THE BIOLOGY OF Acia lineatifrons (NAUDE) (HOMOPTERA: CICADELLIDAE)ON GRAPEVINES IN THE WESTERN CAPE

THESIS

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Acia lineatifrons (Naudé) : female

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CHAPTER 1. INTRODUCTION

Leafhoppers (Homoptera: Cicadellidae) are economically important pests on a large variety of agricultural and commercial crops all over the world. Grapevines in Europe and North America are attacked by numerous leafhopper species, e.g. Empoasca flavescens Fabr., Scaphoideus littoralis Ball, Erythroneura elegantula Osborn and E. ziczac Walsh (Schvester et al, 1962; Kido & Stafford, 1965; McKenzie & Beirne, 1972). Leafhoppers penetrate the xylem, phloem or mesophyll of the host plant with their stylets and feed on the plant sap, causing symptoms like "spotting" or "hopper-burn" as described by Flaherty et al (1982) and Moutous (1979). Many leafhopper species are known disease vectors, e.g. S. littoralis which transmits Flavescence dorée, a disease caused by a mycoplasma-like organism (Schvester et al, 1962). According to Hopkins (1977) at least 26 leafhopper species transmit Pierce's disease on grapevines in North America. The vectors must be xylem feeders as the disease bacteria are restricted to the xylem tissues of the host plant (Purcell & Finlay, 1979).

South African grapevines were not known to be attacked by leafhoppers until 1978 when leafhopper damage was first identified on grapevines in the Tulbagh district (De Klerk, 1981). Since then reports of leafhopper damage to grapevines have been received from all over the Western Cape Province. The leafhopper attacking the vines was identified as Acia lineatifrons (Naudé) (Theron, 1982). It is widely distributed across tropical Africa: specimens have been collected in Ethiopia, Sudan, Nigeria, Ivory Coast, Zaire, Zimbabwe and Madagascar. The first specimen recorded in South Africa was collected on "blackberries" at Hilton Road, Natal in 1917. Since 1968 A. lineatifrons has been collected regularly in the Western Cape. Appendix 1 contains the available records of the specimens collected in Africa.

Acia lineatifrons belongs to the sub-family Typhlocibinae in the family Cicadellidae. Naudé originally described it as Empoasca lineatifrons in 1926 (Theron, 1982) but in 1981 Dworakowska revised the genus Acia and it was reclassified as Acia lineatifrons (Naudé). The face and pronotum are characteristic of this species. There are two big white, oval patches in the centre of each half of the vertex anteriorly and a dark pattern on the pronotum forming indistinct longitudinal stripes. The face is described as dull whitish with the frontoclypeus light brown-testaceous at the sides. There are six dark brown longitudinal narrow streaks apically and seven similar streaks in the lower part of the face (Fig.1) - hence the specific name "lineatifrons" (Dworakowska, 1981).

Figure 2. Symptoms caused by Acia lineatifrons on Chenin blanc grapevines.

The typical symptoms caused by A. lineatifrons feeding on grapevines are browning or discolouration of the leaves from the perimeter inwards and the forming of characteristic concentric bands or fronts of discolouration (Fig.2). These symptoms resemble the "hopper-burn" symptoms described by Moutous (1979) for Empoasca vitis Goethe on grapevines in the southwest of France and appear to be the result of a phytotoxic reaction.

Initially the browned areas of the leaves are leathery, but they soon become dry and brittle and the leaves have a scorched look. This injury reduces photosynthetic activity by reducing effective leaf surface. Discoloured leaves together with the petioles are often abscised. This is in contrast to the symptoms of Pierce's disease where the petioles remain after abscision of the affected leaves. Heavy defoliation before harvest can result in sunburn damage to the grapes, a particularly serious problem in table grapes. Premature leaf loss after harvest adversely affects the ripening of the canes and the accumulation of reserves. This, in turn, can have a detrimental effect on budding and blooming of the vines in the next growing season.

As yet no evidence has been found to indicate that A. lineatifrons is a vector of any grapevine pathogen. The possibility of this insect acquiring a pathogen through exposure to infected hosts cannot, however, be ruled out *a priori*. Experiments to determine whether A. lineatifrons can transmit any of the important grapevine pathogens occurring in South Africa will have to be conducted before definite conclusions can be drawn.

The ultimate objects of research on A. lineatifrons are the development of a reliable crop-linked predictive model and methods for monitoring pest populations, as well as efficient short- and long- term control measures and pest management techniques. The biology of A. lineatifrons has not been studied before, therefore this research project was aimed at obtaining some basic information on the biology and population dynamics of the insect as well as to help identify priorities for future research.

The life cycle of A. lineatifrons and its developmental period were studied under controlled conditions (Chapter 3). Chapter 4 deals with the population dynamics of A. lineatifrons. Its seasonal occurrence on grapevines, overwintering, alternative hosts, host preference, movement between overwintering host and grapevines and sex ratio were investigated.

Because A. lineatifrons is an indigenous insect, the question arises "why did it only recently become a pest on grapevines?" In 1971 Chaboussou suggested that the replacement of inorganic fungicides with organic ones, especially the dithiocarbamates, contributed to the uncommon outbreak of Empoasca flavescens in France by altering the nitrogen content of the grapevines. The possibility that the use of such fungicides could be responsible for local outbreaks of leafhoppers was investigated, although the fact that outbreaks also occurred in vineyards where such fungicides were not used, seems to indicate that this is not the only cause of local leafhopper outbreaks. Laboratory experiments and a field trial on the effects of such a fungicide on the fecundity and population build-up of A. lineatifrons were conducted and are described and discussed in Chapter 5. Alternative possible explanations for the sudden pest status of the leafhopper on grapevines are discussed in Chapter 6.

The methods used as well as the experimental lay-outs of the field trials and sampling programmes are described in Chapter 2.

CHAPTER 2. MATERIALS AND METHODS

2.1. Life cycle and developmental period of Acia lineatifrons

Nymphs were collected from an infested vineyard and placed on potted grapevines in a screen cage kept in a constant temperature room at 26°C. Plants of the cultivar Chenin blanc, grafted onto 99 Richter rootstocks, were chosen for all laboratory experiments because this was the cultivar on which the field work was carried out. A long photoperiod of eighteen hours was selected and special growth lights ("Grolux" neon tubes) were used to ensure normal, vigorous vine growth. Virgin adult leafhoppers were collected as they emerged, sexed and paired (one female with one or two males, depending on availability) in small cages enclosing single vine leaves. All newly hatched nymphs produced by these adults were removed and placed singly in similar cages on single vine leaves. Daily observations were made and the dates of hatching, moulting and adult emergence recorded to determine the number of larval instars and development time. Exuviae were removed from the cages after every moult. The development time from hatching to adult emergence was also determined at 20°C. Observations to determine the incubation period of the eggs at 26°C were made concurrently with the experiments on leafhopper fecundity described in Section 2.2.

2.2. Fecundity, pre-oviposition period and incubation period of eggs

The fecundity of A. lineatifrons was determined concurrently with the experiment on the influence of an organic dithiocarbamate fungicide on the fecundity of the females in the laboratory. Potted Chenin blanc vines grafted onto 99 Richter rootstocks were again used. The plants were divided into two treatment groups: the control group received no organic fungicides, while the test group received two applications of Mikal-M (active ingredient Fosetyl AL/mancozeb) six and three weeks before being exposed to leafhoppers. A. lineatifrons nymphs, preferably

first, second and third instar, were collected from Rubus chrysocarpus in the field in spring before the leafhoppers had moved onto the grapevines. Half of the nymphs were placed on untreated control plants in a screen cage and the other half on Mikal-M treated plants in another cage in the same room. A constant temperature of 26°C and a photoperiod of eighteen hours was maintained. Virgin adults which were collected from these colonies as they emerged, were sexed and paired (one female with one or two males, depending on availability) in gauze sleeve cages fitted over the two or three terminal leaves of potted vine shoots. Adults from the vines treated with Mikal-M were caged on vines treated with Mikal-M, and adults from the untreated vines were caged on untreated control plants. Due to their fragility and agility the females were transferred to fresh leaves only every two to three days. Males dying before the females were not replaced. Daily observations were made and the dates and number of nymphs hatched per female for the two treatments were recorded. The mean incubation period of the eggs was also calculated from these data.

A further experiment to determine the fecundity of the females on untreated vines was carried out at a mean constant temperature of 24,6°C. Two different procedures were employed. In the first, females were transfered to fresh leaves every day or two in order to determine the pre-oviposition period of the females as above. In the second, fecundity was also measured on single leaves taken from grapevines growing outdoors in a vineyard. The leaf petioles were cut underwater and inserted into water saturated "Oasis". The leaves were then placed singly in large Petri dishes and a pair of leafhoppers added to each dish. Leaves were exchanged for fresh ones every second or third day and those exposed to leafhoppers were kept and checked daily for the presence of nymphs. Nymphs were then counted as before.

2.3. Host preference

Leaves of R. chrysocarpus and grapevines were collected in the field, the petioles cut off under water and embedded in saturated "Oasis". One vine leaf and one

Rubus leaf of similar size and age were placed together in a large petri dish (145 mm diameter). R. chrysocarpus and grapevine leaves infested with A. lineatifrons nymphs were collected in the field. Two or three nymphs were placed in each prepared dish, equidistant from both leaves. Observations regarding the kind of leaves the nymphs were on were made 90 minutes after the release of the nymphs as well as on the following morning. The movements of each nymph were recorded individually. The same method was used to determine whether the adults of A. lineatifrons prefer grapevines to Rubus.

2.4. Seasonal occurrence in the field

Part of an infested vineyard (Chenin blanc grafted onto 99 Richter rootstocks) near Simondium in the south-western Cape was divided into 100 plots of six vines each. These 100 plots were divided into five blocks each of 20 plots and one plot selected randomly from each of the five blocks was sampled every week with a D-Vac suction sampler for one minute on one side of the row only. Thus each plot was sampled only once every twenty weeks during the season, which allowed the leafhopper population time to re-establish before the next sampling. The catch for each plot was isolated, killed, and the number of adult A. lineatifrons counted. This sampling method was not efficient for collecting nymphs which cling to the leaves, and the number of nymphs collected was not used in the population curves. Three adjacent patches of R. chrysocarpus (each approx. 2-3 m in diameter) separated from the vineyard by a gravel road were sampled alternately for one minute every week during the growing season and every second week during winter. These were the only patches of R. chrysocarpus near the vineyard. As this sampling regime did not allow the leafhopper population enough time to re-establish properly, these counts serve only as an indication of the presence or absence of A. lineatifrons in the immediate vicinity of the vines, and does not truly reflect its numbers on the Rubus. Sampling was carried out over three seasons, viz. 1981/82, 1982/83 and 1983/84.

2.5. Sex ratio of field populations

On six occasions during the winter of 1986 patches of R. chrysocarpus at sites near Simondium and Lynedoch were sampled with a D-Vac suction sampler. The catches were killed with ethyl acetate and the numbers of A. lineatifrons males and females counted. During the spring and summer of 1986/87 the grapevines near Simondium and the adjacent Rubus patches were sampled weekly from October 1986 until March 1987 and the sex ratio of A. lineatifrons determined. Data for the grapevines were obtained from the plots used in the experiment on the influence of Mikal-M on the population build-up of A. lineatifrons. The experimental lay-out is described in Section 2.8.

2.6. Sticky traps

The movement of leafhoppers between the Rubus and the grapevines were monitored with yellow sticky traps. Cylindrical traps were used to minimize the problems with air currents and slip streams associated with flat board traps. Large coffee tins (130 mm diameter, height 190 mm) were painted yellow and nailed upside-down onto 1,5 meter high wooden posts planted in the ground. Transparent film of the type used for overhead projectors was taped around the tins and coated with Revertex, a transparent, sticky substance. The placement of the traps is illustrated in Fig. 3. The sides facing towards the Rubus and the vines were marked on each sticky strip. The sticky strips were replaced every one or two weeks and the catches counted in the laboratory.

2.7. Measurements to test for flight dimorphism in leafhopper populations

Adults of A. lineatifrons collected on R. chrysocarpus and grapevines for sex ratio determination were also measured to investigate the possibility that flight dimorphism similar to that recorded for Cicadulina mbila by Rose (1972b) exists in these leafhoppper populations. The total length of the front wing was measured

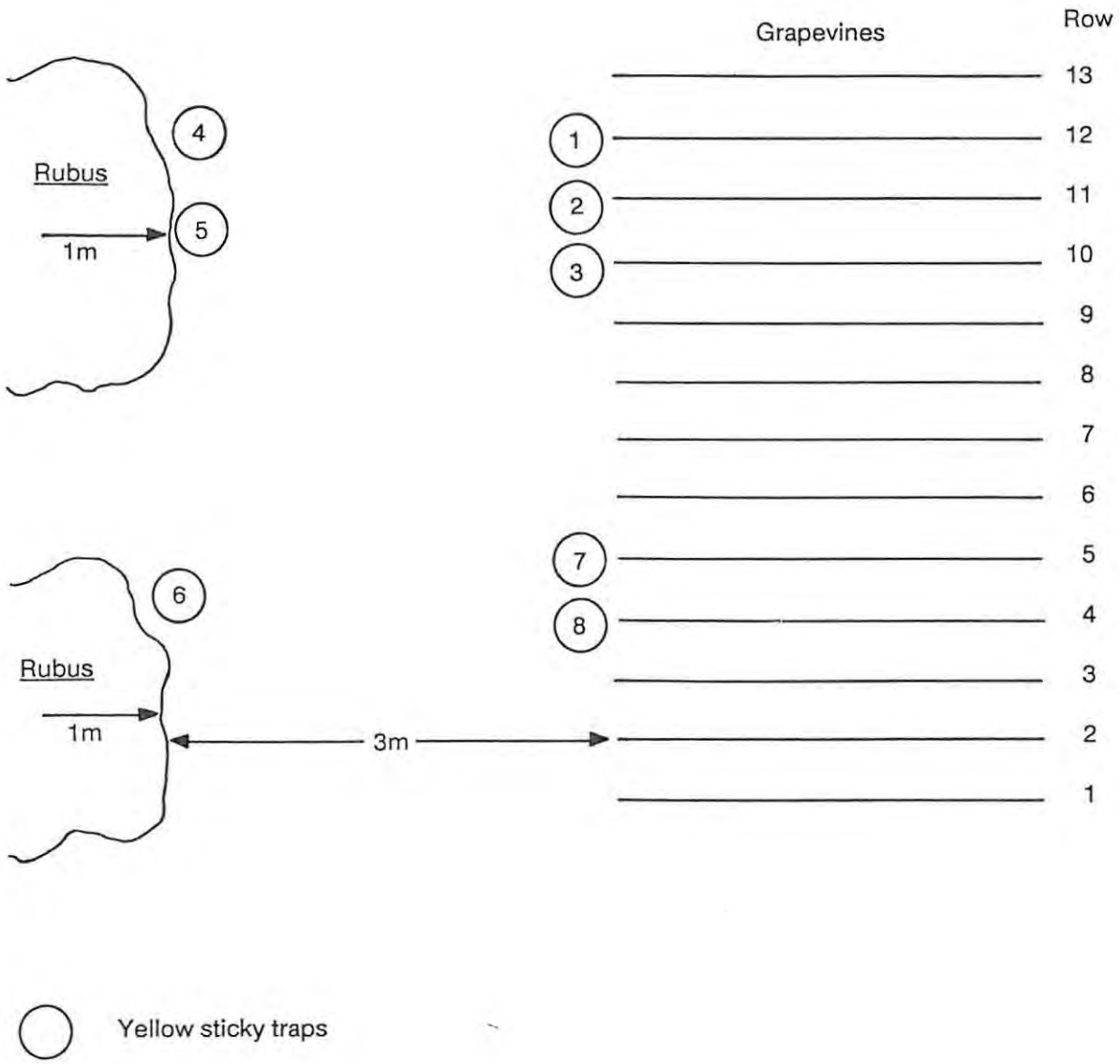


Figure 3. Positions of yellow sticky traps at Simondium.

with a micrometer eyepiece mounted on a dissection microscope. The distance that the wings extended beyond the tip of the abdomen was also measured (Rose, 1972b).

2.8. Effect of an organic fungicide on the population build-up of A. lineatifrons in the field

The experiment was carried out in the vineyard near Simondium described in Section 2.4. Four rows of eleven plots each were sprayed with an organic dithiocarbamate (Mikal-M: active ingredient Fosetyl AL/mancozeb) on 4-12-86 and again on 22-12-86, according to the registered recommendations for downy mildew control. The rest of the vineyard was sprayed with copper oxychloride, an inorganic fungicide. Four of these latter rows were chosen as controls. The rows in every treatment were divided into three blocks: three plots closest to the Rubus patches, the four in the middle and four plots furthest from the Rubus. Every week three plots from each treatment, one selected randomly from each of the three blocks per treatment, were sampled as described in Section 2.4 to monitor the leafhopper population.

2.9. Determination of total leaf nitrogen

Potted vine leaves were analysed to determine whether the application of Mikal-M alters the total nitrogen of the leaves, which could alter the fecundity of A. lineatifrons on the vines. The experiment was carried out on potted Chenin blanc vines grafted onto 99 Richter rootstocks and grown in a green house. Ten vines exhibiting uniform growth and vigour were selected and leaf samples were taken. Five of the vines were then treated with Mikal-M and the other five kept as untreated controls. Thirteen days after treatment leaf samples were taken from both groups of plants. Three weeks after the first application of Mikal-M, a second application was made in accordance with the registered recommendations. Two weeks later the third and final set of leaf samples was taken. The samples were dried at 70°C for 24 hours and milled to pass through a 40 mesh sieve. Total nitrogen was determined in a selenious acid/sulphuric acid digest by means of an automated colorimetric method as described by Warner and Jones (1970).

2.10. Cultivation of potted grapevines for experiments

Cuttings of Chenin blanc vines were grafted onto 99 Richter rootstocks and planted in black plastic bags. Plants were watered with a nutrient solution containing all essential macro- and micro-elements (Chemicult Hydroponic Solution) every second week and with pure water in between. By the time plants were big enough to be used, they were three years old.

CHAPTER 3. THE LIFE CYCLE OF Acia lineatifrons (NAUDE) ON GRAPEVINES (Vitis vinifera)

INTRODUCTION

The life cycles of leafhoppers have been studied extensively on a wide variety of host plants in North America, Europe and Africa. Leafhoppers are hemimetabolous insects and it was established that the nymphs hatching from the eggs pass through five larval stages or instars, the fifth moult terminating in adult emergence (Schvester et al, 1962; Coupe & Schulz, 1968; Metcalfe, 1970; McKenzie & Beirne, 1972; Rose, 1973; Van Rensburg, 1980; Parh & Taylor, 1981; Prestidge, 1982). Certain conditions have been known to cause some leafhopper species to pass through only four or as many as six larval instars (DeLong, 1971). The incubation period of the eggs, development time of the nymphs, adult longevity and the number of generations produced per year are presumably determined by intrinsic factors and can be modified by variations in weather conditions, notably temperature (Hughes, Jones & Gutierrez, 1984).

Some leafhoppers are univoltine and produce only one generation per year, e.g. Scaphoideus littoralis which in Europe occurs on grapevines only and overwinters as diapause eggs (Schvester et al, 1962). Other species are bivoltine. Erythroneura ziczac produces two generations per year on grapevines in the Okanagan Valley, British Columbia and overwinters in the adult stage among fallen leaves and grass (McKenzie & Beirne, 1972). Many leafhopper species are multivoltine. Empoasca flavescens occurs on grapevines in Europe and produces three to four generations per year. Adults overwinter on a variety of other green plants (Schvester et al, 1962; Moutous, 1979). The overwintering adults are in a reproductive diapause.

In multivoltine species the number of generations per year also depends on environmental factors which influence the developmental rate. Research has shown that the growth and developmental rate of leafhoppers are very sensitive to temperature changes and that temperature increases within the tolerance limits of the leafhopper species lead to an increase in the developmental rate (Davis, 1966; Kouskolekas & Decker, 1966; Coupe & Schulz, 1968; Rose, 1973; Van Rensburg, 1980; Parh & Taylor, 1981). An increase in developmental rate shortens the exposure time of eggs and nymphs to predators and

parasites, thus further increasing the number of leafhoppers reaching the reproductive stage. Even one extra generation per year, especially towards the end of the season, can cause a significant increase in crop damage and it also increases the size of the overwintering population, which could result in heavier primary infestation of the crop in the following season.

Generation time, i.e. the time from the hatching of one generation of nymphs until the appearance of the next generation of nymphs, is used to estimate the number of generations that can be produced per season and to estimate the potential growth rate of a population. The generation time of a species consists of the development period of the nymphs, the pre-oviposition period of the females and the incubation period of the eggs.

The life cycle of A. lineatifrons was studied on grapevines in a constant temperature room in order to determine the pre-oviposition period of the females, the incubation period of the eggs and the duration of nymphal development. The latter was done at two different constant temperatures (20 and 26°C) to gain some indication of how strongly the developmental rate is influenced by temperature. The fecundity of the females on grapevines was also investigated on potted grapevines and on single leaves from grapevines in a vineyard.

TECHNIQUES

The methods used in determining the incubation period of the eggs, development time from hatching to adult emergence, pre-oviposition period and fecundity are described in Chapter 2, Sections 2.1 and 2.2. Females of A. lineatifrons are easily injured during handling, therefore they were transferred to fresh leaves every second or third day only. As a result the date of oviposition for each nymph was not known exactly, and the incubation period is given as a range over two or three days.

RESULTS

The female has a well developed ovipositor (Fig. 4) with which she inserts the eggs under the epidermis of the host plant leaves. The mean incubation period of the eggs at 26°C was between nine and eleven days, as is shown in Table 1.

It was confirmed that there are five larval or nymphal instars. Table 2 shows the instar duration in days for A. lineatifrons at constant temperatures of 20 and 26°C and a photoperiod of eighteen hours. Data from all nymphs that died or were lost before adult emergence were excluded. At 26°C the mean duration of the first, second, third and fourth instars was two and a half to three days, whereas the fifth instar took four days on average to complete. The mean development time from the hatching of the nymphs until adult emergence was fifteen days. At 20°C the duration of the individual instars were not recorded. The mean development time from hatching until adult emergence was 25 days. This clearly illustrates how a decrease in temperature retards nymphal development.

Table 3(a) shows the the fecundity of A. lineatifrons females on potted grapevines at a mean temperature of 26°C. The lifespan of the females is given as the number of days from the pairing of the male and female until the death of the female. Due to the difficulty of finding the leafhopper eggs in the vine leaf tissue fecundity was measured as the number of nymphs produced per female. The total number of nymphs produced per female are given. A total of 52 females were caged on potted vines, but only 20 produced any offspring - i.e. only 38,5 percent of the females. The mean number of nymphs produced per female was very low compared to the fecundities measured for other leafhopper species (refer to Appendix 2), therefore the experiment was repeated on potted vines at a mean constant temperature of 24,6°C as well as on potted vines outdoors. The latter was done in an attempt to determine whether the artificial conditions in the insectary were responsible for the low fecundity measured.

Only three out of 33 females produced nymphs at 24,6°C and only two out of eight produced nymphs outdoors. The laboratory results indicate that the low recorded fecundities in the earlier experiment were not due to chance. The results of the outdoor test suggest that these low fecundities are not due to any simple effect of laboratory conditions.

Figure 4. Ovipositor of A. lineatifrons female

TABLE 1. Incubation period of A. lineatifrons eggs at 26°C given as a range over two to three days. Females are easily injured during handling, therefore they were transferred to fresh leaves every two or three days and not daily. This meant that the exact date of oviposition for an egg was not known, hence the range over two or three days.

No.	Incubation period (days)
1	9 - 12
2	9 - 11
3	9 - 11
4	11 - 13
5	14 - 16
6	8 - 11
7	7 - 10
8	8 - 11
9	8 - 11
10	9 - 12
11	7 - 10
12	7 - 10
13	8 - 11
14	7 - 9
15	9 - 11
16	10 - 13
Mean	9 - 11

TABLE 2. Nymphal development period of A. lineatifrons measured to the nearest whole day from hatching until adult emergence at two different temperatures.

		Development period to nearest whole day					
		Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
	Mean	2,7	2,5	2,9	2,9	4,1	15,1
26°C	Range	2-4	2-4	2-5	1-4	1-6	12-20
N=24	SD	0,69	0,78	0,95	0,83	0,83	1,96
	Mean						25,0
20°C	Range						21-30
N=17	SD						2,39

TABLE 3. Fecundity (no. nymphs produced) of A. lineatifrons on potted Chenin blanc grapevines treated with Mikal-M and on untreated controls at 26°C. Only data from females that produced nymphs are given.

	(a)		(b)	
	CONTROL		MIKAL-M	
No.	Lifespan	Fecundity	Lifespan	Fecundity
1	9	13	9	5
2	9	8	16	14
3	34	19	12	1
4	21	20	33	18
5	31	18	34	15
6	17	6	35	3
7	22	24	25	6
8	33	20	8	2
9	30	14	21	4
10	22	6	23	6
11	10	3	23	7
12	12	1	14	2
13	3	1	15	3
14	3	1	22	1
15	4	2	7	1
16	3	4	11	4
17	12	1	11	4
18	20	3	16	1
19	5	2	40	14
20	17	4	3	1
21			15	2
22			24	9
23			16	6
24			6	10
25			18	3
26			16	1
27			18	2
28			14	8
29			9	3
30			6	1
31			12	2
Mean	15,9	8,5	17,2	5,1
Range	3-34	1-24	3-40	1-18
SD	10,5	62,1	9,2	22,1

Further experiments were conducted using single vine leaves in the laboratory and outdoors to investigate the possibility that the fact that potted vines were used could be responsible for the low fecundities measured. These experiments failed, because the leaves dried out before the eggs hatched.

There is reason to believe that the poor results of the second laboratory test may have been due to manipulation of the leafhoppers. During the repeat of the fecundity experiment at 24,6°C in the insectary most of the females were transfered to fresh leaves every day so that the pre-oviposition period of the females could be established. All of these females died without producing any offspring. The three females that produced nymphs had all been left undisturbed on the leaves for more than seven days at a time. As a result data from the previous fecundity experiment at 26°C had to be used to calculate a minimum pre-oviposition period. Females had been transferred to fresh leaves every second or third day only. The number of days each female spent on the leaf or leaves from which no nymphs hatched, was counted. This indicates the minimum pre-oviposition period only, because the number of days before the first eggs were laid on the leaf where the first nymphs hatched, is not known. Table 4 contains these minimum pre-oviposition periods.

DISCUSSION

Generation time and the growth rate of a population are important factors in the study of the population dynamics of a species. A mean incubation period of nine to eleven days, a mean nymphal development time of fifteen days and a minimum pre-oviposition period of five to ten days add up to a mean generation time of between 29 and 36 days at a constant temperature of 26°C. The experiments on the influence of temperature on nymphal development rate showed that generation time and therefore also the number of generations per season will be strongly influenced by the climatological conditions experienced by the leafhoppers. Generation time is an important factor to consider when estimating the growth rate of a population. The field studies (Chapter 4) showed that A. lineatifrons does not produce discreet generations, but that generations overlap. Adult longevity as indicated by the female lifespan recorded in the fecundity experiments supports this: the mean lifespan of those females producing nymphs exceeds the mean

TABLE 4. Minimum pre-oviposition period of A. lineatifrons females at 26°C.

No.	Min. pre-oviposition period (days)
1	5
2	7
3	9
4	7
5	7
6	6
7	6
8	6
9	6
10	10
11	7
12	7
13	5
14	7
15	7
Mean	6,8
Range	5 - 10

incubation period of the eggs (refer Table 1 and 3). Due to the overlapping of generations the number of generations per season in the field cannot be determined accurately.

However, the number of generations that could be produced per season can be estimated. Temperature varies greatly under field conditions and according to the meteorological data obtained from the weather station at Elsenburg (see Chapter 4), the mean daily temperature rarely exceeds 26°C in the field. Therefore, the generation time of A. lineatifrons at 20°C appears to be more applicable. The nymphal development period was 25 days at 20°C compared to 15 days at 26°C. Presuming that all stages of the life cycle are affected to the same degree by a drop in temperature, extrapolation of the data at 26°C gives a generation time of 47 to 60 days at 20°C. This means that four to five leafhopper generations could be produced during a growing season from September until March/April.

Fecundity as well as generation time play a major role in determining the rate of a population's increase. According to Andrewartha (1970) the intrinsic rate of natural increase of a population depends on the mean generation time and the net reproduction rate of the species, the latter being largely determined by fecundity. In all of the experiments on the fecundity of A. lineatifrons both the number of females producing nymphs and the number of nymphs produced per female were very low, even when compared to the lowest leafhopper fecundities recorded thus far, viz. 16 eggs per female for Graminella nigrifrons (Forbes) (DeLong, 1971). This low value may be the result of several factors:

(i) The fecundity of A. lineatifrons is expressed as the mean number of nymphs produced per female, whereas most other authors express it as the mean number of eggs laid per female. The number of eggs that hatch can differ considerably from the number of eggs laid by the female, even in the absence of egg predation and parasitism. Stoner and Gustin (1967) reported that only 61,2 percent of the eggs of Graminella nigrifrons hatched. According to Gustin and Stoner (1968) 51,1 percent of the eggs of Deltocephalus sonorus Ball hatched and Rose (1973) found that less than 20 percent of the eggs of Cicadulina mbila (Naudé) hatched in his laboratory experiments. The cause for this is not known, but Strong, Lawton and Southwood (1984) mention that mortality can occur in eggs inserted

into plant tissues due to crushing by the growing plant tissues.

(ii) Kieckhefer and Medler (1964) demonstrated that the fecundity of Empoasca fabae (Harris) is influenced by temperature and photoperiod. At 27°C ten pairs of leafhoppers produced a mean of 103 nymphs, compared to 520 nymphs by ten pairs at 24°C on broad beans (Vicia faba L.). This shows that fecundity can vary greatly with relatively small changes in temperature. Because the optimal temperature for mating and oviposition is not known for A. lineatifrons it is possible that the temperature regimes in the insectary were not optimal for mating and oviposition.

(iii) The nutritional status of the host plant, particularly with regard to the nitrogen compounds, has a major influence on leafhopper fecundity. Prestidge (1982) found that egg production and the oviposition rate of three feeding types of grassland leafhoppers, viz. Dicranotropis hamata Boheman and Elymana sulphurella Zetterstedt (phloem feeders), Eucelis incisus Kirschbaum (xylem feeder) and Zyginidia scutellaris Herrich-Schaeffer (mesophyll feeder), increased with increases in available nitrogen due to fertilizer applications. Leafhopper females oviposit throughout most of their adult lives (DeLong, 1971; Parh & Taylor, 1981; Prestidge, 1982) with only a few eggs maturing at a time. Studies on Erythroneura elegantula Osborn in California, U.S.A, showed that ovigenesis in females continues with feeding on host plants (Flaherty et al, 1982). Changes in host nutrient quality during a female's lifetime can affect her fecundity. Grapevines are woody perennials and the fact that they had been confined to pots for three years when used in the experiments could have influenced their nutritional status for A. lineatifrons which, in turn, could have affected female fecundity. For this reason single leaves from grapevines growing in a vineyard were also used in fecundity experiments. Only three females out of 30 produced two nymphs each in this experiment, therefore no conclusions regarding the effect of potting on the quality of the vines as hosts can de drawn. Fecundity could not be assessed on grapevines in the field, because the cages were torn from the shoots by the prevailing south-easterly winds.

(iv) The necessary handling of females in the laboratory may have contributed to the low fecundities.

Knowledge of the life cycle of an insect pest under controlled conditions provides a starting-point from which extrapolations to field conditions can be made, but it is the behaviour of the field populations that is of immediate concern to the farmers, therefore the population dynamics of A. lineatifrons were studied in an infested vineyard.

CHAPTER 4. POPULATION DYNAMICS OF A. lineatifrons ON GRAPEVINES

INTRODUCTION

Efficient pest management strategies can only be devised if the population dynamics of the relevant pest are understood. In the case of A. lineatifrons chemical control will have to be applied as a short-term solution until long-term biological or integrated pest management strategies have been developed. In order to be able to predict leafhopper outbreaks and to enable farmers to time chemical control correctly for maximum efficiency it is necessary to know when the pest enters the vineyards, when peak populations can be expected, when damage symptoms appear and where the leafhopper overwinters. To this end regular sampling of A. lineatifrons was undertaken over three years in a vineyard where this pest had caused damage. Inspection of the adjacent natural vegetation showed A. lineatifrons to be present on the wild brambles, Rubus chrysocarpus and R. pinnatus Willd. It was decided to include the brambles in the sampling programme.

The rate of increase of a population is an important determining factor in predicting outbreaks of pest populations. According to Chapman (1931) the reproductive potential of a species is determined by the sex ratio of the population, i.e. the percentage of females in the population, and the fecundity of the females, i.e. the number of young produced per female in a unit of time. Robinson (1980) illustrated that a decrease in the proportion of females in onion fly (Delia antiqua Meigen) colonies led to a significant increase in the fecundity of the females by increasing the oviposition rate. This insect maintains its reproductive potential by compensating for changes in sex ratio by adapting female fecundity and *vice versa.* Because of the importance of the sex ratio in the rate of increase of the population the sex ratio of the leafhopper populations on the overwintering hosts as well as on the grapevines was monitored during the winter of 1986 and the spring and summer of 1986/87.

Erythroneura elegantula Osborn is native to California, U.S.A, and these leafhoppers overwinter as adults in reproductive diapause on weeds in or near the vineyards. In spring there is a definite migration from the overwintering sites into the vineyards. Yellow sticky

traps were erected to determine if A. lineatifrons migrates from nearby Rubus to the grapevines at the beginning of the season, and if the leafhoppers show a tendency for directional movement one way or the other between the vines and Rubus during the course of the season.

Rose (1972b) found that populations of Cicadulina mbila (Naudé), C. parazeae Ghauri and C. storeyi China consist of short- and long-distance fliers. Long- and short-bodied forms of Cicadulina were distinguished with the highest proportion of short-bodied forms amongst the long-distance fliers and the highest proportion of long-bodied forms amongst short-distance and non-fliers. The long-bodied poor fliers predominated in breeding populations and higher proportions of short-bodied strong fliers occurred in the migrating populations. Rose measured the wing lengths of the leafhoppers as well as the distance that the wing tips extend beyond the abdomen. He classified females as short-bodied if the wing tip extended beyond the body by more than an eighth of the length of the wing and in males by more than a quarter of the length. The same measurements were made for A. lineatifrons to determine whether there is any evidence for the existence of a similar flight polymorphism in populations of this species. If this were the case, the production of short-bodied forms on the natural host plant could provide prior warning of migration to the vineyards.

A host preference study was done to determine if the move of A. lineatifrons onto the grapevines was the result of a preference for grapevines to its wild plant hosts.

TECHNIQUES

Various methods of surveying and sampling leafhopper populations in the field have been reported. Hosny and El-Dessouki (1968) used sweep nets to sample Empoasca spp. on cotton. Twenty-five net sweeps consituted one replicate. Lynn, Jensen and Flaherty (1965) used nymphal counts to monitor leafhopper populations in vineyards. Ten leaves in a plot of ninety vines in a row were examined and the mean number of nymphs per leaf calculated. This constituted one replicate. This method was also used by Jayaraj (1966), with each replicate consisting of nine castor leaves. Hosny and El-Dessouki (1968) used nymphal counts as well to sample leafhoppers on cotton.

Yellow sticky traps have been used by a number of researchers to monitor leafhopper populations (Kido et al, 1984; Purcell & Suslow, 1984; Williams, 1984). Meyerdirk and Hessein (1985) recommended yellow traps with a wavelength of 570 nanometers as the most efficient for catching the beet leafhopper, Circulifer tenellus (Baker). The traps were made of metal or plastic sheets coated with a sticky substance and attached vertically to poles or suspended from branches or trellising wires. The traps are usually changed every two weeks. Rose (1972a) and Waloff (1977) used fixed suction traps situated from 1,2 to 19,8 meters above ground to monitor dispersal flights of various leafhoppers. Heinrichs et al (1982) used a D-Vac suction sampler to sample Nilaparvata lugens (Stal) on rice.

Nymphal counts have an advantage over the other sampling methods in that it does not destroy or remove part of the insect population, whereas all the others are destructive sampling methods where specimens are removed. In a preliminary trial nymphal counts and a D-Vac suction sampler were tested for sampling A. lineatifrons. With a sample size of thirty leaves per plot of six vines, well over the number recommended by the previously mentioned authors, the nymphal counts obtained for successive samples in the same plot were highly variable - for example, four successive samples from the same plot gave counts of 0, 2, 6 and 17 nymphs per 30 leaves respectively. This was not considered a reliable method to use. The brambles are very thorny and this presents difficulties for using sweep nets. The D-Vac suction sampler was selected for the field studies on the population dynamics of A. lineatifrons. The sampling procedures and experimental lay-outs for these studies are described in Chapter 2, sections 2.3, 2.4, 2.5, 2.6 and 2.7.

RESULTS

Seasonal occurrence

Fig. 5 shows the weekly counts of A. lineatifrons on grapevines over three seasons. Each point on the graph is the mean of five replicates. Months during which no leafhoppers occurred on the vines, viz. July, August and September, were omitted from the graphs. Sampling commenced after budding of the vines and the first adults were collected from late October to early November. The population peaks occurred between the middle of February and the end of March. After completion of leaf fall no more leafhoppers were

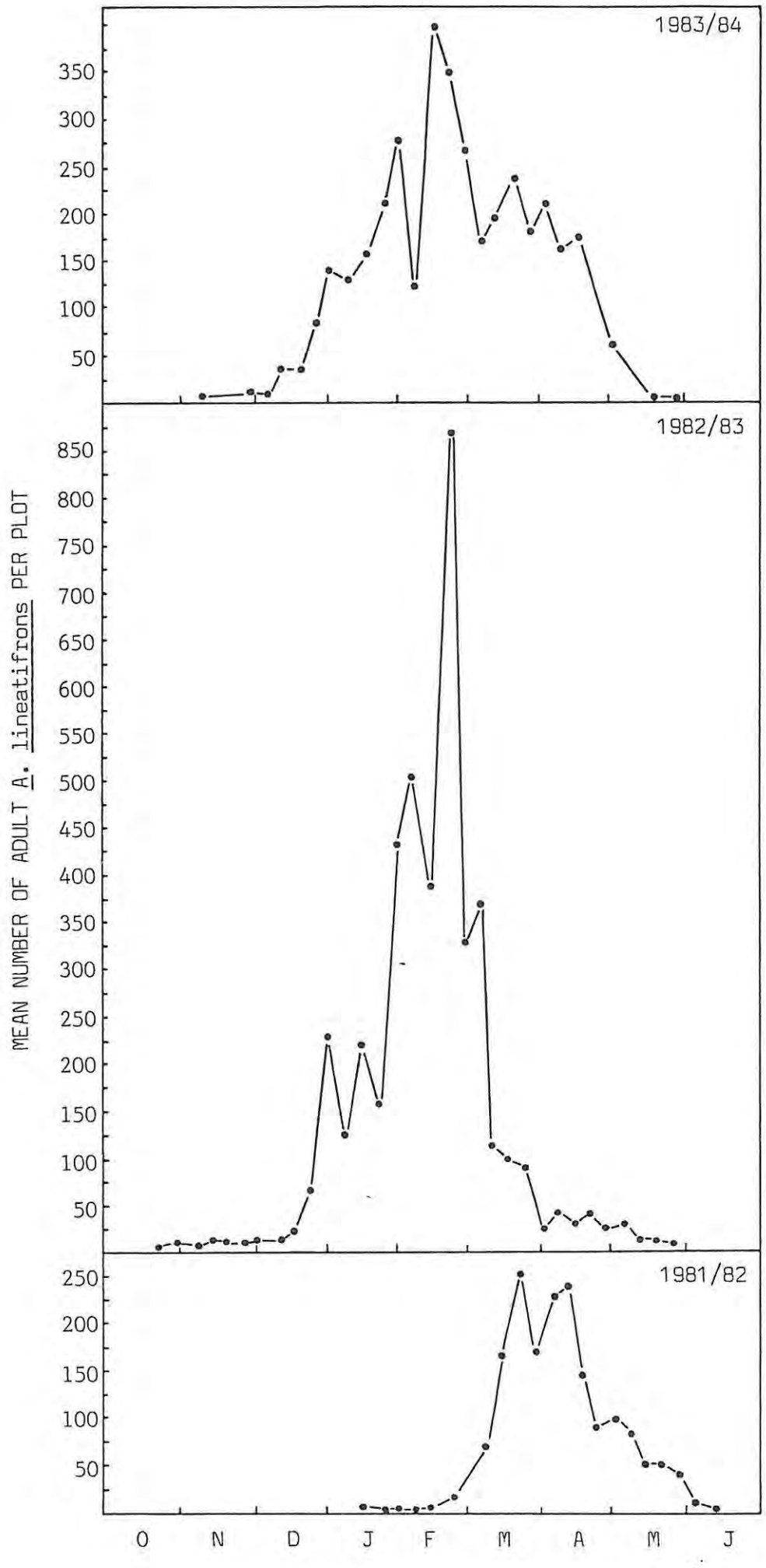


Figure 5. Seasonal occurrence of Acia lineatifrons on grapevines at Simondium over three seasons.

found on the vines or on the weeds in the vineyard. Symptoms of leafhopper damage appeared shortly before the population peaks were reached on the vines.

Fig. 6 shows the counts of adult A. lineatifrons on R. chrysocarpus sampled weekly during the growing season and biweekly during winter. During the season adults and nymphs occurred, but only adults were found during winter. From this it is concluded that A. lineatifrons overwinters in the adult stage.

The daily maximum temperatures, daily minimum temperatures and daily rainfall figures for the period January 1982 until June 1984 were obtained from the meteorological station at Elsenburg near Stellenbosch. Data from the Mountain Vineyards station, the closest weather station to the experimental site at Simondium were used. A series of multiple linear regressions were carried out to see whether any correlation between the temperature and rainfall data and the population curves could be found which could explain the population fluctuations observed. Since the number of adults present at any given sampling date would depend largely on the survival and development rate of the nymphs, the meteorological data were averaged over 1, 2, 3 etc. to 20 days prior to sampling and multiple linear regressions of leafhopper counts on each of maximum temperature, minimum temperature and daily rainfall done for each case. The only significant correlations were between leafhopper counts and minimum temperature averaged over 2, 3, 5, 9 and 10 days prior to sampling.

Sex ratio

Fig. 7 shows the sex ratio of A. lineatifrons on Rubus and grapevines. The sex ratio of the overwintering population on R. chrysocarpus was heavily female biased. With the advent of spring there was a marked swing towards a predominantly male biased sex ratio. The sex ratio on the grapevines was female biased when the first leafhoppers began to move onto the vines (29/10/86), although the sex ratio on the Rubus had already changed to male biased at that time. Soon after, however, the ratio on the vines also became male biased. Although the sex ratio attained a 1:1 proportion on several occasions, the overall trend during the season was male biased on both host plants.

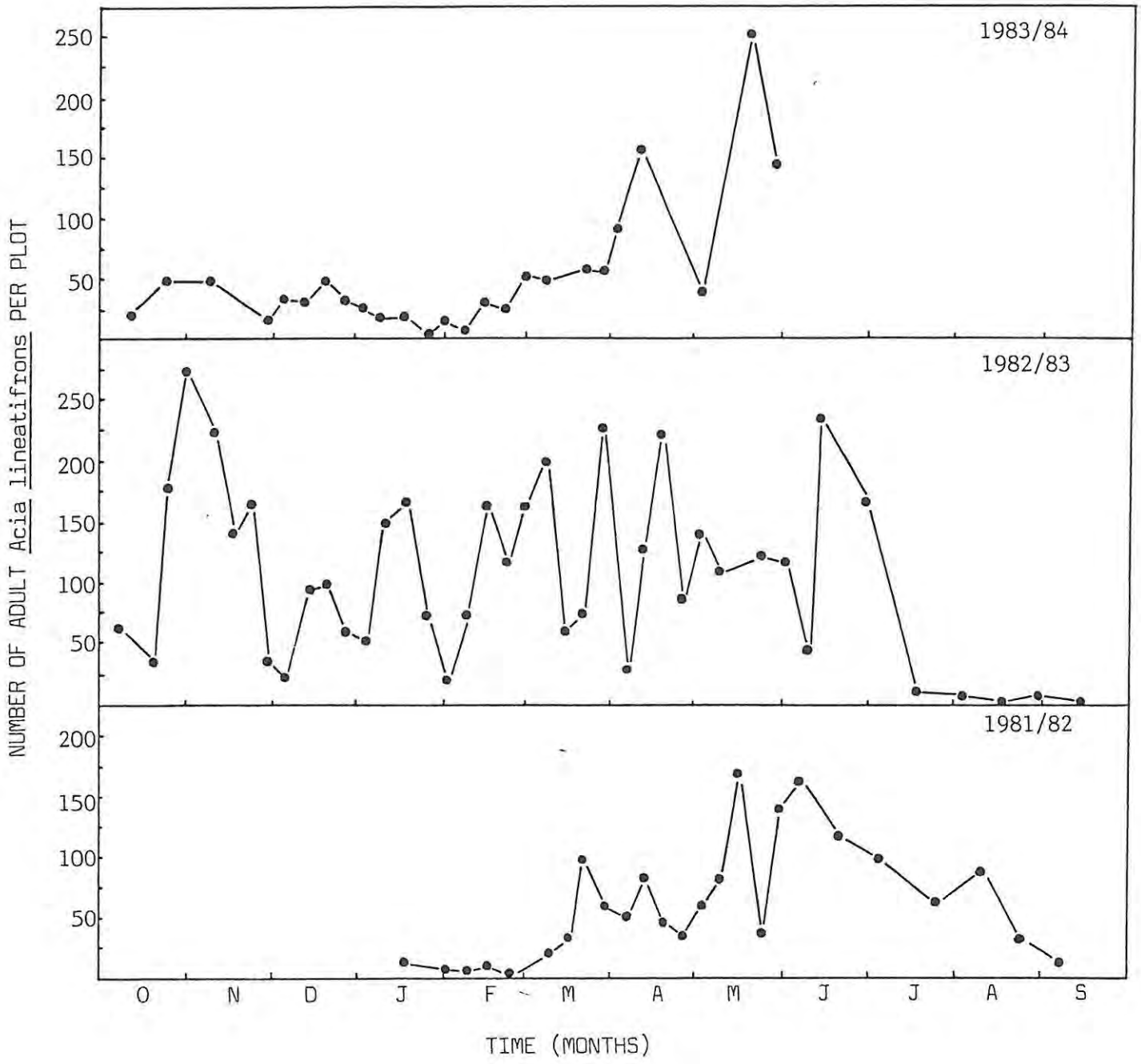
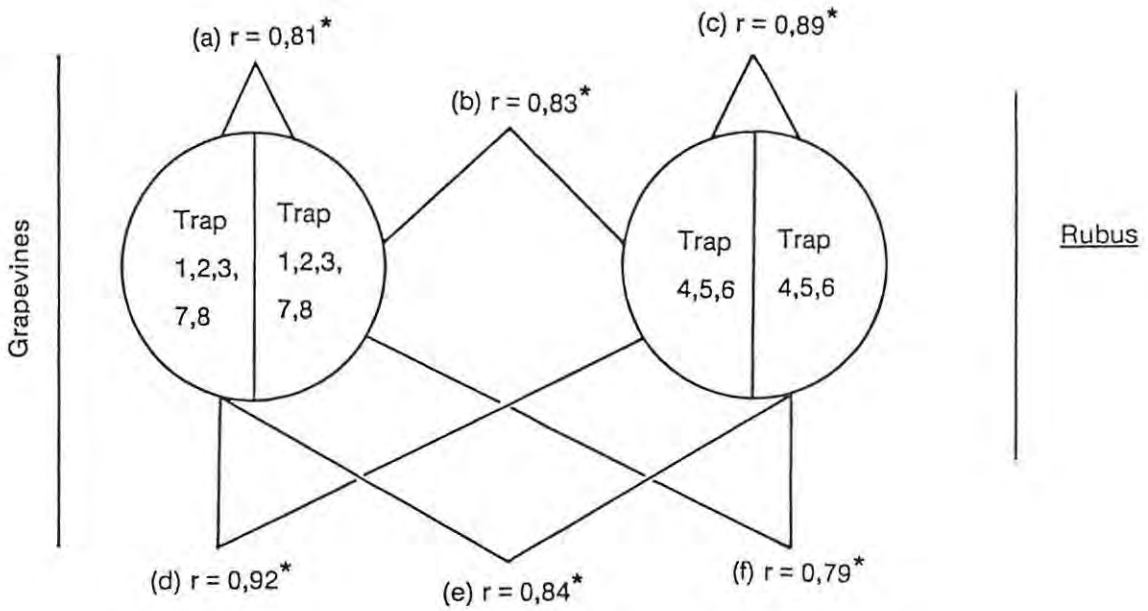
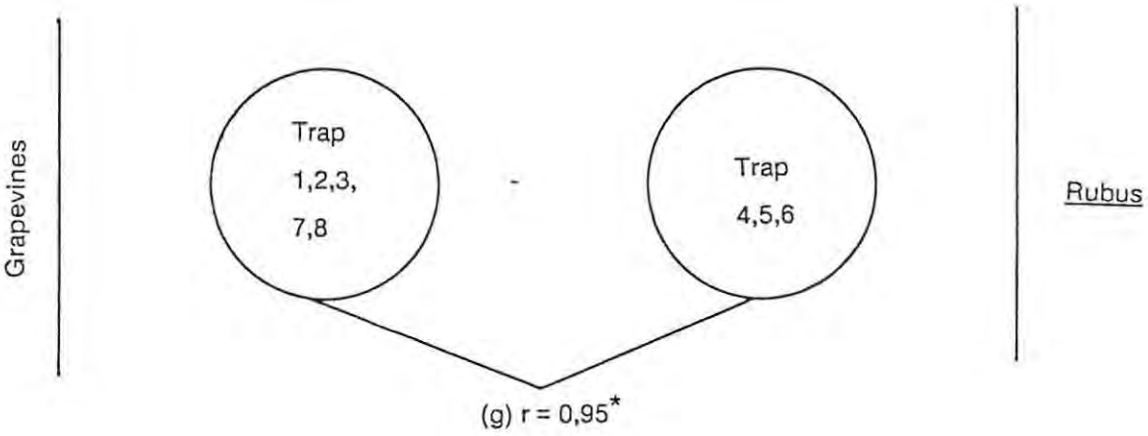


Figure 6. Seasonal occurrence of Acia lineatifrons on Rubus chrysocarpus at Simondium over three seasons.



Critical value for r = 0,576 at alpha = 0,05 for 10 degrees of freedom

n = 12



Critical value for r = 0,666 at alpha = 0,05 for seven degrees of freedom

n = 9

* Correlation significant at alpha = 0,05

Figure 8. Correlations of sticky trap catches of Acia lineatifrons moving between Rubus and grapevines at Simondium. See Fig. 3 for layout of traps in the field.

Migration

The results obtained with the sticky traps from 22/10/86 when the leafhoppers began to enter the vineyard until 3/3/87 are presented in Table 5. In an attempt to determine the direction of leafhopper movement, the catches of the two halves of each cylindrical trap (i.e. facing towards the vines and facing towards the Rubus - see Fig.3) were counted separately. Fig. 8 shows the correlation coefficients for the catches in the different directions on the different traps compared to each other. The mean catches for all the traps closest to the vines (no. 1, 2, 3, 7 & 8), the mean catches for the traps closest to the Rubus (no. 4, 5 & 6) as well as the mean catches for all eight traps together were correlated (Table 6) with the total number of adult leafhoppers collected over six vines plots during the field experiment on the effect of organic fungicides on the population build-up of A. lineatifrons on grapevines (see Chapter 5). Samples from 10/12/86 when the population of the leafhoppers in the vineyard was beginning to increase more rapidly were used.

In view of the significance of all the correlations, it appears that the catches of the sticky traps do not reflect a directional movement of leafhoppers. This is indicated by the significant correlations between the catches on the two sides of the same traps for those near the vines and those near the Rubus. The significant correlations between the sticky trap catches and population build-up in the vineyard indicate that the traps rather reflect the build-up of the leafhopper population on the vines, which raises the possibility that sticky traps could be used to monitor leafhopper build-up in the vineyards. This clearly warrants investigation.

The catches during the beginning of the season when the leafhoppers begin to colonize the vines do not indicate any marked unidirectional movement from the Rubus to the grapevines.

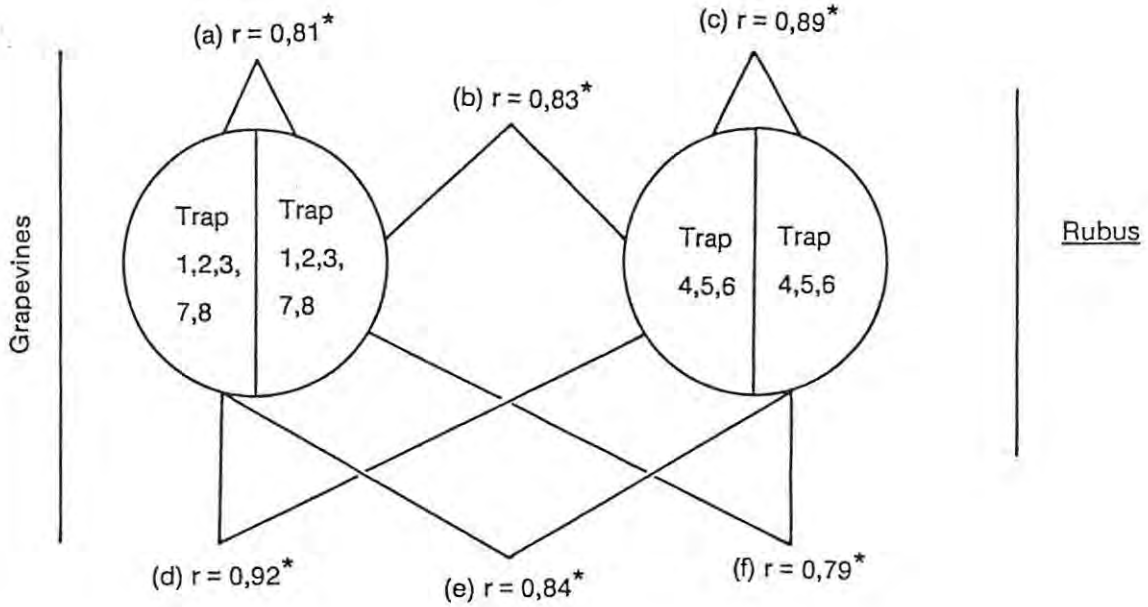
Flight dimorphism

The ratio of wing lengths to the distance that the wings extend beyond the body (Rose, 1972b) were calculated for A. lineatifrons. Only three individuals could be classified as long-bodied according to Rose's ratio. Scatter plots of the data were constructed (Fig.9a-f) to see whether the lack of distinctive morphs was due to the fact that the critical ratios of wing length in A. lineatifrons were different from those in Cicadulina spp. No distinctive

TABLE 5. Numbers of A. lineatifrons adults caught on the eight yellow sticky traps at Simondium.

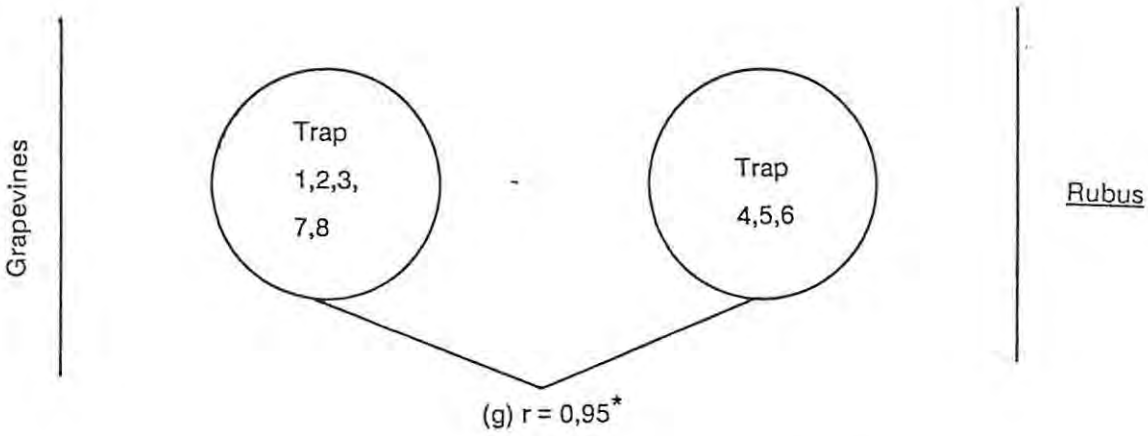
Sampling date	No. leafhoppers per trap on side facing vines								
	1	2	3	4	5	6	7	8	Total
22-10-86	0	0	0	x	2	0	0	0	2
29-10-86	0	0	0	1	x	x	0	0	1
13-11-86	1	0	2	1	0	0	0	0	4
26-11-86	8	5	0	0	4	0	0	0	17
10-12-86	1	0	3	0	0	0	2	0	6
30-12-86	0	15	6	4	2	1	4	1	33
14-01-87	30	10	9	12	3	1	5	4	74
28-01-87	9	x	x	x	5	x	x	4	18
4-02-87	10	12	8	7	2	2	3	5	49
11-02-87	35	27	16	8	6	1	2	10	105
18-02-87	39	25	16	12	8	3	5	19	127
25-02-87	38	15	8	6	2	0	2	12	83
3-03-87	54	23	18	14	10	2	3	10	134
	No. leafhoppers per trap on side facing Rubus								
	1	2	3	4	5	6	7	8	Total
22-10-86	0	0	0	0	3	0	0	1	4
29-10-86	2	1	0	0	x	x	1	0	4
13-11-86	0	0	1	0	1	1	0	0	3
26-11-86	2	1	2	0	0	0	0	2	7
10-12-86	0	1	0	1	1	0	1	0	4
30-12-86	0	0	2	1	1	0	0	1	5
14-01-87	10	21	10	11	6	1	7	8	74
28-01-87	3	x	x	x	5	x	4	x	12
4-02-87	14	6	2	3	4	1	0	1	31
11-02-87	21	12	6	3	4	3	1	0	50
18-02-87	31	14	11	14	13	4	6	6	99
25-02-87	16	13	4	5	10	3	3	6	60
3-03-87	26	22	2	14	18	4	9	16	111

x - Traps lost due to rain



Critical value for r = 0,576 at alpha = 0,05 for 10 degrees of freedom

n = 12



Critical value for r = 0,666 at alpha = 0,05 for seven degrees of freedom

n = 9

* Correlation significant at alpha = 0,05

Figure 8. Correlations of sticky trap catches of Acia lineatifrons moving between Rubus and grapevines at Simondium. See Fig. 3 for layout of traps in the field.

TABLE 6. Correlation of the numbers of A. lineatifrons caught with the sticky traps with the numbers of leafhoppers sampled in the vineyard in the experiment on the effect of an organic fungicide on the population build-up of the leafhoppers in the field (see Chapter 5).

Sampling date	Mean no. leafhoppers per trap			Tot. no. leafhoppers in 6 plots
	Traps near Rubus 4,5,6	Traps near vines 1,2,3,7,8	All traps 1-8	
10-12-86	0,67	1,60	1,25	67
30-12-86	3,00	5,80	4,75	230
14-01-87	11,33	22,80	18,50	157
28-01-87	3,33	4,00	10,00	187
4-02-87	6,33	12,20	10,00	458
11-02-87	8,33	26,00	19,38	311
18-02-87	18,00	34,40	28,25	421
25-02-87	8,67	23,40	17,88	342
3-03-87	20,67	36,60	30,63	454
	r=0,67*	r=0,67*	r=0,66*	

Critical value for r = 0,666 at alpha = 0,05 for one degree of freedom.

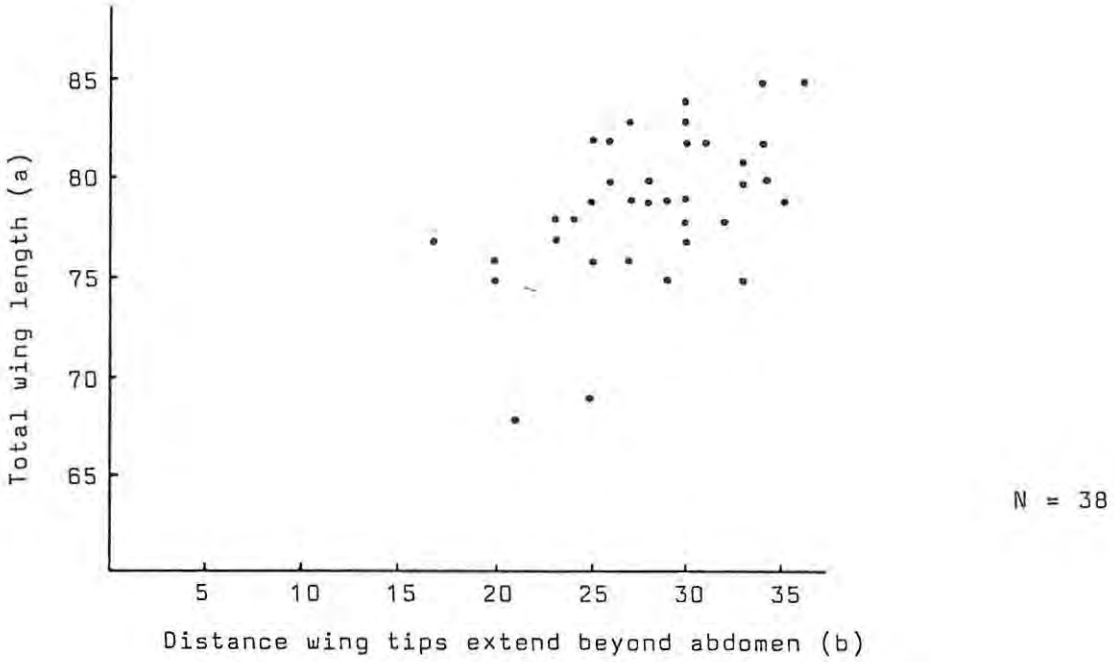


Figure 9 (a). Total wing length of A. lineatifrons males on R. chrysocarpus during September and October 1986 plotted against the distance that the wingtips extend beyond the abdomen, measured in eyepiece micrometer units (30 units = 1 mm).

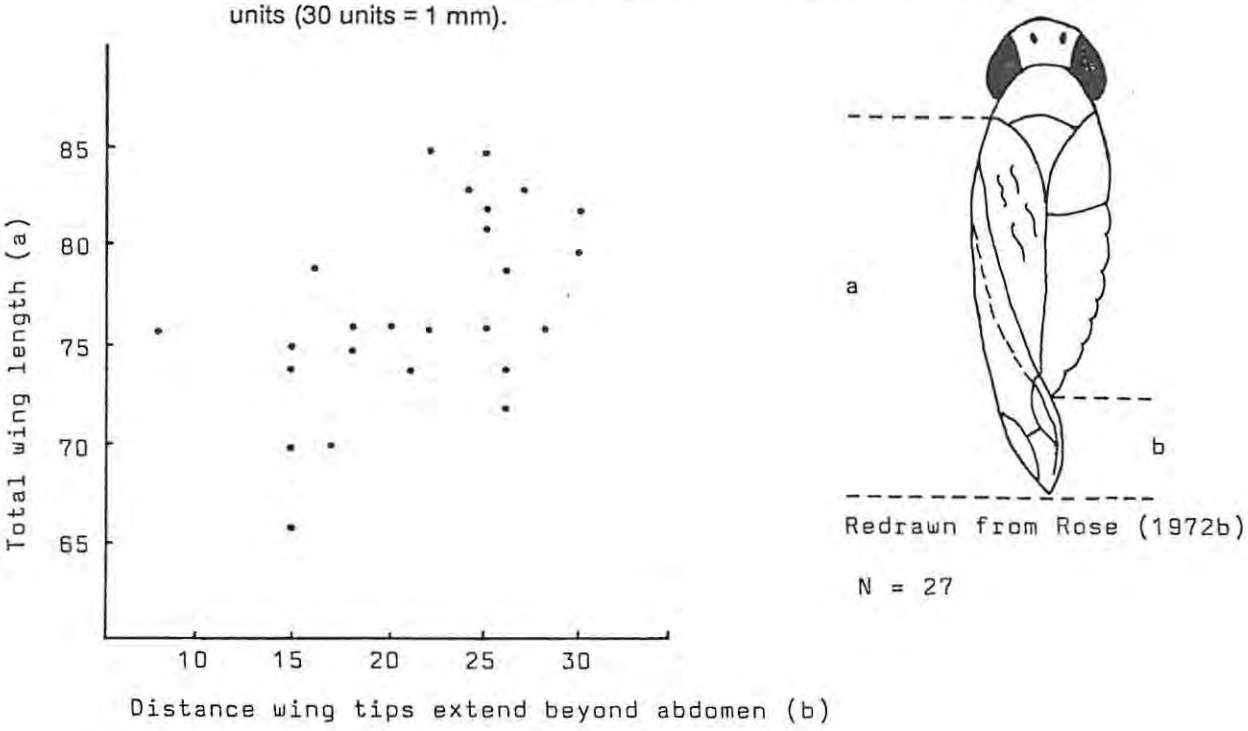


Figure 9 (b). Total wing length of A. lineatifrons males on R. chrysocarpus during November 1986 until January 1987 plotted against the distance that the wingtips extend beyond the abdomen, measured in eyepiece micrometer units (30 units = 1 mm).

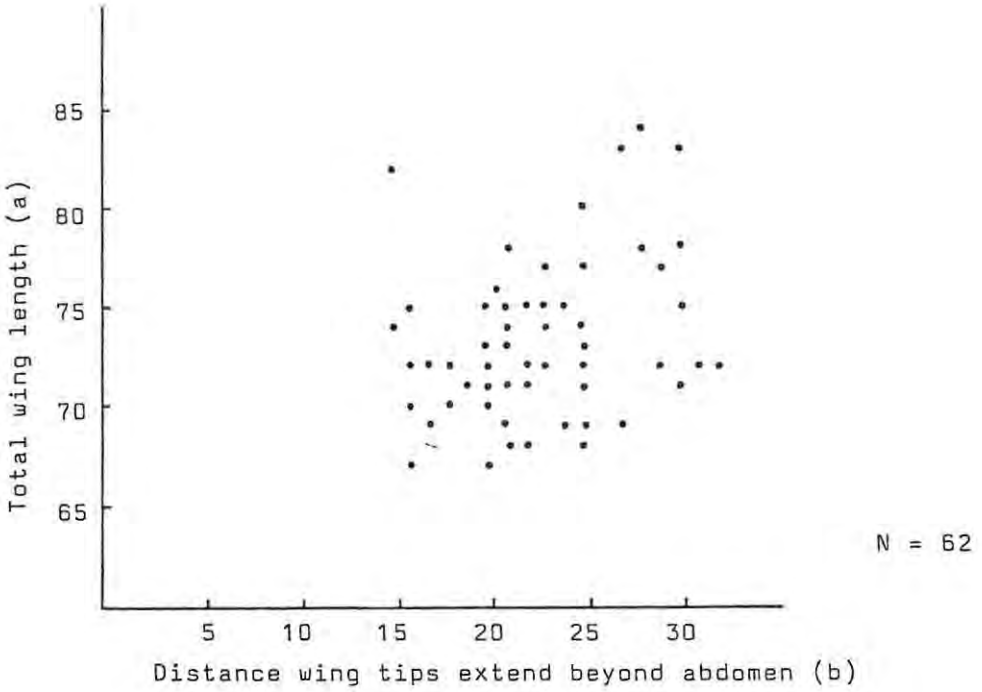


Figure 9 (c). Total wing length of A. lineatifrons males on grapevines during November 1986 until February 1987 plotted against the distance that the wingtips extend beyond the abdomen, measured in eyepiece micrometer units (30 units = 1 mm).

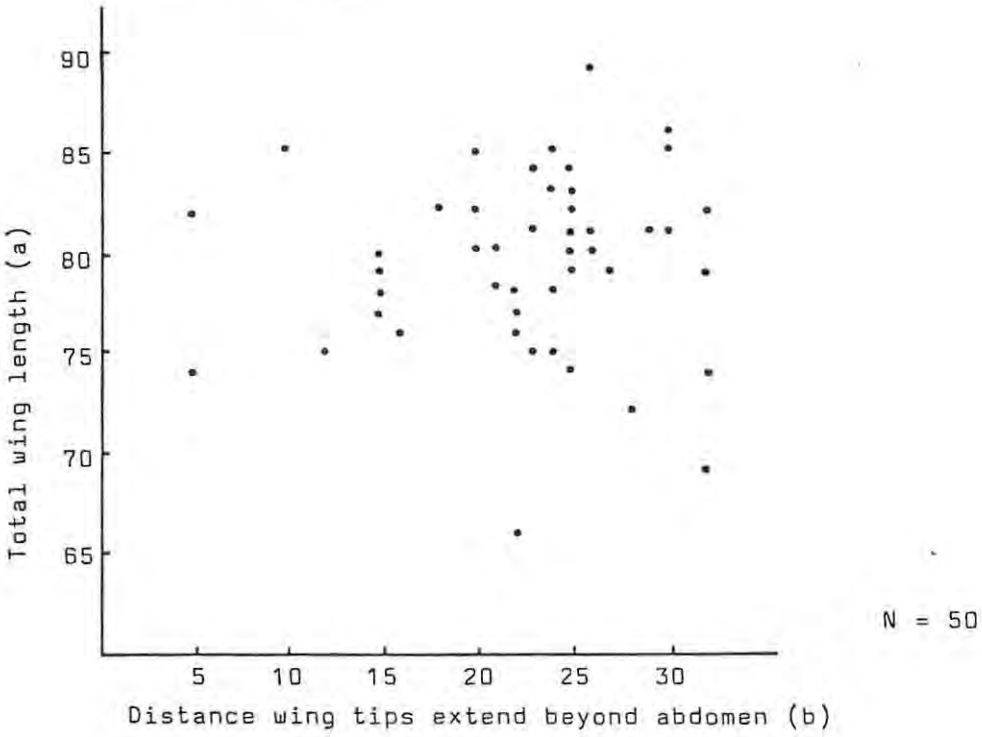


Figure 9 (d). Total wing length of A. lineatifrons females on R. chrysocarpus during September and October 1986 plotted against the distance that the wingtips extend beyond the abdomen, measured in eyepiece micrometer units (30 units = 1 mm).

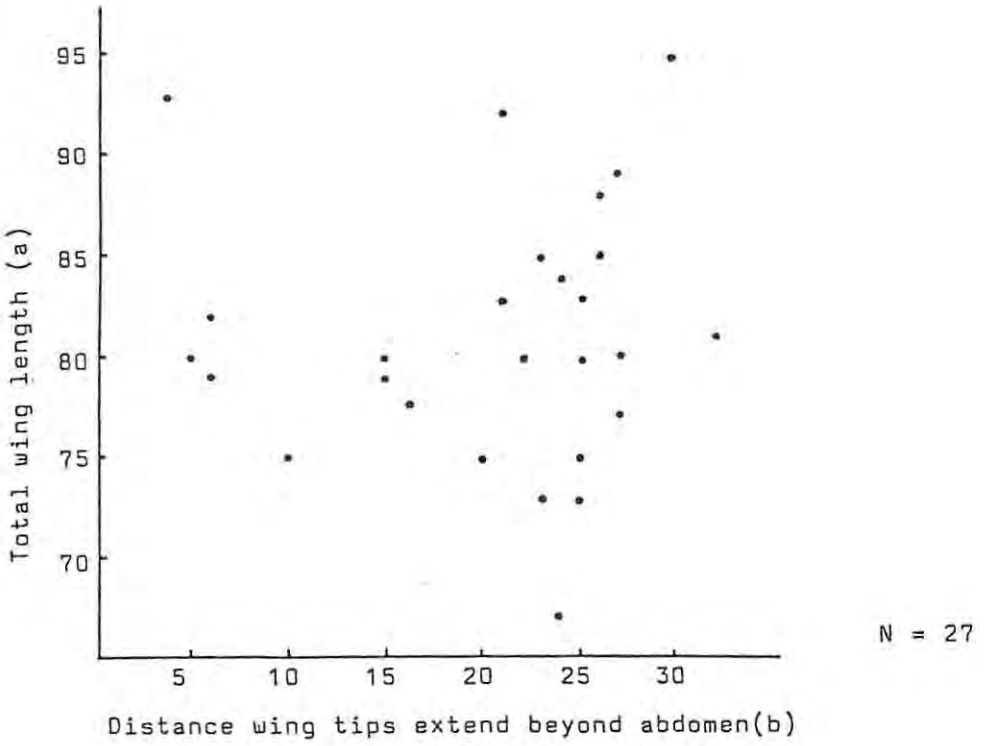


Figure 9 (e). Total wing length of A. lineatifrons females on R. chrysocarpus during November 1986 until January 1987 plotted against the distance that the wingtips extend beyond the abdomen, measured in eyepiece micrometer units (30 units = 1 mm).

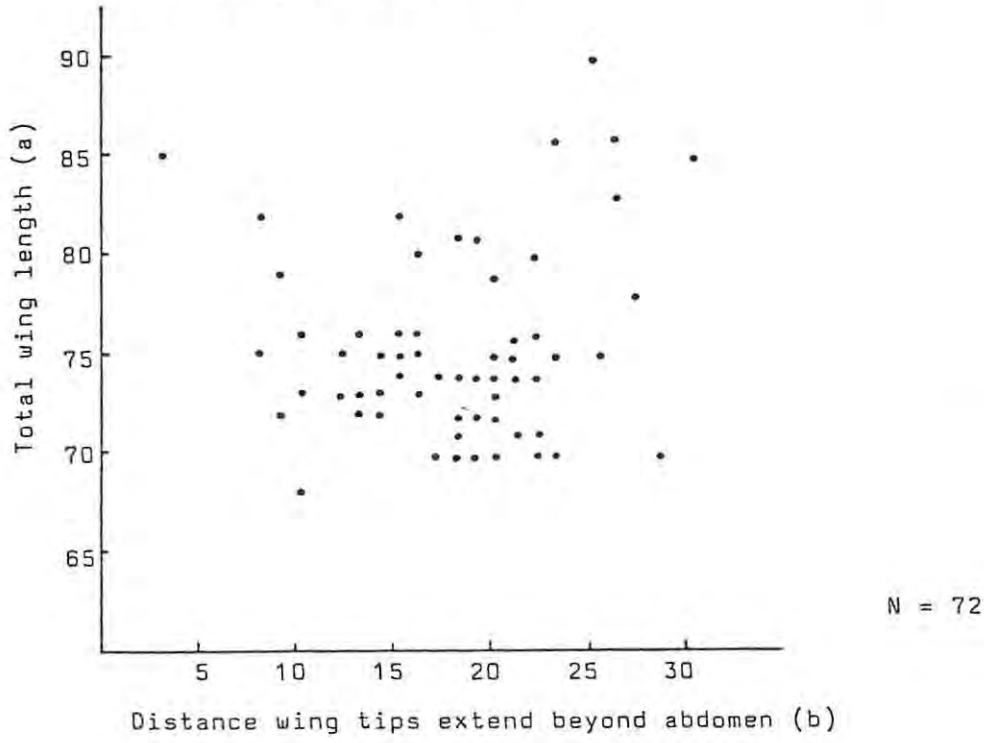


Figure 9 (f). Total wing length of A. lineatifrons females on grapevines during November 1986 until February 1987 plotted against the distance that the wingtips extend beyond the abdomen, measured in eyepiece micrometer units (30 units = 1 mm).

grouping or clusters are evident, which indicates that the population is unlikely to be divisible into two distinct morphological groups based on wing and body length.

Host preference

Host preference tests were conducted with A. lineatifrons nymphs and adults collected on grapevines and on Rubus. The results of these tests appear in Table 7(a) and (b) and in Table 8 (a) and (b). Chi-square independence tests done for each replicate (see Appendix 3 for contingency tables) indicated independence, therefore Chi-square values were calculated for each replicate and for the combined results of each experiment. The first experiment was carried out with nymphs from grapevines. The first replicate showed no significant preference for either host plant. In the second replicate, a significant preference for Rubus was shown 90 minutes after the nymphs were released, but the observations the following morning indicated no significant preference. The combined results indicate a significant preference for Rubus after 90 minutes but not overnight.

The experiment with nymphs from Rubus consisted of five replicates. The second replicate indicated a significant preference for grapevines after 90 minutes and overnight. Although the other replicates did not show significant preferences, the highly significant preferences in the second replicate are responsible for the significant preference for grapevines indicated by the combined result.

According to the combined results, nymphs from grapevines prefer Rubus and nymphs from Rubus prefer grapevines, even though it was the first time that these nymphs encountered the host other than the one they hatched on. Biologically there seems to be no reasonable explanation for this. Furthermore, in the case of nymphs from grapevines it was observed that 26 out of the 36 nymphs remained on their first choice of host overnight, but 10 nymphs changed to the other host overnight. In the case of nymphs from Rubus 47 out of 70 remained on the first choice and 23 changed host overnight. In view of these considerations, it is felt that although a significant result was obtained in both cases where only totals are considered, the result should be treated with caution.

The available data allow no definite conclusions to be drawn. Repeating the experiments

TABLE 7 (a). Host preference of A. lineatifrons nymphs taken from grapevines. The number of nymphs on each kind of leaf was recorded 90 minutes after the release of the nymphs and on the following morning.

Nymphs from Grapevines						
Repl	Time after release	Rubus	Grapevines	Container surface	X^2	N
1	90 min.	11	7	2	0,89	20
	overnight	9	8	3	0.06	
2	90 min.	11	3	2	4,57*	16
	overnight	9	7	0	0,25	
Comb	90 min.	22	10	4	4,50*	36
	overnight	18	15	3	0,27	

Critical value for X^2 = 3,84 at alpha = 0,05 for one degree of freedom

Note: the numbers of nymphs recorded on the container surface were not taken into account when Chi-square values were calculated.

TABLE 7 (b). Host preference of A. lineatifrons nymphs from Rubus recorded 90 minutes after release and on the following morning.

Nymphs from Rubus						
Repl	Time after release	Rubus	Grapevines	Container surface	X^2	N
1	90 min.	8	9	1	0.06	18
	overnight	10	7	1	0,53	
2	90 min.	0	13	1	13,00*	14
	overnight	1	13	0	10,29*	
3	90 min.	5	7	1	0,33	13
	overnight	7	6	0	0,08	
4	90 min.	3	10	0	3,77	13
	overnight	3	10	0	3,77	
5	90 min.	9	3	0	3,00	12
	overnight	5	7	0	0,33	
Comb	90 min.	25	42	3	4,31*	70
	overnight	26	43	1	4,19*	

Critical value for X^2 = 3,84 at alpha = 0,05 for one degree of freedom

Note: the numbers of nymphs recorded on the container surface were not taken into account when Chi-square values were calculated.

TABLE 8 (a). Host preference of A. lineatifrons adults from grapevines. The number of nymphs on each kind of leaf was recorded 90 minutes after release of the nymphs and on the following morning.

Adults from Grapevines						
Repl	Time after release	Rubus	Grapevines	Container surface	X^2	N
1	90 min.	4	6	4	0,40	14
	overnight	8	4	2	1,33	
2	90 nim.	3	9	0	3,00	12
	overnight	6	5	1	0,09	
3	90 min	5	11	5	2,25	21
	overnight	12	9	0	0,43	
4	90 min.	10	11	4	0,05	25
	overnight	13	12	0	0,04	
Comb	90 min.	22	37	13	3,81	72
	overnight	39	30	3	1,17	

Critical value for X^2 = 3,84 at alpha = 0,05 for one degree of freedom

Note: the numbers of adults recorded on the container surface were not taken into account when Chi-square values were calculated.

TABLE 8 (b). Host preference of A. lineatifrons adults from Rubus. The number of nymphs on each kind of leaf was recorded 90 minutes after release of the nymphs and on the following morning.

Adults from Rubus						
Repl	Time after release	Rubus	Grapevines	Container surface	X^2	N
1	90 min.	6	13	2	2,58	21
	overnight	11	10	0	0,05	
2	90 min.	9	11	4	0,20	24
	overnight	12	10	2	0,18	
3	90 min	7	11	2	0,89	20
	overnight	6	12	2	2,00	
Comb	90 min.	22	35	8	2,97	65
	overnight	29	32	4	0,15	

Critical value for X^2 = 3,84 at alpha = 0,05 for one degree of freedom

Note: the numbers of adults recorded on the container surface were not taken into account when Chi-square values were calculated.

with even greater numbers of nymphs may reduce the variation in the results sufficiently to make the results more conclusive. Care must be taken to exclude any factors that may temporarily affect the relative attractiveness of the leaves to the nymphs in the experiments. The fact that such precautions may be necessary implies no strong preference on the part of the leafhoppers for either host.

The results of the experiment with adults from grapevines indicate no significant preference for either host in any of the four replicates, although the combined result for 90 minutes after release is very close to significance - see Table 8 (a). The experiment with adults from Rubus revealed no significant preference for either host in any of the three replicates or in the overall result. The results of the experiments with adults indicate that the adults of A. lineatifrons have no significant preference for grapevines to Rubus or *vice versa*. From these results it would appear that the colonization of the grapevines at the beginning of the growing season by adults of A. lineatifrons that had overwintered on Rubus is not prompted by a preference for grapevines to Rubus.

If any conclusion can be drawn from the above experiments with nymphs and adults it is that there is unlikely to be any strong preference on the part of A. lineatifrons for either vine or Rubus.

DISCUSSION

It was established that A. lineatifrons overwinters in the adult stage on Rubus chrysocarpus and R. pinnatus. A. lineatifrons can be expected to enter the vineyard during late October to early November, after the new vine leaves have unfurled. According to the field population study peak populations can be expected between the middle of February and the end of March in normal years. The exact number of generations produced per season could not be determined in the field because they overlap, but extrapolation of the data obtained in the life cycle studies indicates that four to five generations could occur in a season where the weather conditions are favourable for rapid leafhopper development (see Chapter 3).

The variation in the population curves from week to week can be ascribed to the fact that the leafhoppers are not uniformly distributed through the vineyard, to fluctuations in the environmental conditions and to sampling error. On colder, windy days the leafhoppers are less active and more inclined to shelter deeper inside the leaf canopy where they are less easily collected.

The comparison of the meteorological data with the population curves showed that only daily minimum temperature was significantly correlated with the weekly leafhopper counts. According to this the minimum temperatures measured were low enough at times to affect the rate of development of the leafhoppers, whereas the maximum temperatures were not consistently high enough to have any significant effect.

During the second and third seasons the peaks occurred earlier than in the first season. On the 18th December 1981 acephate (Orthene) was applied to the vineyard for snout-beetle (Curculionidae) control. According to Marais and De Klerk (1985) acephate is also very effective against A. lineatifrons. It is proposed that this insecticide application was mainly responsible for the initial delay in the population build-up of the leafhoppers during the 1981/82 season. After that time no insecticides were applied to the experimental vines for the duration of the study.

The population peak during the second season was more than twice as high as in the other two seasons, but then the population crashed and for the rest of the season remained at a lower level than the populations in the first and second seasons. The analysis of the meteorological data indicated that the minimum temperatures measured affected leafhopper survival. It was often observed that adults' wings got stuck to wet leaves, resulting in death. Heavy rainfall, particularly when accompanied by low minimum temperatures, can be expected to increase mortality of the overwintering adults, which could delay the population build-up in the following spring. During the winter of 1982 only 619,2 mm of rain fell between May and September compared to 1162,7 mm for the same period in 1983. It is possible that the lower rainfall during 1982 may have resulted in a higher rate of adult survival during winter which, in turn, could have contributed to the higher population peak in the 1982/83 season compared to the 1983/84 season. The possibility that very high leafhopper populations follow winters of low rainfall should be investigated.

From the population survey it is evident that A. lineatifrons does not abandon its overwintering hosts completely in favour of grapevines at the onset of the new growing season in spring. The sticky trap data indicate no directional migration onto the vines. Leafhoppers appear continually to move between at least the nearby Rubus and the vines during the season. Because the leafhopper's indigenous hosts, R. chrysocarpus and R. pinnatus, are evergreen perennials with regular flushes of new growth all year round the leafhopper is not forced to seek alternative hosts. This also ties in with the host preference tests where the adults and probably the nymphs show no clear preference for either host. This is in contrast to the case of Cicadulina spp. where migration occurs when the natural grass hosts begin drying at the end of the rainy season (Rose, 1972a).

The sex ratio of A. lineatifrons on Rubus and grapevines tended to be male biased during the growing season, although it occasionally reached equality. Walker (1984) notes that the sex ratio of a population can change with age due to differential mortality of the sexes caused by sex-biased diapause or to one sex taking more risks than the other. The shift towards a heavily female biased ratio of A. lineatifrons during winter is most likely due to differential mortality of the sexes, with the females better surviving winter conditions. If this is so, it can be expected that mating takes place before winter and that the females store the sperm until the beginning of the next growing season. Futher investigation is needed to determine if this is the case.

When planning pest control strategies, it is very helpful to know the cause or causes for a pest outbreak or any predisposing factors. It may be possible to prevent or reduce outbreaks by eliminating the causes. The knowledge of predisposing factors could also help in predicting outbreaks. Chapter 5 deals with experiments to investigate a possible contributing factor to leafhopper outbreaks on grapevines.

CHAPTER 5. THE EFFECT OF AN ORGANIC FUNGICIDE ON THE FECUNDITY AND POPULATION BUILD-UP OF A. LINEATIFRONS

INTRODUCTION

The nutrient quality of the host plant plays a major role in determining the performance and population dynamics of its insect herbivores. According to House (1969) the digestiblity and nutrient composition of foodstuffs and the nutrient requirements of insects vary considerably. The qualitative nutrient requirements among insects are quite similar, therefore the qualities of a foodstuff as measured by its ability to promote or support growth, etc. depend on how well the nutrient composition of the foodstuff made available by digestion fits the nutrient requirements of the insect.

The influence of nutrient quality, especially the nitrogen compounds, on the reproduction and fecundity of Homoptera is well documented. Van Emden (1966) showed that an increase in the soluble nitrogen levels in Brussels sprout leaves was correlated with an increase in the fecundity and reproductive rate of Myzuz persicae (Sulz.). According to Banks and Macaulay (1970) the reproductive rate and fecundity of Aphis fabae (Scop.) are affected by nutrition during both the larval and adult life. Prestidge (1982) found that egg production and oviposition rate of three feeding types of grassland leafhoppers increased with increases in available nitrogen due to fertilizer application. A maximum was reached at optimum nitrogen concentration and egg production and oviposition rate decreased as the nitrogen levels rose above the optimum. Each species reached its maximum nitrogen utilization efficiency at a different host plant nitrogen level. Metcalfe (1970) found that the application of ammonium sulphate fertilizer increased the nitrogen content of sugar cane leaves which, in turn, resulted in an increase in the egg production of Saccharosydne saccharivora (Westw.) (Delphacidae).

Research on aphids fed on various synthetic diets indicated that certain amino acids have a greater effect on aphid performance (development and fecundity) than others. Some amino acids, either alone or in combination, also act synergistically. It was found that changes in the proportions of these amino acids affected aphid performance even if the total amino acid concentration remained the same (Dadd & Krieger, 1967; Mittler, 1970; Srivastava & Auclair,

1974). On the basis of this evidence it seems logical to suppose that any factor which alters the amino acid balance of the host plant to a significant degree might have an effect, albeit indirect, on insect performance even if the total nitrogen level remains unchanged.

Jayaraj (1967) showed that varieties of castor beans (Ricinus communis) susceptible and tolerant to the leafhopper Empoasca flavescens have a higher nitrogen content (free amino acids and amides) in the foliar tissues than the resistant varieties. Chaboussou (1969) showed that dithiocarbamate fungicides cause an increase in the nitrogen/glucide ratio of vine leaves. Agulhon (1968) found that E. flavescens populations developed faster on plots treated with organic fungicides than on those treated with Bordeaux mixture (copper sulphate + lime) or organo-cupric products partially based on zineb and mancozeb. These findings led Chaboussou (1971) to suggest that the use of organic fungicides was partly responsible for the uncommon outbreak of E. flavescens in France. These fungicides apparently caused an increase in the nitrogen/glucide ratio of the vine leaves which resulted in an increase in the developmental rate and fecundity of the leafhoppers and a decrease in the plants' resistance to the leafhoppers.

The possibility that the use of organic fungicides could contribute to outbreaks of A. lineatifrons on grapevines was investigated. Mikal-M is one of the organic dithiocarbamates recommended against downy mildew (Plasmopara viticola) on wine and raisin grapes. It was selected to test the effect of an organic dithiocarbamate on the fecundity of A. lineatifrons in the laboratory and on the population build-up of the leafhoppers in the field because it was the only such fungicide in stock at the V.O.R.I. at the time. Leaves of treated and untreated grapevines were analysed and the total nitrogen content determined to see whether Mikal-M has an effect on the nitrogen content of the leaves.

TECHNIQUES

The experimental methods are described in Chapter 2 sections 2.2, 2.8 and 2.9.

RESULTS

Fecundity in laboratory

Table 3 contains the results of the experiment on female fecundity at 26°C on potted Chenin blanc grapevines treated with Mikal-M. Only 31 out of 66 females (47%) produced nymphs. Table 3(a) shows the fecundity data of the females on untreated vines and Table 3(b) that for the treated vines. The results presented in Table 3(a) and (b) were obtained at the same time under the same conditions.

The fecundity data of the females that produced nymphs on the treated and control vines were compared and subjected to a Kruskall-Wallis one way analysis of variance (Siegel, 1956). At the five percent confidence level there was no significant difference between the two treatments (Table 9).

Nitrogen content of treated and untreated leaves

Table 10 shows the results of the total nitrogen analysis of the leaves of potted grapevines with and without Mikal-M treatments. Both treatment groups exhibited a decrease in total nitrogen over the experimental period. This decrease was probably caused by the draining of nutrients from the pots with regular watering as well as the effect of the plants having been confined to pots for three years in a green house at the time of the experiment. The decrease in total nitrogen for each replicate in terms of its nitrogen content before treatment are given as well. These ratios were subjected to a two way analysis of variance using Student's t-test for significant differences (Snedecor & Cochran, 1980). At the five percent confidence level there was no significant difference in total nitrogen content between the two treatments.

Field experiment

Fig. 10 represents the data from the experiment on the effect of Mikal-M on leafhopper population build-up in the field. Samples taken from both treatment blocks prior to the treatment indicated no significant difference in the mean number of leafhoppers present. The weekly counts for each of the three plots sampled per treatment appear in Table 11. The data were transformed logarithmically and a two-way analysis of variance using the Student t-test was done. According to the statistical analysis there were significantly more

TABLE 9. Kruskall-Wallis analysis of variance on the data from the experiment on the effect of a dithiocarbamate fungicide (Mikal-M) on the fecundity (no. of nymphs produced) of A. lineatifrons on grapevines in the laboratory at 26°C.

	N	Mean fecundity	Rank sums
Control	20	8,5	29,15
Mikal-M	31	5,1	23,97
Difference			6,18
LSD 5% = 10,91			

TABLE 10. Total nitrogen content (% dry weight) of Mikal-M (Fosetyl AL/Mancozeb) treated and untreated potted Chenin blanc vine leaves before and after one and two treatments.

		CONTROL		MIKAL-M	
Sampling time#	No.	Nitrogen content	Decrease	Nitrogen content	Decrease
A	1	3,4249		4,0732	
	2	3,3242		3,4356	
	3	3,3149		3,5908	
	4	3,2800		3,7145	
	5	3,6407		2,9631	
	Mean	3,3969		3,5554	
B	1	1,8489	0,46 A-B	3,0507	0.25 A-B
	2	2,3583	0,29	2,9904	0,13
	3	1,6047	0,52	3,1375	0,13
	4	2,6473	0,19	2,4492	0,34
	5	2,3201	0,36	2,7074	0,09
	Mean	2,1559	0,36	2,8671	0,19
C	1	1,6311	0,52 A-C	2,3080	0,43 A-C
	2	1,7520	0,47	2,0513	0,40
	3	1,8578	0,44	2,5814	0,28
	4	2,0907	0,36	2,2665	0,39
	5	2,2540	0,38	1,8046	0,39
	Mean	1,9171	0,43	2,2024	0,38
D 10% = 0,157 D 5% = 0,182					

A = Before treatment

B = Two weeks after first treatment

C = Two weeks after second treatment

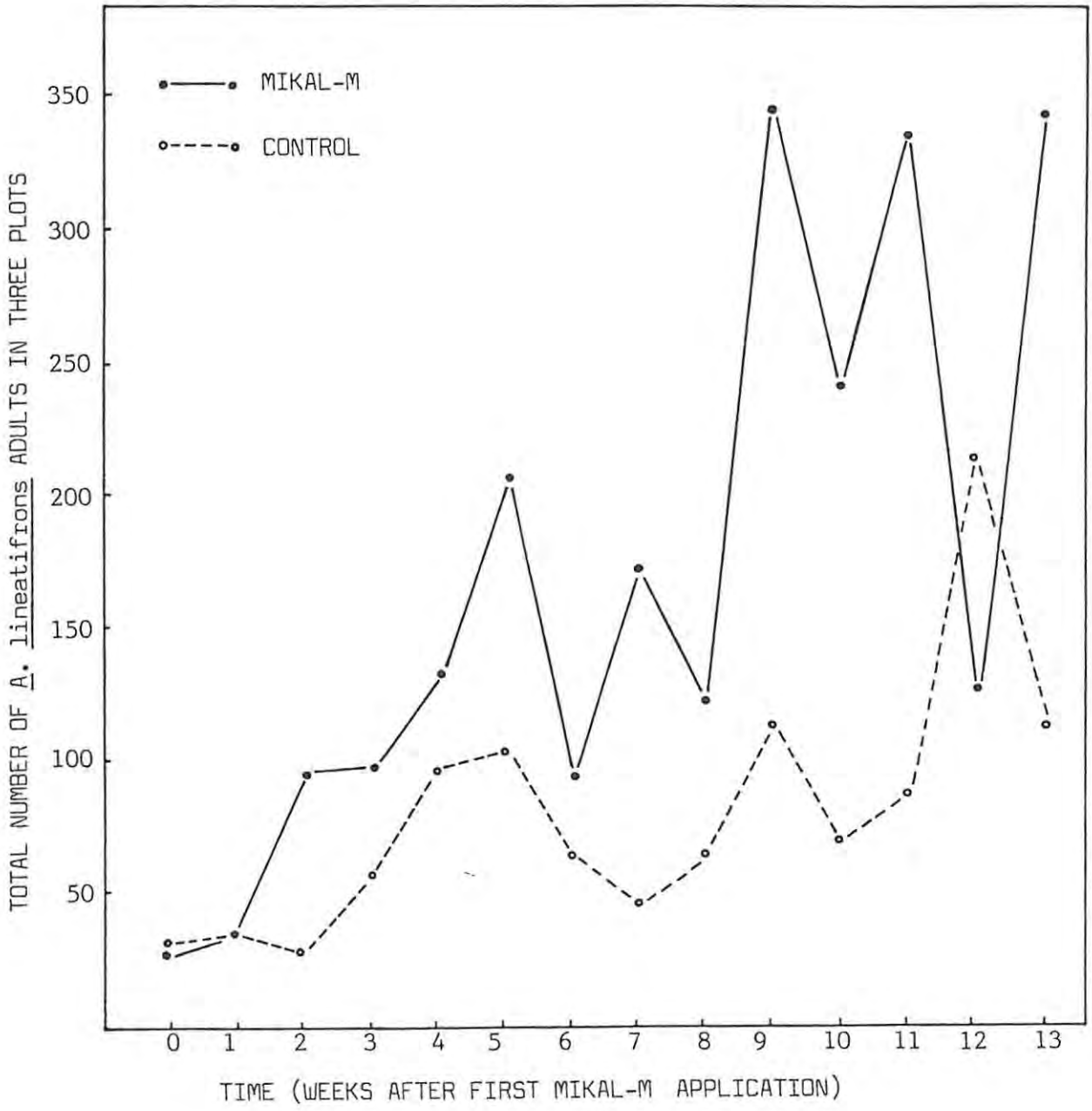


Figure 10. The effect of Mikal-M on the population build-up of Acia lineatifrons on grapevines at Simondium.

TABLE 11. Number of A. lineatifrons adults per plot sampled on untreated grapevines and grapevines treated with Mikal-M at Simondium to determine if a dithiocarbamate fungicide affects the population build-up of the leafhoppers in the field.

	CONTROL				MIKAL-M			
Sampling date	Block			Tot	Block			Tot
	1	2	3		1	2	3	
4-12-86	2	6	25	33	2	7	18	27
10-12-86	24	5	5	34	16	8	9	33
17-12-86	4	9	13	26	49	22	25	96**
22-12-86	5	16	36	57	13	61	24	98**
30-12-86	33	40	24	97	28	44	61	133*
7-01-87	91	11	2	104	145	54	8	207**
14-01-87	44	16	3	63	17	29	48	94*
23-01-87	27	3	15	45	64	85	24	173**
28-01-87	20	16	28	64	24	33	66	123**
4-02-87	73	14	26	113	132	75	138	345**
11-02-87	50	11	9	70	67	134	40	241**
18-02-87	42	10	34	86	88	112	135	335**
25-02-87	145	62	6	213	37	55	37	129**
3-03-87	57	29	25	111	122	121	100	343**

D-values for data after logarithmic transformation

D 5% = 0,153*

D 1% = 0,204**

leafhoppers in the plots treated with Mikal-M than in the control plots treated with copper oxychloride, an inorganic fungicide.

DISCUSSION

The low proportion of females producing nymphs and the low fecundities recorded were discussed in Chapter 3. There was no significant difference in leafhopper fecundity or total leaf nitrogen between the Mikal-M treatments and the controls, which seems to suggest that Mikal-M would not affect leafhopper populations. However, the field experiment indicates that Mikal-M does indeed have some influence on the build-up of leafhopper populations.

In view of the low fecundities recorded on treated and control plants in the laboratory experiments, it seems possible that some other limiting factor or factors responsible for the poor performance of the leafhoppers may have masked the effect of the fungicide. Although no significant difference in the total nitrogen content of the vine leaves were measured, it does not necessarily mean that Mikal-M does not affect the nitrogen balance of the leaves at all. The ratio of soluble to insoluble nitrogen may be changed or the proportions of certain key amino acids altered. As discussed at the beginning of the chapter, changes such as these can affect insect performance or the host plant's resistance to the pest.

According to the above results, the possibility exists that organic fungicides may influence the population build-up of A. lineatifrons. Since organic fungicides are included in the regular preventative spraying programmes against fungal diseases followed by farmers in all the vine-growing areas of South Africa, further research on the effects of these fungicides on leafhopper populations is needed to confirm the generality of the above result.

CHAPTER 6. GENERAL DISCUSSION AND CONCLUSIONS

It was established that the mean generation time for A. lineatifrons at 26°C is from 29 to 36 days. Taking into account the effects of varying environmental conditions on generation time length as discussed in Chapter 3, it appears that four to five A. lineatifrons generations can be produced per season. The population levels of univoltine species are more closely dependent on the survival rate of the overwintering population during the preceding winter because of the single generation per year. Multivoltine species are better able to compensate for heavy mortality during winter to reach high population levels towards the end of the season. This implies that reducing the overwintering population of A. lineatifrons by chemical control, for instance, will not necessarily guarantee that population levels will not reach pest status later in the season if the environmental conditions favour rapid development. Furthermore, the presence of A. lineatifrons on species of Rubus throughout the year provides a continuous source of infestation. This is a further reason why the application of chemical control early in the season when population levels are still low may not be effective in preventing the leafhoppers from reaching pest status on the vines. Since such an early, largely ineffective insecticide application might have a deleterious effect on natural enemies of both A. lineatifrons and other pest species, it seems desirable that chemical control should only be applied when the population nears damaging levels. Leaf symptoms, indicating leafhopper damage, occurred shortly before the population peaks were reached. According to the studies on the seasonal occurrence of A. lineatifrons peak populations can be expected from mid-summer onwards, which means that it is unlikely that a leafhopper population reduced by an insecticide application at this stage will be able to recover to damaging levels again before the end of the season.

Also important in the timing of chemical control are the questions of economic damage and economic threshold levels, i.e. the population density where economic loss occurs and the population density where the increase in yield after control is greater than the cost of control. To determine these levels the relationship between population density and economic crop damage must be determined. Assessing the effects of leafhopper damage later in the season on the budding and blooming of the next season, as discussed in Chapter 1, presents great difficulty, as there are so many other factors which also influence these events. Methods for the assessment of economic damage and the determination of the relationship between population density and economic damage must clearly receive

highest priority in future research. Chemical control has many disadvantages, notably environmental pollution, disruption of the ecological equilibrium and high costs. In future one will most likely strive towards an integrated pest management system consisting of adjustments in management, the conservation of natural enemies and careful, strategic insecticide applications. To implement such a system, it is essential to establish an economic threshold level.

Studies of other leafhopper species indicate that the population levels at which economic damage occurs may be higher than might be expected. Research on Erythroneura elegantula and E. comes Say in the U.S.A. indicates that grapevines have a fairly high tolerance for leafhoppers. According to Flaherty et al (1982) defoliation studies to simulate damage by E. elegantula showed that vines can lose up to 20 percent of their leaves without any yield or maturity loss, provided the leaves are not removed until about a month after fruit set. Studies with varying levels of leafhoppers also indicated a fairly high tolerance for leafhopper damage: 20 nymphs per leaf for the first brood and 10 to 15 nymphs per leaf for the second and third broods on Thompson Seedless grapes for raisins or wine, providing leaf loss does not exceed 20 percent. Tolerance levels can also be expressed as nymphal days by multiplying the number of nymphs per leaf by the number of days' exposure. However, these tolerance levels do not take the impact of the adult populations into account.

Jubb, Danko and Haeseler (1983) studied the impact of E. comes on "Concord " grapevines (Vitis labruscana Bailey cv. "Concord"). Caged vines were artificially infested with "low" and "high" leafhopper populations. The "high" populations, comparable to natural populations in commercial vineyards, did not result in significant differences in foliage injury, vine vigour, fruit yield or juice quality compared to uninfested vines. Apparently these vines can withstand greater injury from the first and second generations of E. comes than previously believed, so that the empirical treatment threshold of 15 percent of the leaves injured could be raised.

A subjective survey of symptom development was conducted during the latter part of the 1983/84 season in the experimental vineyard at Simondium. The five plots sampled every week were scored for symptom development on a scale of I to V, based on the percentage of leaves per plot showing symptoms of leafhopper damage (Table 12). This survey showed

TABLE 12. Survey of "hopper-burn" symptom development due to A. lineatifrons on grapevines in five plots at Simondium. On the first two sampling dates the plots were not scored individually, but an overall estimate of symptom development was recorded, hence the mean values only.

Sampling date	Index of symptom development					"Mean"
	1	2	3	4	5	
18-1-84						I
26-1-84						I
29-2-84	II	IV	II	IV	V	III
8-3-84	I	III	II	III	III	II
14-3-84	I	I	II	IV	IV	II
22-3-84	II	II	IV	II	IV	III
28-3-84	I	I	III	II	IV	II
4-4-84	III	II	III	IV	III	III
11-4-84	I	I	III	III	III	II
18-4-84	I		III	II		III
2-5-84	I	III	III	II	II	II

I = 0 - 20% leaves with symptoms

II = 20 - 40% leaves with symptoms

III = 40 - 60% leaves with symptoms

IV = 60 - 80% leaves with symptoms

V = 80 - 100% leaves with symptoms

that the symptoms do not appear evenly through the vineyard, but appeared rather to break out in patches. It also showed that obvious symptoms appeared only shortly before the population peaks were reached (see Table 12 and Fig. 5). It thus appears that it may be too late to spray when a high percentage of leaves show symptoms of leafhopper damage, because the damage may already have been done. This raises the possibility that an insecticide application earlier when the first symptoms can be found could significantly reduce the leafhopper population before its rapid increase begins and so prevent it from reaching damaging population levels. It is evident that the relationship between population density and symptom development must be studied to see if and how symptom development can be used to time chemical control.

The question as to why A. lineatifrons became a pest only recently was raised in Chapter 1. There are three possibilities to consider: (1) that A. lineatifrons is a species of tropical origin which has moved down the continent and became established in the Western Cape only relatively recently, (2) that A. lineatifrons has been in the Western Cape at least as long as the grapevines, but that it required prolonged exposure to establish itself on the new host plant, and (3) that it has been on the grapevines for many years, but only in very small numbers and that it was noticed only when recent outbreaks occurred on the vines. Various factors may have been responsible for these outbreaks.

(1) To investigate the possibility that A. lineatifrons is a more recent arrival in the Western Cape all the available records on the collection of A. lineatifrons were obtained from the University of Stellenbosch's Insect Collection housed at the Department of Entomology, the National Collection of Insects in Pretoria and from literature. These are summarised in Appendix 1. The first recorded collection was from "blackberries" at Hilton Road, Natal in 1917. The earliest record outside the Republic of South Africa was in 1940 when A. lineatifrons was collected in Zaire. Rubus pinnatus, one of the host plants of A. lineatifrons, occurs from the slopes of the eastern escarpment in Transvaal through the Natal midlands and the Drakensberg slopes, down the coastline into Transkei and southwards along the coastline as far as Simonstown in the Cape (Smith, 1966). Apparently it prefers the mistbelts. This means that a corridor existed through which A. lineatifrons could have moved down from the north to the Western Cape. The lack of records prior to 1917 and the fact that the collections outside the RSA were all made later than this precludes any definite

conclusions. However, the fact that it was collected only once in South Africa prior to 1968, in spite of the high concentration of entomological activity in this country, means that the possibility that A. lineatifrons is a recent arrival in the Western Cape cannot be excluded.

(2) If A. lineatifrons has been in the Cape as long as or longer than the grapevines, a possible reason for its recent pest status may be that the insect required prolonged exposure to establish itself on the new host plant. Grapevines belong to the family Vitaceae which is unrelated to the family Rosaceae under which Rubus spp fall. Since it appears to have no feeding preference for grapevines to Rubus, the question "why did A. lineatifrons move onto the vines?" arises. The insect's wide distribution in Africa leads one to suspect a high degree of polyphagy. According to Strong et al (1984) polyphagous insect species often colonize introduced plants belonging to tribes and families unrelated to their original host plants. Several possible reasons for the move onto grapevines are suggested. In the first place there is what Strong et al (1984) refer to as ecological opportunity, that is the close proximity of widespread and abundant normal hosts to the new food plant. Rubus spp are abundant along the numerous streams on the mountain slopes in the Western Cape where grapevines are cultivated. A. lineatifrons therefore had ample opportunity to encounter grapevines. Disturbance of its natural habitat may also have contributed to the shift of the leafhopper onto grapevines. During the last two decades many high mountain slopes, previously untillable, have been cleared with the help of heavy machinery and planted with grapevines. In the process a lot of the natural vegetation, including stands of Rubus, have been destroyed which reduced the natural hosts available to A. lineatifrons and presumably exposed a much greater part of the A. lineatifrons population to grapevines.

Symptoms of leafhopper damage occur to a far lesser degree on Rubus than on grapevines (Chapter 3), which suggests that Rubus has a much higher tolerance for leafhopper damage and/or that the leafhoppers are more abundant on the grapevines than on the Rubus. A higher degree of tolerance in what appears to be the normal host plant, at least in South Africa, is not unexpected and the abundance of insects on introduced hosts compared to the original hosts is often observed. This abundance, often leading to the insect attaining pest status on the new host, can be due to several factors:

(i) The resource concentration hypothesis according to Root (1973) states that "herbivores

are more likely to find and remain on hosts that are growing in dense or nearly pure stands". Finding suitable hosts in the mixed stands of natural vegetation is more difficult for A. lineatifrons than in the grapevine monocultures.

(ii) Furthermore, fertilizers and other management practices maintain a high plant quality which, in view of the effects of nutrient quality on insect performance discussed in Chapter 5, could favour rapid development of the leafhoppers on the grapevines.

(iii) Reduction in the regulating effects of natural enemies (predators and parasites) on insect populations under cultivated conditions also favours high insect population levels. Natural enemies are often more susceptible to toxic chemicals used for pest and disease control than the insect pests, according to Van Emden, 1974. According to Vinson (1976) insect parasitoids often use visual, olfactory and tactile stimuli from the host plant when searching for prey. When an insect moves onto a new host, particularly if unrelated to its normal hosts, one can expect that the insect's parasitoids and indeed all its natural enemies using some host plant cue in finding prey may not be so effective in locating the pest. This may apply to A. lineatifrons on grapevines. Vineyards do not provide such stable habitats for natural enemies with requirements outside the crop for alternate prey or adult food. When the vines begin to grow again in spring, they must be colonized by natural enemies from outside and it may take time until pest numbers reach attractive levels (Van Emden, 1974). However, research to identify the natural enemies of A. lineatifrons on its normal hosts and their abundance in vineyards will have to be done to determine their potential for regulating leafhopper populations in vineyards in an integrated pest management system.

(iv) Pesticides can cause outbreaks of pest populations by means other than their effects on natural enemies. The effects of organic fungicides on leafhopper outbreaks by increasing the available plant nitrogen and lowering plant resistance as suggested by Chaboussou (1971) were dicussed in Chapter 5. Various insecticides have also been found to cause outbreaks and resurgences of pests. Apparently the insecticides affect the insects directly or indirectly via their effects on the host plants. Heinrichs et al (1982) reported that applications of carbofuran, decamethrin and methyl parathion induced resurgences of Nilaparvata lugens (Stal) populations on rice in the Philppines. Stimulation of N. lugens reproduction appeared to be more significant in causing the resurgence than the

destruction of natural enemies. Chelliah and Heirichs (1980) demonstrated that some insecticides applied at sub-lethal doses caused a decrease in the length of the life cycle of N. lugens and increased its feeding activity and reproductive rate. Other cases of insecticide-induced pest resurgences were reported by Dittrich, Streibert and Bathe (1974), Shepard et al (1977), Bottrell and Rummel (1978) and Ball and Su (1979).

(3) It is also possible that A. lineatifrons has been established on the grapevines for some time, but that it occurred in such insignificant numbers that it was not noticed before. Recent outbreaks caused by changes in cultural practices brought it to the attention of farmers and researchers. A number of factors could have contributed to these outbreaks. The possible effects of organic fungicides on leafhopper populations have already been discussed in Chapter 5, but since outbreaks also occurred in vineyards where these fungicides were not applied, it is evident that this is not the only cause of outbreaks. In the experimental vineyard at Simondium pyrethroids were introduced for snoutbeetle control shortly before the first leafhopper outbreaks were reported. The effect of the pyrethroids on natural enemies may have contributed to the outbreaks in this case. From this it appears that there is no single factor which can be singled out as the main cause of leafhopper outbreaks in local vineyards.

The ultimate objectives of the research on A. lineatifrons stated in Chapter 1 are the development of a reliable crop-linked predictive model and methods for monitoring pest populations, as well as efficient short- and long- term control measures. All of these are needed for an efficient and cost-effective pest management system to be established. This research project identified several research priorities aimed at attaining these objectives, namely:

(1) To determine whether A. lineatifrons can aquire and transmit any of the known grapevine virusses, as this would affect the economic damage potential of the pest considerably

(2) To investigate the use of sticky traps to monitor leafhopper populations in vineyards

(3) To identify other alternative host plants of A. lineatifrons

(4) To determine the relationship between population level and symptom development related to economic damage, in order to see if symptom development could be used as an indicator in timing chemical control

(5) To develop a method or methods for assessing economic leafhopper damage

(6) To determine an economic damage level for A. lineatifrons on grapevines

(7) To identify the natural enemies of A. lineatifrons and to determine their abundance and impact on the leafhopper population - this will help to assess their potential as biocontrol agents

(8) To identify and determine the effects of any predisposing factors for outbreaks of A. lineatifrons on grapevines, such as the possible effects of organic fungicides on leafhopper build-up

(9) all of the above will ultimately enable the establishment of an economic threshold level for A. lineatifrons on grapevines. This is essential in an efficient integrated pest management system.

In conclusion, the basic biology of A. lineatifrons and its seasonal occurrence have been determined with the laboratory and field studies. The results of the studies on the effect of organic fungicides on leafhopper populations indicate a priority for further investigation in this field, as this holds serious implications for the farming industry. Some of the other possible reasons for the sudden pest status of A. lineatifrons on grapevines were examined, but due to the lack of conclusive evidence no definite conclusions can be drawn. Furthermore, priorities for further research aimed at attaining the ultimate goal of an efficient integrated pest management system were identified.

SUMMARY

The leafhopper, Acia lineatifrons (Naudé) was identified as a pest on grapevines near Tulbagh in 1978 and has since been reported on grapevines all over the South Western Cape. A. lineatifrons causes browning of the leaves which often results in the shedding of the discoloured leaves. Heavy defoliation before harvest can result in sunburn damage to the grapes, whilst premature leaf loss after harvest adversely affects the ripening of the canes and the accumulation of reserves.

This project was aimed at obtaining basic information on the biology and population dynamics of A. lineatifrons as well as to identify priorities for future research. This information is needed to develop a reliable crop-linked predictive model, methods for monitoring pest populations as well as to develop efficient short- and long-term control measures and pest management strategies.

The life cycle of A. lineatifrons was studied in the laboratory. At 26°C the mean incubation period of the eggs was nine to eleven days, the mean developmental period for the five nymphal instars was 15 days and the minimum pre-oviposition period five to ten days. This adds up to a mean generation time of 29 to 36 days at 26°C. At 20°C the mean nymphal development period was 25 days, confirming the strong influence of temperature on the development rate. Fecundity was determined in the laboratory as the number of nymphs produced per female. The mean of 8,5 nymphs per female recorded at 26°C is very low compared to that of other leafhopper species (see Appendix 2). The low fecundity measured was most likely due to sub-optimal environmental conditions in the laboratory, a reduction in the suitability of the host plant under these conditions and handling of the females.

The seasonal occurrence of A. lineatifrons on grapevines was studied over three seasons. It was found that the leafhoppers overwinter in the adult stage on indigenous Rubus spp, and that they enter the vineyard from the end of October until the beginning of November. Peak

populations occurred between the middle of February and the end of March after which the population declined steadily towards the end of the season as the vine leaves were shed. The sex ratio of the overwintering population on R. chrysocarpus was heavily female biased, possibly due to differential mortality of the sexes. During the growing season the sex ratio was slightly male biased and reached equality on several occasions, both on the Rubus and on the grapevines.

The movement of A lineatifrons between the Rubus and the grapevines was investigated, but no evidence of a directional migration from the Rubus to the grapevines was found. Furthermore, no evidence was found to indicate that morphologically distinct short- and long-distance fliers, as found in Cicadulina species by Rose (1972b), exist in the A. lineatifrons population. Host preference tests also showed that adult leafhoppers apparently have no significant preference for grapevines to Rubus or *vice versa*. It seems, therefore, that the leafhoppers' move onto the grapevines at the beginning of the growing season is not prompted by a host preference.

Chaboussou (1971) suggested that certain organic fungicides may cause leafhopper outbreaks because they affect the suitability of the vines as host plants and alter leafhopper fecundity. The effect of Mikal-M (active ingredient Fosetyl AL/Mancozeb), a systemic dithiocarbamate fungicide, on A. lineatifrons was investigated. Laboratory experiments showed no significant effect on fecundity and leaf analysis of potted vines treated with Mikal-M indicated no significant difference in total leaf nitrogen compared to untreated control plants. However, the field experiment on the effect of Mikal-M on the population build-up of the leafhopper showed that significantly more leafhoppers occurred on the vines treated with Mikal-M than on those treated with a conventional inorganic fungicide, copper oxychloride. In view of the far-reaching implications this can have on the viticultural industry, further research on the effects of organic fungicides on leafhopper populations is recommended to confirm the generality of these results so that recommendations regarding the use of these fungicides may be made.

The question as to why A. lineatifrons became a pest only recently was raised. Three possibilities were considered, namely (1) that A. lineatifrons is a species of tropical origin which moved down the continent and became established in the Western Cape only

recently, (2) that is has been in the Western Cape at least as long as the grapevines, but required prolonged exposure to establish itself on the new host and (3) that is has been on the vines for some time, but was noticed only recently when outbreaks occurred. These outbreaks could have been caused by the introduction of organic fungicides or the depletion of natural enemies by insecticides used to control other insects in the vineyards. Due to the lack of evidence this question could not be answered conclusively.

Other research priorities that were established are the development of methods for damage assessment and monitoring of leafhopper populations, determining if A. lineatifrons can transmit grapevine virusses, the development of an economic threshold level and the identification of natural enemies of A. lineatifrons to enable the development of efficient pest management strategies.

APPENDIX 1 (a). Records on the distribution and collection of Acia lineatifrons (Naudé) in South Africa obtained from the University of Stellenbosch collection, the National Collection of Insects in Pretoria and from literature (Theron, 1982).

RSA		
Date	Location	Collector
20-03-1917	Hilton Rd, Natal	E.S. Cogan
18-05-1968	Stellenbosch	J.G. Theron
11-12-1968	Stellenbosch	J.G. Theron
22-03-1969	Stellenbosch	J.G. Theron
04-01-1970	Stellenbosch	J.G. Theron
24-03-1971	Stellenbosch	J.G. Theron
09-11-1971	Citrusdal	F. Honiball
03-05-1972	Wemmershoek	H. Geertsema
03-07-1973	Montagu	J.G. Theron
11-12-1973	Swellendam (Bontebok park)	J.G. Theron
10-04-1974	Rawsonville	J.G. Theron
-12-1974	East London	J.G. Theron
01-2-1975	Stellenbosch	J.G. Theron
10-03-1978	Tulbagh	J.G. Theron
-04-1978	Saron	J.H. Giliomee
11-04-1978	Wellington	J.G. Theron
21-04-1978	Rawsonville	C.A. de Klerk
14-05-1979	Wellington	J.G. Theron
18-03-1980	Simondium	J.G. Theron

APPENDIX 1 (b). Records on the distribution and collection of A. lineatifrons in the rest of Africa.

Outside RSA*		
Date	Location	Collector
1940	Zaire (Lubumbashi)	H.J. Brédo
1959	Madagascar (Ankarafantsika forest)	E.S. Ross
1962	Madagascar (Majunga province)	E.D. Cashatt
1963	Sudan (near Gilo)	
1963	Sudan (Lotti forest)	
1963	Ethiopia (Belleta forest)	
1968	Zimbabwe (Victoria Falls)	P. Spangler
1973	Nigeria (Olokemeji forest)	
1973	Nigeria (Nsukka)	
1973	Nigeria (Abakaliki)	
1973	Ivory Coast (Goumere)	R. Linnavuori

* Dworakowska, 1981.

APPENDIX 2. Comparison of adult longevity and female fecundity (no. eggs or nymphs per female) of Acia lineatifrons (Naudé) with other leafhopper species.

Species	Host	Temp. (°C)	Longevity	Fecundity	Reference
Acia lineatifrons (Naudé)	grapevines	26	16,9 (female) 6,7 (male)	8,5 nymphs	
Endria inimica (Say)	durum wheat	24,4		44 nymphs	Coupe & Schulz, 1968
Cicadulina mbila (Naudé)	dwarf wheat seedlings	28 26	28 (f) 23 (m)	54,0 eggs 68,9 eggs	Van Rensburg, 1980 Rose, 1973
Empoasca dolichi Paoli	cowpeas	21 - 32	38,3 (f) 31,0 (m)	116 eggs	Parh & Taylor, 1981
Dalbulus maidis (DeLong & Wolcott)	maize seedlings	21	26 - 51 (f & m)	151 eggs	Davis, 1966
Deltocephalus sonorus (Ball)	sweet corn seedlings	21	23,5 (f & m)	27 eggs	Gustin & Stoner, 1968
Graminella nigrifrons (Forbes)	sweet corn seedlings	21 - 24	29,4 (f)	16 eggs	Stoner & Gustin, 1967
Homalodisca insolita (Walker)	Sorghum halepense (L.)	uncontrolled		560 eggs (F1) 250 eggs (F2)	Pollard, 1965

APPENDIX 3(a). Contingency tables for Chi-square independence tests on the host preference experiments with nymphs of A. lineatifrons (Chapter 4).

Nymphs from Grapevines	
Replicate No.	Chi-square value
1	0,22
2	1,65

Nymphs from Rubus	
Replicate No.	Chi-square value
1	0,46
2	0,96
3	0,35
4	0,00
5	2,74

Critical value for $X^2 = 3,84$ at alpha = 0,05 for one degree of freedom

Note: the numbers of nymphs recorded on the container surface were not taken into account when Chi-square values were calculated.

APPENDIX 3(b). Contingency tables for Chi-square independence tests on the host preference experiments with adults of A. lineatifrons (Chapter 4).

Adults from Grapevines	
Replicate No.	Chi-square value
1	1,55
2	2,08
3	2,44
4	0,08

Adults from Rubus	
Replicate No.	Chi-square value
1	1,75
2	0,38
3	0,10

Critical value for $X^2 = 3,84$ at alpha = 0,05 for one degree of freedom

Note: the numbers of nymphs recorded on the container surface were not taken into account when Chi-square values were calculated.

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