.0000        0,4066
     380.0000        0,3600
```

```
THE INTERCEPT (YINTER), REGRESSION COEFFICIENT
(RCOEF) AND THE DISTANCE EXPONENT (C) ARE SHOWN
TOGETHER WITH SUMS OF SQUARES (RESIDUAL) AND THE
REGRESSION AND RESIDUAL MEAN SQUARES.

FINAL RESULTS ARE
-----------------
RCOEF  =     -0.2747
YINTER =      3.7327
REG MS =   1001.4435
RES SS =     16.2902
RES MS =      0.9582
C      =      0.4800
FRATIO =   1045.0797
```

APPENDIX 3

```
PROGRAM CTER.
============

C  THIS PROGRAM PROVIDES AN ITERATIVE FIT OF THE GENERAL
C  EQUATION (TAYLOR 1978) TO DATA FOR THE DISPERSAL OF
C  D.AUSTRINUS CRAWLERS. THE PROGRAM INCORPORATES TWO
C  SUBROUTINES (AUXPLEX AND FLEXPLEX) FOR NON LINEAR
C  OPTIMIZATION, WHOSE CODING WAS DEVELOPED BY DR P.D.TERRY
C  (APPLIED MATHEMATICS DEPARTMENT, RHODES UNIVERSITY,
C  GRAHAMSTOWN) FROM A PROGRAM IN HIMMELBLAU (1972) BASED
C  ON AN ALGORITHM OF NELDER & MEAD (1964). THE SUBROUTINE
C  AUXPLEX SETS UP THE INITIAL APPROXIMATION OF THE LOCATION
C  OF THE MINIMUM FOR THE FUNCTION WHICH IS LOCATED USING
C  FLEXPLEX.

      MASTER GUNN
      EXTERNAL FUN
      DIMENSION X(5,8),XMAX(4),XMIN(4),GUESS(4)
      COMMON XP(100),YP(100),NP
      DATA XMAX,XMIN/4*1.0E70,4*-1.0E70/

C  NUMBER OF VARIABLES IN THE FUNCTION ENTERED.

      N=3
      TOTYP=0
      WRITE(6,600)

C  THE NUMBER OF CATCH-DISTANCE DATA ENTRIES IN THE ANALYSIS SET.

      READ(5,500)NP

C  CATCH-DISTANCE VALUES ARE READ IN AND PRINTED.

      DO 1 I=1,NP
      READ(5,501) XP(I),YP(I)
      TOTYP=TOTYP+YP(I)
      WRITE(6,601)XP(I),YP(I)
1     CONTINUE

C  THE VALUES FOR THE INTERCEPT (A), REGRESSION COEFFICIENT (B)
C  AND THE DISTANCE EXPONENT (C) ARE READ TO PROVIDE THE
C  INITIAL LOCATION OF THE MINIMUM FOR THE FUNCTION.

      READ(5,502) GUESS(1),GUESS(2),GUESS(3)

C  INITIAL PARAMETERS ARE SET.

      DELTA=0.1
      IM=5
      JM=8
      TOL=0.0001
      ITMAX=200

C  SUBROUTINE AUXPLEX USED TO SET UP THE INITIAL MATRIX X FOR
C  THE INITIAL CALL TO FLEXPLEX.
```

```
      CALL AUXPLEX(X,GUESS,DELTA,N,IM,JM)

C  ATTEMPT TO MINIMISE NON LINEAR SUMS OF SQUARES.

      CALL FLEXPLEX(FUN,N,X,IM,JM,XMAX,XMIN,TOL,ITMAX)
      WRITE(6,602) (X(I,N+2),I=1,N),TOL,ITMAX
      IF(ITMAX.LT.0)STOP
      RESSS=0
      REGMS=0

C  CALCULATION OF ESTIMATED CATCHES, SUMS OF SQUARES AND MEAN
C  SQUARES. THESE ARE PRINTED OUT FOR THE FUNCTION VALUES
C  WHICH PROVIDE THE MINIMUM RESIDUAL DEVIATION.

      DO 10 I=1,NP
      F=EXP(X(1,N+2)+X(2,N+2)*XP(I)**X(3,N+2))
      YT=F-TOTYP/NP
      G=YP(I)-F
      WRITE(6,603) I,F,YP(I),G,YT
      REGMS=REGMS+YT*YT
10    RESSS=RESSS+G*G
      RESMS=RESSS/(NP-3)
      FRAT=REGMS/RESMS
      WRITE(6,604)RESSS,REGMS,RESMS,FRAT
      STOP

500   FORMAT(I2)
501   FORMAT(2F0.0)
502   FORMAT(3F0.0)
600   FORMAT(1H1,6X,8HDISTANCE,7X,5HCATCH,/,7X,8(1H=),7X,5(1H=))
601   FORMAT(1X,2F12.2)
602   FORMAT(1H ,6X,5HY INT,3X,8HREG COEF,8X,1HC,9X,3HTOL,5X,
     15HITMAX,/,5X,49(1H*),//,3(4X,F7.4),5X,F7.3,5X,I2,/,5X,
     249(1H*),//////,9X,1HI,3X,10HEST. CATCH,3X,5HCATCH,9X,
     31HG,9X,2HYT,/,6X,50(1H*),/)
603   FORMAT(1H ,5X,I4,4(5X,F6.2))
604   FORMAT(1H ,5X,50(1H*),/////,8X,6HRES SS,9X,6HREG MS,10X,
     16HRES MS,7X,7HF RATIO,/,8X,52(1H*),//,4(5X,F10.4),/,8X,
     252(1H*))
      END
      SUBROUTINE AUXPLEX (X,G,D,N,IM,JM)

C GENERATE INITIAL SIMPLEX FOR USE WITH FLEXPLEX SUBROUTINE

C X     RECTANGULAR ARRAY OF DIMENSION  X(IM,JM)  IN CALLING SEGMENT
C       IM  MUST BE AT LEAST  N+1  AND  JM  MUST BE AT LEAST  N+4
C       ON EXIT   X(I,J) ,J=1,N+1   CONTAINS  N+1  INITIAL
C       APPROXIMATIONS TO THE LOCATION OF THE DESIRED
C       MINIMUM/MAXIMUM.   EACH COLUMN OF THE MATRIX REPRESENTS A
C       DIFFERENT APPROXIMATION, EACH ROW GIVING CORRESPONDING
C       COORDS.

C N     NUMBER OF VARIABLES
C D     SIZE OF SEARCH AREA

C G     ARRAY OF COORDINATES FOR STARTING VECTOR, DIMENSION N

      DIMENSION X(IM,JM),G(N)
      EN=N
      NP1=N+1
      D2=D/(1.414236*EN)
```

```
      D1=D2*(SQRT(EN+1.0)+EN-1.0)
      D2=D2*(SQRT(EN+1.0)-1.0)
      DO 10 I=1,N
10    X(I,1)=0.0
      DO 20 I=1,N
      DO 20 J=2,NP1
      X(I,J)=D2
20    X(J-1,J)=D1
      DO 30 I=1,N
      DO 30 J=1,NP1
30    X(I,J)=X(I,J)+G(I)
      RETURN
      END

      SUBROUTINE FLEXPLEX (FUNCT,N,X,IM,JM,XMAX,XMIN,TOL,ITMAX)
      EXTERNAL FUNCT

C DETERMINE LOCATION OF MINIMUM OR MAXIMUM OF FUNCTION  FUNCT
C WHICH IS A FUNCTION OF  N  VARIABLES

C X     RECTANGULAR ARRAY OF DIMENSION X(IM,JM) IN CALLING
C       SEGMENT IM MUST BE AT LEAST N+1 AND JM MUST BE
C       AT LEAST N+4. ON ENTRY X(I,J) ,J=1,N+1 CONTAINS
C       N+1 INITIAL APPROXIMATIONS TO THE LOCATION OF THE
C       DESIRED MINIMUM/MAXIMUM. EACH COLUMN OF THE MATRIX
C       REPRESENTS A DIFFERENT APPROXIMATION, EACH ROW
C       GIVING CORRESPONDING COORDS.ON EXIT X(I,N+2), I=1,N
C       GIVES THE BEST APPROXIMATION TO THE LOCATION OF THE
C       MINIMUM/MAXIMUM, AND X(N+1,N+2) GIVES THE CORRESPONDING
C       VALUE OF THE FUNCTION
C       THE FIRST N+1 COLUMNS ARE THUS SUITABLE FOR RE-ENTRY
C       TO THE ROUTINE TO PRESS FOR GREATER ACCURACY.

C XMAX,XMIN   - REAL ARRAYS, DIMENSION  N  GIVING THE LIMITS  (MAX
C       AND MIN) ALLOWED FOR COORDINATES  1  TO  N.  IF COMPLETELY
C       UNCONSTRAINED, SET ALL XMIN(I)=-1.0E70  AND ALL
C       XMAX(I)=+1.0E70

C TOL  ACCURACY REQUIRED (SEE NOTES).  RETURNED AS ACCURACY ATTAINE

C ITMAX  MAXIMUM NUMBER OF ITERATIONS ALLOWED.  SET  ITMAX  TO A
C       NEGATIVE NUMBER IF MAXIMISING FUNCTION, AND TO A POSITIVE
C       NUMBER IF MINIMISING FUNCTION.  ITMAX  IS RETURNED AS THE
C       NUMBER OF ITERATIONS NEEDED TO REACH  TOL , OR AS -1  IF
C       CONVERGENCE  WAS UNSATISFACTORY, AS -2  IF INITIAL SIMPLEX
C       WAS USELESS, OR AS -3  IF THE DIMENSIONS OF ARRAY X ARE
C       INADEQUATE.

C USER MUST SUPPLY AN EXTERNAL FUNCTION

C       FUNCTION  FUNCT  (X,N)
C WHERE  X IS A REAL ARRAY OF THE  N  VARIABLE VALUES FOR WHICH THE
C FUNCTION IS TO BE EVALUATED

C REFERENCES: NELDER AND MEAD: COMPUTER JOURNAL VOL 7, PAGE 308
C             (1964)HIMMELBLAU "APPLIED NONLINEAR OPTIMIZATION"
C             (MCGRAW-HILL 1972) PAGES 148-157 AND 451-454
C             (BEWARE OF MISPRINTS)
C             MORGAN AND DEMING , ANAL.CHEM, VOL 46,PAGE 1170
C             (1974).
```

```
      LOGICAL FLAG,NOPRNT
      DIMENSION X(IM,JM),XMAX(N),XMIN(N)
      COMMON /FLEX1/ MON

C SET INITIAL PARAMETERS

      NOPRNT=MON.NE.1
      ITERMAX=IABS(ITMAX)
      SIGN=1.0
      IF (ITMAX.LT.0) SIGN=-1.0
      N1=N+1
      N2=N+2
      N3=N+3
      N4=N+4
      IF (N4.GT.JM.OR.N1.GT.IM) GO TO 300
      ALPHA=1.0
      BETA=0.5
      GAMMA=2.0
      ALPH1=1.0+ALPHA
      BET1=1.0-BETA
      GAM1=1.0-GAMMA
      DEN=1.0/FLOAT(N)

C CALCULATE AND CHECK INITIAL VALUES OF FUNCTION

      DO 20 J=1,N1
      DO 10 I=1,N
      IF (X(I,J).GT.XMAX(I).OR.X(I,J).LT.XMIN(I)) GO TO 290
10    CONTINUE
20    X(N1,J)=FUNCT(X(1,J),N)*SIGN

C START ITERATIVE LOOP

      DO 260 ITMAX=1,ITERMAX

C FIND BEST AND WORST RESPONSES

      BEST=X(N1,1)
      WORST=X(N1,1)
      JBEST=1
      JWORST=1
      DO 40 J=2,N1
      IF (X(N1,J).GT.BEST) GO TO 30
      BEST=X(N1,J)
      JBEST=J
      GO TO 40
30    IF (X(N1,J).LT.WORST) GO TO 40
      WORST=X(N1,J)
      JWORST=J
40    CONTINUE

C FIND CENTROID OF POINTS OTHER THAN WORST

      FLAG=.FALSE.
      DO 60 I=1,N
      SUM=0.0
      DO 50 J=1,N1
50    SUM=SUM+X(I,J)
      X(I,N2)=DEN*(SUM-X(I,JWORST))

C FIND REFLECTION OF WORST POINT THROUGH CENTROID
```

```
      X(I,N3)=ALPH1*X(I,N2)-ALPHA*X(I,JWORST)
60    IF (X(I,N3).GT.XMAX(I).OR.X(I,N3).LT.XMIN(I)) FLAG=.TRUE.
      X(N1,N3)=1.0E70
      IF (FLAG) GO TO 70

C CALCULATE VALUE OF FUNCTION AT REFLECTED POINT

      X(N1,N3)=FUNCT(X(1,N3),N)*SIGN
70    IF (X(N1,N3).GT.BEST) GO TO 120

C EXPAND IF REFLECTION HAS PRODUCED A BETTER MINIMUM

      FLAG=.FALSE.
      DO 80 I=1,N
      X(I,N4)=GAM1*X(I,N2)+GAMMA*X(I,N3)
80    IF (X(I,N4).GT.XMAX(I).OR.X(I,N4).LT.XMIN(I)) FLAG=.TRUE.
      X(N1,N4)=1.0E70
      IF (FLAG) GO TO 90

C CALCULATE VALUE OF FUNCTION AT EXPANDED POINT

      X(N1,N4)=FUNCT(X(1,N4),N)*SIGN
90    NEW=N4
      IF (X(N1,N4).GT.BEST) NEW=N3
      GO TO 200

C SELECT SECOND WORST VALUE

120   SECWORST=X(N1,1)
      IF (JWORST.EQ.1) SECWORST=X(N1,2)
      DO 130 J=1,N1
      IF (J.EQ.JWORST.OR.X(N1,J).LE.SECWORST) GO TO 130
      SECWORST=X(N1,J)
130   CONTINUE

C IF REFLECTED VALUE BETTER THAN NEXT-TO-WORST, REPLACE WORST
C BY REFLECTED VALUES

      NEW=N3
      IF (X(N1,N3).LE.SECWORST) GO TO 200

C CONTRACTION NEEDED

      IF (X(N1,N3).GT.WORST) GO TO 150
      DO 140 I=1,N1
140   X(I,JWORST)=X(I,N3)
150   FLAG=.FALSE.
      DO 160 I=1,N
      X(I,N4)=BETA*X(I,JWORST)+BET1*X(I,N2)
160   IF (X(I,N4).GT.XMAX(I).OR.X(I,N4).LT.XMIN(I)) FLAG=.TRUE.
      X(N1,N4)=1.0E70
      IF (FLAG) GO TO 170
      X(N1,N4)=FUNCT(X(1,N4),N)*SIGN
170   NEW=N4
      IF (WORST.GT.X(N1,N4)) GO TO 200

C REDUCE SIMPLEX BY HALF IF REFLECTION PRODUCES A WORSE VALUE
C THAN THE MAXIMUM SO FAR

      DO 180 I=1,N
```

```
      DO 180 J=1,N1
180   X(I,J)=0.5*(X(I,J)+X(I,JBEST))
      DO 190 J=1,N1
190   X(N1,J)=FUNCT(X(1,J),N)*SIGN
      GO TO 220

C REPLACE ONE VECTOR IN THE SIMPLEX BY A BETTER ONE

200   DO 210 I=1,N1
210   X(I,JWORST)=X(I,NEW)

C TEST FOR POSSIBLE CONVERGENCE

220   X(N1,N2)=FUNCT(X(1,N2),N)*SIGN
      SUM=0.0
      DO 230 J=1,N1
230   SUM=SUM+(X(N1,J)-X(N1,N2))**2
      SUM=DEN*SQRT(SUM)
      IF (NOPRNT) GO TO 250

C OPTIONAL MONITOR PRINT (CONTROLLED BY COMMON BLOCK)

      VALUE=SIGN*X(N1,NEW)
      WRITE (6,6000) (X(I,NEW),I=1,N),VALUE
250   IF (SUM.LT.TOL) GO TO 270
260   CONTINUE

C CONVERGENCE HAS FAILED

      ITMAX=-1

C RETURN BEST VECTOR OF SIMPLEX IN FIRST COLUMN

270   TOL=SUM
      DO 280 I=1,N1
280   X(I,N2)=X(I,JWORST)
      X(N1,N2)=SIGN*X(N1,N2)
      RETURN

C ERROR EXIT IF INITIAL SIMPLEX IS USELESS

290   ITMAX=-2
      TOL=1.0E55
      RETURN

C ERROR EXIT IF DIMENSIONS OF MATRIX ALL WRONG

300   ITMAX=-3
      TOL=1.0E55
      RETURN

6000  FORMAT (1H ,1P6E12.4)
      END

      FUNCTION FUN(X,N)
      DIMENSION X(N)
      COMMON XP(100),YP(100),NP
      FUN=0.0
      DO 10 I=1,NP
      G=EXP(X(1)+X(2)*XP(I)**X(3))-YP(I)
10    FUN=FUN+G*G
      RETURN
      END
      FINISH
```

```
DATA INPUT FORMAT FOR PROGRAM CTER.
===================================

THE DATA USED TO ILLUSTRATE THE INPUT/OUTPUT FORMATS FOR
THIS PROGRAM ARE THE CATCH-DISTANCE DATA FOR THE DISPERSAL
OF DROSOPHILA PSEUDOOBSCURA FROL (DOBZHANSKY & WRIGHT 1943)
QUOTED BY TAYLOR (1978).

THE INITIAL VALUE SETS THE NUMBER OF CATCH-DISTANCE DATA ENTRIES
TO BE USED IN THE ANALYSIS.
20

THE CATCH-DISTANCE VALUES ARE LISTED.
1.0  31.65
20.0  12.11
40.0  11.66
60.0  4.96
80.0  5.52
100.0  2.74
120.0  1.94
140.0  1.76
160.0  1.40
180.0  2.06
200.0  1.49
220.0  1.30
240.0  1.12
260.0  0.69
280.0  0.72
300.0  0.64
320.0  0.60
340.0  0.72
360.0  0.44
380.0  0.17

THE VALUES OBTAINED FOR THE INTERCEPT (A), REGRESSION
COEFFICIENT (B) AND THE DISTANCE EXPONENT (C) USING
PROGRAM SINA ARE LISTED TO SET THE INITIAL APPROXIMATION
OF THE MINIMUM OF THE FUNCTION USING THE SUBROUTINE
AUXPLEX.
3.7327  -0.2747  0.48
```

```
OUTPUT FORMAT FOR PROGRAM CTER
==============================

THE CATCH-DISTANCE DATA PRINTED.

      DISTANCE        CATCH
      --------        -----
        1.00        31.65
       20.00        12.11
       40.00        11.66
       60.00         4.96
       80.00         5.52
      100.00         2.74
      120.00         1.94
      140.00         1.76
      160.00         1.40
      180.00         2.06
      200.00         1.49
      220.00         1.30
      240.00         1.12
      260.00         0.69
      280.00         0.72
      300.00         0.64
      320.00         0.60
      340.00         0.72
      360.00         0.44
      380.00         0.17

THE VALUES FOR THE INTERCEPT (Y INT), REGRESSION
COEFFICIENT (REG COEF) AND THE DISTANCE EXPONENT
(C) GIVING THE LOCATION OF THE MINIMUM FOR THE FUNCTION
ARE PRINTED TOGETHER WITH THE DEGREE OF TOLERANCE
REQUESTED AND THE NUMBER OF ITERATIONS THAT WERE
REQUIRED TO LOCATE THE MINIMUM.

      Y INT   REG COEF         C            TOL     ITMAX
    **************************************************

    3.6950    -0.2432     0.4996       0.000      43
    **************************************************


THE ESTIMATED CATCH AND CATCH SHOWN TOGETHER WITH
THE DEVIATION OF ESTIMATED CATCH FROM THE CATCH
AND ESTIMATED CATCH FROM THE MEAN CATCH.

          I   EST. CATCH   CATCH           G            YT
     ***************************************************

          1        31.56      31.65        0.09        27.37
          2        13.58      12.11       -1.47         9.40
          3         8.67      11.66        2.99         4.48
          4         6.14       4.96       -1.18         1.95
          5         4.59       5.52        0.93         0.41
          6         3.55       2.74       -0.81        -0.63
          7         2.82       1.94       -0.88        -1.37
```

```
         8        2.28         1.76        -0.52        -1.91
         9        1.87         1.40        -0.47        -2.32
        10        1.55         2.06         0.51        -2.63
        11        1.30         1.49         0.19        -2.88
        12        1.10         1.30         0.20        -3.08
        13        0.94         1.12         0.18        -3.25
        14        0.80         0.69        -0.11        -3.38
        15        0.69         0.72         0.03        -3.49
        16        0.60         0.64         0.04        -3.58
        17        0.52         0.60         0.08        -3.66
        18        0.46         0.72         0.26        -3.73
        19        0.40         0.44         0.04        -3.78
        20        0.36         0.17        -0.19        -3.83
      *********************************************


RESIDUAL SUMS OF SQUARES AND THE REGRESSION AND RESIDUAL
MEAN SQUARES ARE SHOWN TOGETHER WITH THE F RATIO.

      RES SS        REG MS          RES MS       F RATIO
      ***********************************************

      15.8125     1000.9800         0.9301     1076.1534
      ***********************************************
```

APPENDIX 4

```
C   PROGRAMS: EQU1 AND EQU2.
C   ========================

C   THESE PROGRAMS COMBINE REGRESSION ESTIMATES OF THE TWO
C   HOURLY CATCHES OF WIND DISPERSED D.AUSTRINUS CRAWLERS WITH
C   THE EQUIVALENT TWO HOURLY WIND DIRECTION SCORES TO ALLOCATE
C   THE ESTIMATED CATCHES IN THE FOUR CARDINAL AND SEMICARDINAL
C   DIRECTIONS. THE DATA SUBFILE CONTAINS THE HOURLY READINGS OF
C   TEMPERATURE (H   13 C), WINDRUN (KM) AND THE WIND DIRECTION
C   SCORES IN ALL EIGHT DIRECTIONS FROM 0600 TO 2000 EACH DAY.
C   PROGRAM EQU1 GIVES REGRESSION ESTIMATES OF THE CATCH BASED
C   ON TEMPERATURE AND WINDRUN AND EQU2 ON TEMPERATURE X WINDRUN.
C   THE PROGRAMS ARE IDENTICAL APART FROM THE FUNCTIONS AND THE
C   PARTIAL REGRESSION COEFFICIENTS USED TO DETERMINE THE CATCH.
C   THE ESTIMATED CATCH IN EACH DIRECTION IS DETERMINED FOR TWO
C   HOURLY, DAILY AND TOTAL PERIOD OF THE ANALYSIS (SEE OUTPUT
C   FORMAT.

       MASTER CATCH9
       DIMENSION DIRECO(8),WINDOT(8),DIREC2(8),DIREC(8),STTOT(8)
       DIMENSION DSTOT(8),WIND(8)
       LOGICAL EQUALI

C   PARTIAL REGRESSION COEFFICIENTS A, B AND C OF THE REGRESSION
C   FUNCTION RELATING THE VARIANCE IN THE CATCH WITH TEMPERATURE
C   AND WINDRUN. THE PARTIAL REGRESSION COEFFICIENTS (A AND B) FOR
C   PROGRAM EQU2 ARE -5.071 AND 0.113 RESPECTIVELY.

       DATA A,B,C,BLANK/-21.386,1.252,1.525,8H
1      CATCH=0.0
2      READ(5,5000) DATE

C   TERMINATOR FOR DATA INPUT.

       IF(EQUALI(DATE,BLANK)) GO TO 9999

C   ANALYSIS OF HOURLY DATA FROM 0600 TO 2000.
C   ==========================================

       DO 5 I=1,8
       WINDOT(I)=0.0
5      DSTOT(I)=0.0

C   DATE OF ANALYSIS PRINTED.

       WRITE(6,6000) DATE
       DO 30 I=1,7
       TOT1=0.0
       TOT2=0.0

C   TIME, TEMPERATURE (H   13 C), WINDRUN (KM) AND THE WIND
C   DIRECTION SCORES FOR EACH HOUR ARE READ FROM THE DATA
C   SUBFILE (SEE EXAMPLE DATA INPUT FORMAT).

       READ(5,5001) TIME,TEMP,WINDR,(DIREC(J),J=1,8)
       READ(5,5001) TIME2,TEMP2,WINDR2,(DIREC2(J),J=1,8)
```

```
C   HOURLY TEMPERATURE AND WINDRUN VALUES COMBINED TO PROVIDE
C   TWO HOURLY TOTALS.

        TEMP=TEMP+TEMP2
        WINDR=WINDR+WINDR2

C   CATCH FOR TWO HOUR PERIOD ESTIMATED USING THE FUNCTION
C   RELATING THE CATCH TO THE TWO HOURLY TEMPERATURE AND
C   WINDRUN READINGS. THE FUNCTION FOR PROGRAM EQU2 IS; CATCH
C   =A+B(TEMP+WINDRUN).

        CATCH=A+B*TEMP+C*WINDR

C   TOTAL WIND DIRECTION SCORES FOR FIRST AND SECOND HOUR OF EACH
C   TWO HOURLY PERIOD OBTAINED.

        DO 10 J=1,8
        TOT1=TOT1+DIREC(J)
10      TOT2=TOT2+DIREC2(J)

C   WIND SCORE RATIOS FOR TWO HOUR PERIODS DETERMINED,

        FACT1=0.0
        FACT2=0.0
        IF(TOT1.NE.0.0) FACT1=1.0/TOT1
        IF(TOT2.NE.0.0) FACT2=1.0/TOT2
        DO 20 J=1,8
        FACT=FACT1*DIREC(J)    +    FACT2*DIREC2(J)

C   ESTIMATED TWO HOURLY CATCH ALLOCATED IN EACH DIRECTION.

        DIRECO(J) = FACT/2*CATCH
        IF(DIRECO(J).LT.0.0) DIRECO(J)=0.0

C   TWO HOURLY CATCHES IN EACH DIRECTION TOTALLED TO GIVE
C   DAILY TOTAL OF ESTIMATED CATCH IN EACH DIRECTION, THE
C   DAILY WINDRUN TIMES IN EACH DIRECTION ARE ALSO OBTAINED.

        WINDOT(J)=WINDOT(J)+FACT*60.0
20      DSTOT(J)=DSTOT(J)+DIRECO(J)

C   THE TWO HOURLY READINGS OF TIME, TEMPERATURE, WINDRUN
C   AND THE ESTIMATED CATCH IN EACH DIRECTION ARE PRINTED.

30      WRITE(6,6001) TIME2,TEMP,WINDR,(DIRECO(J),J=1,8)

C   DAILY TOTALS FOR CATCH AND WINDRUN TIME IN EACH DIRECTION
C   PRINTED.

        WRITE(6,6002)(DSTOT(J),J=1,8),(WINDOT(J),J=1,8)

C   CUMULATIVE TOTALS OF DAILY CATCH AND WINDRUN IN EACH DIRECTION.

        DO 40 I=1,8
        WIND(I)=WIND(I)+WINDOT(I)
40      STTOT(I)=STTOT(I)+DSTOT(I)

C   RETURN STATEMENT TO START ANALYSIS OF THE FOLLOWING DAY
C   RETURN STATEMENT TO BEGIN ANALYSIS OF DATA FOR THE NEXT DAY.
```

```
      GO TO 2
9999  IF(CATCH.EQ.0.0) STOP

C  THE TOTAL ESTIMATED CATCH AND WINDRUN TIMES IN EACH DIRECTION
C  FOR THE TOTAL PERIOD OF ANALYSIS ARE PRINTED.

      WRITE(6,6003) (STTOT(J),J=1,8),(WIND(J),J=1,8)
      DO 50 I=1,8
50    STTOT(I)=0.0
      GO TO 1

5000  FORMAT(A8)
5001  FORMAT(11F0.0)


6000  FORMAT(1H1,//,6X,17HSAMPLE TAKEN ON, ,A8,///,
     16X,4HTIME,4X,4HTEMP,4X,5HWIND.,4X,
     21HN,7X,2HNE,6X,1HE,7X,2HSE,6X,1HS,7X,2HSW,6X,1HW,7X,2HNW)
6001  FORMAT(1H ,6X,F3.0,4X,F4.1,9(3X,F5.1))
6002  FORMAT (1H ,28X,61(1H*),/,5X,15HESTIMATED CATCH,6X,
     18(3X,F5.1),//,5X,10HTIME (MIN),11X,8(3X,F5.1),/,28X,
     261(1H*))
6003  FORMAT (1H1,///,26X,1HN,7X,2HNE,6X,1HE,7X,2HSE,6X,1HS,7X,
     12HSW,7X,1HW,7X,2HNW,/,21X,65(1H*),//,1X,16HTOTAL EST. CATCH,
     24X,8F8.1,//,1X,10HTIME (MIN),10X,8F8.1,//,21X,65(1H*))
      STOP
      END
      FINISH
```

```
DATA INPUT FORMAT: PROGRAMS EQU1 AND EQU2.
==========================================

THE TIME, TEMPERATURE (H° >13 C), WINDRUN (KM) AND THE WIND
DIRECTION SCORES IN THE FOUR CARDINAL AND FOUR SEMICARDINAL
DIRECTIONS FOR EACH HOUR FROM 0600 TO 2000 ARE LISTED.

25.01.78
7.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
8.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
9.  13.0  6.6  100.  15.  0.  0.  0.  0.  0.  70.
10.  15.5  8.0  100.  30.  0.  0.  0.  0.  10.  75.
11.  17.0  9.0  100.  30.  0.  0.  0.  0.  15.  75.
12.  18.0  7.0  100.  50.  5.  5.  5.  20.  50.  85.
13.  19.5  6.1  100.  35.  5.  5.  10.  30.  40.  90.
14.  19.5  5.7  40.  20.  10.  20.  50.  70.  60.  60.
15.  17.0  6.0  20.  5.  10.  70.  75.  90.  55.  20.
16.  16.0  9.0  0.  5.  25.  85.  100.  90.  25.  5.
17.  12.0  4.3  5.  40.  40.  65.  65.  20.  10.  0.
18.  6.0  6.0  40.  10.  0.  5.  10.  10.  10.  40.
19.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
20.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
26.01.78
7.  8.0  4.8  90.  10.  0.  0.  0.  0.  5.  60.
8.  9.5  8.5  70.  10.  0.  0.  0.  0.  5.  70.
9.  10.5  6.3  25.  10.  5.  10.  65.  90.  85.  35.
10.  10.5  5.2  35.  0.  0.  5.  50.  90.  85.  45.
11.  10.0  9.5  5.  5.  5.  10.  90.  100.  70.  10.
12.  10.0  6.0  40.  10.  15.  10.  85.  100.  95.  65.
13.  9.0  5.0  10.  0.  0.  10.  70.  80.  80.  45.
14.  8.0  4.6  100.  0.  5.  5.  10.  30.  45.  95.
15.  11.5  4.5  95.  20.  0.  0.  0.  5.  10.  65.
16.  10.0  4.8  30.  20.  0.  10.  30.  55.  50.  30.
17.  8.0  11.6  5.  0.  0.  20.  100.  100.  40.  10.
18.  4.0  11.0  10.  10.  5.  20.  100.  100.  80.  50.
19.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
20.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
```

```
OUTPUT FORMAT; PROGRAMS EQU1 AND EQU2.
=====================================

THE ESTIMATED CATCHES IN EACH DIRECTION FOR TWO HOURLY,DAILY AND THE
TOTAL PERIOD OF THE ANALYSIS ARE SHOWN.

      SAMPLE TAKEN ON, 25,01.78


      TIME      TEMP      WIND.      N         NE         E         SE         S         SW         W         NW
       8.        0,0       0,0      0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0
      10.       28.5      14,6     18,4       4,0       0,0       0,0       0.0       0,0       0,9      13,3
      12.       35,0      16,0     18,0       6,9       0,4       0,4       0.4       1,5       5,3      14,2
      14.       39,0      11,8     10,0       3,9       1,0       1,7       4,2       7,0       7,0      10,6
      16.       33.0      15,0      1,2       0,6       2,2       9,8      11,0      11,3       5,0       1,6
      18.       18,0      10,3      2,9       2,1       1,4       2,6       2,9       1,4       1,0       2,7
      20.        0,0       0,0      0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0
                                 ************************************************************************
     ESTIMATED CATCH               50,4      17,5       5,0      14,4      18,5      21,1      19,1      42.4

     TIME (MIN)                   156,6      57,5      19,7      51,2      63,6      63,7      56,1     131,7
                                 ***********************************************************************


      SAMPLE TAKEN ON, 26,01,78


      TIME      TEMP      WIND.      N         NE         E         SE         S         SW         W         NW
       8.       17,5      13,3     10,4       1,3       0,0       0,0       0,0       0,0       0,7       8,5
      10.       21,0      11,5      2,1       0,3       0,2       0,5       4,1       6,4       6,0       2,8
      12.       20,0      15,5      1,5       0,6       0,7       0,8       6,9       7,9       6,3       2,6
      14.       17,0       9,6      2,8       0,0       0,1       0,4       2,0       2,7       3,1       3,5
      16.       21,5       9,3      6,1       1,9       0,0       0,4       1,3       2,7       2,7       4,6
      18.       12,0      22,6      0,6       0,4       0,2       1,8       8,9       8,9       5,0       2,4
      20.        0,0       0,0      0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0
                                 ************************************************************************
     ESTIMATED CATCH               23,5       4,5       1,2       3,9      23,1      28,5      23,8      24.4

     TIME (MIN)                   140,6      24,9       5,9      19,6     114,2     145,2     127,2     142,4
                                 ***********************************************************************


                                N        NE         E         SE         S         SW         W         NW
                         **********************************************************************

TOTAL EST. CATCH           74.       22.        6.        18.       42.       50.       43.       67.

TIME (MIN)               297.2      82,3      25.6      70,8     177.9     208.8     183.3     274,0

                         **********************************************************************
```

APPENDIX 5

```
PROGRAMS: WIN1 AND WIN2.
========================

C  THESE PROGRAMS ALLOCATE HOURLY WINDRUN (WIN1) AND HOURLY
C  WINDRUN X TEMPERATURE VALUES BETWEEN 0600 AND 2000 TO THE
C  FOUR CARDINAL AND SEMICARDINAL DIRECTIONS TO PROVIDE AN
C  AN ESTIMATED CATCH RATIO. THE PROGRAMS ARE INDENTICAL APART
C  FROM THE PARAMETERS WINDRUN AND WINDRUN X TEMPERATURE USED
C  TO ESTIMATE THE CATCH. ALLOCATION OF THESE VALUES TO THE
C  DIFFERENT DIRECTIONS IS ON THE BASIS OF THE WIND DIRECTION
C  SCORE IN EACH DIRECTION. IN ADDITION, WIN1 ALSO GIVES THE
C  MEAN WIND VELOCITY (M/SEC) IN EACH DIRECTION.

      MASTER CATCH9
      DIMENSION DIRECO(8),WINDOT(8),DIREC(8),STTOT(8),DSTOT(8)
      DIMENSION WIND(8),RUNT(8)
      LOGICAL EQUALI
      DATA BLANK/8H        /
1     CATCH=0.0
2     READ(5,5000) DATE

C  TERMINATOR FOR DATA INPUT.

      IF(EQUALI(DATE,BLANK)) GO TO 9999

      DO 5 I=1,8
      WINDOT(I)=0.0
5     DSTOT(I)=0.0

C  ANALYSIS OF HOURLY DATA FROM 0600 TO 2000
C  ========================================

      WRITE(6,6000) DATE
      DO 30 I=1,14
      TOT1=0.0

C  TIME, TEMPERATURE (H   13 C), WINDRUN, AND THE
C  WIND DIRECTION SCORES FOR EACH HOUR ARE READ FROM THE
C  DATA SUBFILE (SEE EXAMPLE DATA INPUT FORMAT).

      READ(5,5001) TIME,TEMP,WINDR,(DIREC(J),J=1,8)

C  THE WINDRUN FOR EACH HOUR IS USED AS THE ESTIMATE FOR
C  THE CATCH RATIO IN EACH DIRECTION.
C  FOR PROGRAM WIN2: CATCH=WINDR*TEMP.

      CATCH=WINDR

C  TOTAL WIND DIRECTION SCORES FOR EACH HOUR OBTAINED.

      DO 10 J=1,8
10    TOT1=TOT1+DIREC(J)
      FACT1=0.0
      IF(TOT1.NE.0.0) FACT1=1.0/TOT1

C  WINDRUN (CATCH) IS ALLOCATED IN EACH DIRECTION ON THE BASIS
```

```
C  OF THE HOURLY WIND DIRECTION SCORE RATIOS.

      DO 20 J=1,8
      FACT=FACT1*DIREC(J)
      DIRECO(J)=FACT*CATCH

C  HOURLY WINDRUN AND WINDRUN TIME IN EACH DIRECTION TOTALLED
C  TO GIVE DAILY TOTAL OF WINDRUN AND WINDRUN TIMES IN EACH
C  DIRECTION.

      WINDOT(J)=WINDOT(J)+FACT*60.0
20    DSTOT(J)=DSTOT(J)+DIRECO(J)

C  HOURLY READINGS OF TIME, TEMPERATURE AND WINDRUN, TOGETHER
C  WITH THE WINDRUN IN EACH DIRECTION PRINTED.

30    WRITE(6,6001) TIME,TEMP,WINDR,(DIRECO(J),J=1,8)

C  DAILY WINDRUN AND WINDRUN TIMES IN EACH DIRECTION PRINTED.
C  THESE VALUES SERVE AS THE ESTIMATED CATCH RATIO IN
C  EACH DIRECTION.

      WRITE(6,6002)(DSTOT(J),J=1,8),(WINDOT(J),J=1,8)

C  CUMULATIVE TOTAL OF WINDRUN AND WINDRUN TIME IN EACH
C  DIRECTION OBTAINED.

      DO 40 I=1,8
      WIND(I)=WIND(I)+WINDOT(I)
40    STTOT(I)=STTOT(I)+DSTOT(I)

C  RETURN STATEMENT TO REPEAT THE ANALYSIS FOR THE NEXT PERIOD
C  0600 TO 2000.
      GO TO 2

C  CALCULATION OF THE MEAN WIND VELOCITY (M/SEC) IN EACH
C  DIRECTION.

9999  DO 60 I=1,8
60    RUNT(I)=(STTOT(I)*1000.0)/(WIND(I)*60)

C  THE CUMULATIVE TOTALS FOR WINDRUN, WINDRUN TIMES AND THE MEAN
C  WIND VELOCITIES IN EACH DIRECTION FOR THE COMPLETE PERIOD OF
C  THE ANALYSIS ARE PRINTED. THE WINDRUN AND WINDRUN TIME VALUES
C  SERVE AS THE ESTIMATED CATCH RATIO.

      WRITE(6,6003) (STTOT(J),J=1,8),(WIND(J),J=1,8),(RUNT(J),J=1,8)
      IF(CATCH.EQ.0.0) STOP
      DO 50 I=1,8
50    STTOT(I)=0.0
      GO TO 1

5000  FORMAT(A8)
5001  FORMAT(11F0.0)


6000  FORMAT(1H1,//,6X,17HSAMPLE TAKEN ON, ,A8,///,
     16X,4HTIME,4X,4HTEMP,4X,5HWIND.,4X,
     21HN,7X,2HNE,6X,1HE,7X,2HSE,6X,1HS,7X,2HSW,6X,1HW,7X,2HNW)
6001  FORMAT(1H ,6X,F3.0,4X,F4.1,9(3X,F5.1))
6002  FORMAT (1H ,28X,61(1H*),/,5X,16HEST. CATCH RATIO,5X,
```

```
     18(3X,F5.1),//,5X,10HTIME (MIN),11X,8(3X,F5.1),/,28X,
     261(1H*))
6003  FORMAT (1H1,///,26X,1HN,7X,2HNE,6X,1HE,7X,2HSE,6X,1HS,7X,
     12HSW,7X,1HW,7X,2HNW,/,21X,65(1H*),//,1X,16HEST. CATCH RATIO,
     24X,8F8.1,//,1X,10HTIME (MIN),10X,8F8.1,//,1X,
     319HWIND VELOCITY (M/S),1X,8F8.1,//,21X,65(1H*))
      STOP
      END
      FINISH
```

DATA INPUT FORMAT: PROGRAMS WIN1 AND WIN2.

THE TIME, TEMPERATURE (H° > 13 C), WINDRUN (KM) AND THE WIND DIRECTION SCORES IN THE FOUR CARDINAL AND FOUR SEMICARDINAL DIRECTIONS FOR EACH HOUR FROM 0600 TO 2000 ARE LISTED.

```
25.01.78
7.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
8.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
9.  13.0  6.6  100.  15.  0.  0.  0.  0.  0.  70.
10.  15.5  8.0  100.  30.  0.  0.  0.  0.  10.  75.
11.  17.0  9.0  100.  30.  0.  0.  0.  0.  15.  75.
12.  18.0  7.0  100.  50.  5.  5.  5.  20.  50.  85.
13.  19.5  6.1  100.  35.  5.  5.  10.  30.  40.  90.
14.  19.5  5.7  40.  20.  10.  20.  50.  70.  60.  60.
15.  17.0  6.0  20.  5.  10.  70.  75.  90.  55.  20.
16.  16.0  9.0  0.  5.  25.  85.  100.  90.  25.  5.
17.  12.0  4.3  5.  40.  40.  65.  65.  20.  10.  0.
18.  6.0  6.0  40.  10.  0.  5.  10.  10.  10.  40.
19.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
20.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
26.01.78
7.  8.0  4.8  90.  10.  0.  0.  0.  0.  5.  60.
8.  9.5  8.5  70.  10.  0.  0.  0.  0.  5.  70.
9.  10.5  6.3  25.  10.  5.  10.  65.  90.  85.  35.
10.  10.5  5.2  35.  0.  0.  5.  50.  90.  85.  45.
11.  10.0  9.5  5.  5.  5.  10.  90.  100.  70.  10.
12.  10.0  6.0  40.  10.  15.  10.  85.  100.  95.  65.
13.  9.0  5.0  10.  0.  0.  10.  70.  80.  80.  45.
14.  8.0  4.6  100.  0.  5.  5.  10.  30.  45.  95.
15.  11.5  4.5  95.  20.  0.  0.  0.  5.  10.  65.
16.  10.0  4.8  30.  20.  0.  10.  30.  55.  50.  30.
17.  8.0  11.6  5.  0.  0.  20.  100.  100.  40.  10.
18.  4.0  11.0  10.  10.  5.  20.  100.  100.  80.  50.
19.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
20.  0.  0.  0.  0.  0.  0.  0.  0.  0.  0.
```

```
OUTPUT FORMAT: PROGRAM WIN1.
==========================

THE HOURLY, DAILY AND TOTAL WINDRUN AND WINDRUN TIMES
IN EACH DIRECTION ARE SHOWN, THESE VALUES SERVE AS THE
ESTIMATED CATCH RATIOS. IN ADDITION THE MEAN WIND VELOCITY
IN EACH DIRECTION FOR THE TOTAL PERIOD OF THE ANALYSIS
ARE SHOWN


     SAMPLE TAKEN ON, 25.01.78

     TIME     TEMP     WIND.    N        NE       E        SE       S        SW       W        NW
       7.      0.0      0.0    0.0      0.0      0.0      0.0      0.0      0.0      0.0      0.0
       8.      0.0      0.0    0.0      0.0      0.0      0.0      0.0      0.0      0.0      0.0
       9.     13.0      6.6    3.6      0.5      0.0      0.0      0.0      0.0      0.0      2.5
      10.     15.5      8.0    3.7      1.1      0.0      0.0      0.0      0.0      0.4      2.8
      11.     17.0      9.0    4.1      1.2      0.0      0.0      0.0      0.0      0.6      3.1
      12.     18.0      7.0    2.2      1.1      0.1      0.1      0.1      0.4      1.1      1.9
      13.     19.5      6.1    1.9      0.7      0.1      0.1      0.2      0.6      0.8      1.7
      14.     19.5      5.7    0.7      0.3      0.2      0.3      0.9      1.2      1.0      1.0
      15.     17.0      6.0    0.3      0.1      0.2      1.2      1.3      1.6      1.0      0.3
      16.     16.0      9.0    0.0      0.1      0.7      2.3      2.7      2.4      0.7      0.1
      17.     12.0      4.3    0.1      0.7      0.7      1.1      1.1      0.4      0.2      0.0
      18.      6.0      6.0    1.9      0.5      0.0      0.2      0.5      0.5      0.5      1.9
      19.      0.0      0.0    0.0      0.0      0.0      0.0      0.0      0.0      0.0      0.0
      20.      0.0      0.0    0.0      0.0      0.0      0.0      0.0      0.0      0.0      0.0
                              ****************************************************************
    EST. CATCH RATIO          18.5      6.4      1.9      5.4      6.8      7.0      6.2     15.4

    TIME (MIN)               156.6     57.5     19.7     51.2     63.6     63.7     56.1    131.7
                             ****************************************************************

     SAMPLE TAKEN ON, 26.01.78

     TIME     TEMP     WIND.    N        NE       E        SE       S        SW       W        NW
       7.      8.0      4.8    2.6      0.3      0.0      0.0      0.0      0.0      0.1      1.7
       8.      9.5      8.5    3.8      0.5      0.0      0.0      0.0      0.0      0.3      3.8
       9.     10.5      6.3    0.5      0.2      0.1      0.2      1.3      1.7      1.6      0.7
      10.     10.5      5.2    0.6      0.0      0.0      0.1      0.8      1.5      1.4      0.8
      11.     10.0      9.5    0.2      0.2      0.2      0.3      2.9      3.2      2.3      0.3
      12.     10.0      6.0    0.6      0.1      0.2      0.1      1.2      1.4      1.4      0.9
      13.      9.0      5.0    0.2      0.0      0.0      0.2      1.2      1.4      1.4      0.8
      14.      8.0      4.6    1.6      0.0      0.1      0.1      0.2      0.5      0.7      1.5
      15.     11.5      4.5    2.2      0.5      0.0      0.0      0.0      0.1      0.2      1.5
      16.     10.0      4.8    0.6      0.4      0.0      0.2      0.6      1.2      1.1      0.6
      17.      8.0     11.6    0.2      0.0      0.0      0.8      4.2      4.2      1.7      0.4
      18.      4.0     11.0    0.3      0.3      0.1      0.6      2.9      2.9      2.3      1.5
      19.      0.0      0.0    0.0      0.0      0.0      0.0      0.0      0.0      0.0      0.0
      20.      0.0      0.0    0.0      0.0      0.0      0.0      0.0      0.0      0.0      0.0
                              ****************************************************************
    EST. CATCH RATIO          13.4      2.5      0.7      2.6     15.3     18.2     14.5     14.6




    TIME (MIN)               140.6     24.9      5.9     19.6    114.2    145.2    127.2    142.4
                             ****************************************************************


                         N        NE        E        SE        S        SW        W        NW
                    ***************************************************************************

EST. CATCH RATIO       31.9      8.9      2.6      8.1     22.1     25.2     20.7     30.0

TIME (MIN)            297.2     82.3     25.6     70.8    177.9    208.8    183.3    274.0

WIND VELOCITY (M/S)     1.8      1.8      1.7      1.9      2.1      2.0      1.9      1.8

                    ***************************************************************************
```

```
OUTPUT FORMAT; PROGRAM WIN2.
===========================

HOURLY, DAILY AND TOTAL VALUES FOR WINDRUN X TEMPERATURE
AND THE WINDRUN TIMES IN EACH DIRECTION ARE SHOWN, THESE
VALUES SERVE AS THE ESTIMATED CATCH RATIO.


   SAMPLE TAKEN ON, 25,01,78

   TIME     TEMP      WIND,      N         NE        E         SE        S         SW        W         NW
    7.       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0
    8.       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0
    9.      13,0       6,6      46,4       7,0       0,0       0,0       0,0       0,0       0,0      32,5
   10.      15,5       8,0      57,7      17,3       0,0       0,0       0,0       0,0       5,8      43.3
   11.      17,0       9,0      69,5      20,9       0,0       0,0       0,0       0,0      10,4      52.2
   12.      18,0       7,0      39,4      19,7       2,0       2,0       2,0       7,9      19,7      33.5
   13.      19,5       6,1      37,8      13,2       1,9       1,9       3,8      11,3      15,1      34.0
   14.      19,5       5,7      13,5       6,7       3,4       6,7      16,8      23,6      20,2      20,2
   15.      17,0       6,0       5,9       1,5       3,0      20,7      22,2      26,6      16,3       5,9
   16.      16,0       9,0       0,0       2,1      10,7      36,5      43,0      38,7      10,7       2,1
   17.      12,0       4,3       1,1       8,4       8,4      13,7      13,7       4,2       2,1       0,0
   18.       6,0       6,0      11,5       2,9       0,0       1,4       2,9       2,9       2,9      11,5
   19.       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0
   20.       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0
                               ***********************************************************************
  EST. CATCH RATIO             282,7      99,7      29,4      83,0     104,3     115,2     103,2     235.1

  TIME (MIN)                   156,6      57,5      19,7      51,2      63,6      63,7      56,1     131.7
                               **********************************************************************


   SAMPLE TAKEN ON, 26,01,78

   TIME     TEMP      WIND,      N         NE        E         SE        S         SW        W         NW
    7.       8,0       4,8      20,9       2,3       0,0       0,0       0,0       0,0       1,2      14.0
    8.       9,5       8,5      36,5       5,2       0,0       0,0       0,0       0,0       2,6      36.5
    9.      10,5       6,3       5,1       2,0       1,0       2,0      13,2      18,3      17,3       7.1
   10.      10,5       5,2       6,2       0,0       0,0       0,9       8,8      15,9      15,0       7.9
   11.      10,0       9,5       1,6       1,6       1,6       3,2      29,0      32,2      22,5       3.2
   12.      10,0       6,0       5,7       1,4       2,1       1,4      12,1      14,3      13,6       9.3
   13.       9,0       5,0       1,5       0,0       0,0       1,5      10,7      12,2      12,2       6.9
   14.       8,0       4,6      12,7       0,0       0,6       0,6       1,3       3,8       5,7      12.1
   15.      11,5       4,5      25,2       5,3       0,0       0,0       0,0       1,3       2,7      17.2
   16.      10,0       4,8       6,4       4,3       0,0       2,1       6,4      11,7      10,7       6.4
   17.       8,0      11,6       1,7       0,0       0,0       6,7      33,7      33,7      13,5       3.4
   18.       4,0      11,0       1,2       1,2       0,6       2,3      11,7      11,7       9,4       5.9
   19.       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0.0
   20.       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0,0       0.0
                               ***********************************************************************
  EST. CATCH RATIO             124,7      23,4       6,0      21,0     127,0     155,2     126,3     129.8

  TIME (MIN)                   140,6      24,9       5,9      19,6     114,2     145,2     127,2     142.4



                               **********************************************************************


                         N         NE        E         SE        S         SW        W         NW
                       *********************************************************************
TOTAL CATCH RATIO      407.4     123.1     35.3     103.9     231.3     270.4     229.5     364.9

TIME (MIN)             297.2      82.3     25.6      70.8     177.9     208.8     183.3     274.0

                       *********************************************************************
```

APPENDIX 6: Two hourly catches (06h00 - 20h00) of wind dispersed *D.austrinus* crawlers trapped on eight horizontal sticky impact traps placed 1 m from a single jointed cactus pla (*O.aurantiaca*) in the four cardinal and four semi-cardinal directions; together with the corresponding values for temperature ($h^o > 13^oC$), windrun (km) humidity (mean hourly % R.H.) and crawler movement. Values for ten days are shown.

Time	Catch	Temperature	Windrun	Humidity	Crawler movement
25.01.78					
06h00-08h00	0	15,5	6,4	82,5	12
08h00-10h00	32	28,5	14,6	53,5	115
10h00-12h00	49	35,0	16,0	41,5	103
12h00-14h00	30	39,0	11,8	37,6	22
14h00-16h00	122	33,0	15,0	49,0	85
16h00-18h00	51	18,0	10,3	78,5	65
18h00-20h00	0	11,0	12,6	84,5	2
26.01.78					
06h00-08h00	8	17,5	13,3	70,0	4
08h00-10h00	10	21,0	11,5	80,0	81
10h00-12h00	32	20,0	15,5	82,5	47
12h00-14h00	16	17,0	9,6	78,5	54
14h00-16h00	14	21,5	9,3	62,5	64
16h00-18h00	21	12,0	22,6	85,0	27
18h00-20h00	2	5,0	19,5	95,5	8
27.01.78					
06h00-08h00	3	1,5	11,3	79,0	27
08h00-10h00	10	5,0	10,9	70,0	38
10h00-12h00	17	11,5	12,5	54,0	69
12h00-14h00	11	12,5	11,6	57,5	47
14h00-16h00	23	9,5	12,8	72,5	26
16h00-18h00	0	7,0	10,0	77,5	19
18h00-20h00	1	4,5	6,9	92,0	5

Time	Catch	Temperature	Windrun	Humidity	Crawler movement
28.01.78					
06h00-08h00	0	5,0	5,9	97,0	4
08h00-10h00	0	5,5	7,0	97,0	6
10h00-12h00	0	11,0	5,8	87,5	5
12h00-14h00	9	16,5	10,4	82,5	20
14h00-16h00	13	17,5	12,0	82,5	41
16h00-18h00	6	15,0	8,8	85,0	13
18h00-20h00	4	9,5	2,5	81,5	8
29.01.78					
06h00-08h00	0	6,0	5,3	81,5	28
08h00-10h00	18	15,0	6,1	60,0	144
10h00-12h00	15	21,0	6,6	51,5	137
12h00-14h00	22	25,0	7,1	45,0	82
14h00-16h00	50	24,0	14,9	65,0	162
16h00-18h00	27	16,0	11,1	67,5	46
18h00-20h00	4	10,5	5,8	95,0	15
30.01.78					
06h00-08h00	0	13,0	2,7	77,5	24
08h00-10h00	13	27,0	8,6	57,7	121
10h00-12h00	26	29,0	11,2	46,5	102
12h00-14h00	46	31,0	14,8	60,0	54
14h00-16h00	43	18,5	29,0	77,5	154
16h00-18h00	19	14,0	19,7	92,0	38
18h00-20h00	8	12,0	17,2	96,0	10
31.01.78					
06h00-08h00	0	10,0	5,2	97,0	13
08h00-10h00	0	9,5	8,7	97,0	12
10h00-12h00	4	14,0	10,0	80,0	14
12h00-14h00	13	14,0	11,8	80,0	37
14h00-16h00	16	15,0	10,8	76,0	53
16h00-18h00	6	11,0	11,0	90,0	26
18h00-20h00	6	10,5	11,5	95,0	8

	Time	Catch	Temperature	Windrun	Humidity	Crawler movement
01.02.78						
	06h00-08h00	0	9,5	9,3	98,0	1
	08h00-10h00	4	15,5	7,5	91,5	33
	10h00-12h00	8	26,0	7,7	65,0	118
	12h00-14h00	13	34,0	6,9	56,0	52
	14h00-16h00	50	30,0	14,2	68,5	115
	16h00-18h00	8	25,5	9,0	79,0	76
	18h00-20h00	4	18,0	12,0	85,0	21
02.02.78						
	06h00-08h00	8	11,0	12,3	85,0	5
	08h00-10h00	23	14,0	21,2	86,5	57
	10h00-12h00	25	17,5	18,9	81,5	61
	12h00-14h00	13	19,5	17,0	75,0	129
	14h00-16h00	47	16,0	17,6	78,0	141
	16h00-18h00	7	11,5	13,4	85,0	37
	18h00-20h00	0	8,5	9,9	88,5	7
03.02.78						
	06h00-08h00	0	10,0	2,0	92,5	5
	08h00-10h00	7	21,0	6,6	70,0	65
	10h00-12h00	22	26,5	7,0	58,5	114
	12h00-14h00	16	35,0	9,4	45,0	41
	14h00-16h00	48	27,5	10,3	56,0	141
	16h00-18h00	24	12,5	14,0	74,0	61
	18h00-20h00	19	12,0	11,9	95,0	28

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