23-11-59.

THE DISTRIBUTION AND ABUNDANCE

OF

NATURAL POPULATIONS

OF

ONCOPERA FASCICULATA (WALKER) (LEPIDOPTERA : HEPIALIDAE),

IN

SOUTH AUSTRALIA

BY

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A thesis submitted to the University of Adelaide in part fulfilment of the requirements for the degree of Doctor of Philosophy.

June, 1955.

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Summary

The underground grass caterpillar, Oncopera fasciculata (Walker), is found in the southern portion of South Australia and Victoria and caused severe damage to improved pastures in the lower South-East of South Australia and the Western District of Victoria during 1948-50. Larvae live in vertical burrows in the soil and emerge to feed on surface herbage.

Preliminary studies on the ecology of O. fasciculata revealed what appeared to be two critical periods during its life cycle. In one case the eggs and young larvae, being on the surface of the ground during the late spring and early summer (October-December), might be exposed to dry conditions; this would be more likely to happen on the well-drained soils. The other critical period appeared to be when mature larvae, prepupae and pupae might be exposed to excess wetness during the late winter and early spring (July-September) if situated on the low-lying soils subject to flooding.

Field and laboratory experiments done to study the influence of environment on the distribution and numbers of O. fasciculata are discussed. These experiments showed that eggs and young larvae are easily killed by dryness and lose water at a rapid rate when exposed to desiccation. As the embryo develops it becomes more susceptible to water-loss, and water lost cannot be regained when free water becomes available. Eggs and young larvae stand a better chance to survive where the herbage is dense, because this cover protects them from heat and dryness. In the field, this sort of cover would be found where

improved pastures (growth consisting of clovers and introduced grasses) have not been heavily grazed or cut for hay.

Larvae, prepupae and pupae may be exposed to excess wetness if the place where they are living should become waterlogged. Deaths may be caused by drowning or these stages may be forced from their subterranean tunnels and exposed to predators, of which birds are of greatest importance, or pathogenic organisms.

Starvation, under certain conditions, has had an influence on the survival-rate of O. fasciculata but has been considered as being caused primarily by weather. Predators have very little influence on the numbers of this species except when assisted by unfavourable weather, and no parasites were found.

The development of the lower South-East for agriculture has greatly increased the area of favourable shelter and the quantity of suitable food. The result has been that O. fasciculata has increased in numbers and is more abundant even during unfavourable periods. However, not all of the suitable places were occupied during the outbreak of 1948-50, nor was all of the food eaten except in restricted areas. With food and shelter available, the numbers reached during the outbreak depended mainly on weather.

The evidence suggests that an increase in the numbers of O. fasciculata in any one year may be expected when there are fewer than about fifty days without rain during the previous October-December, and economic loss to pastures might be expected when there is a succession of such years. On the poorly-drained soils it appears that O. fasciculata is likely to increase in numbers whenever a wet, late spring is followed the next year by a winter in which the rainfall is not severe enough to cause more than about two days of waterlogging during July-September.

The influence of weather on the distribution and abundance of _O. fasciculata_ during 1948-55 is discussed. A series of favourable late springs (1943-47) apparently resulted in the outbreak of 1948-50. The largest numbers during 1948-49 were on the well-drained soils because the low-lying soils were too wet. The winters of 1948-49, however, were very dry and in 1950 the largest numbers of _O. fasciculata_ were on the poorly-drained situations. Dry springs in 1950 and 1951, in addition to the wet winters of these years, caused a dramatic reduction in the numbers of the species on both the well-drained and poorly-drained soils. Kinder weather during 1952-53 resulted in an increase in numbers in 1954. There was a slight reduction in the abundance of _O. fasciculata_ in 1955; the largest numbers were found on the lower portions of both the well-drained and poorly-drained soils.

I INTRODUCTION

The underground grass caterpillar, Oncopera fasciculata (Walker), is an indigenous insect which in recent years has severely damaged improved pastures in the lower South-East of South Australia and the Central and Western districts of Victoria. This insect was first recorded in South Australia in 1896 but it was not until 1935 that damage to pastures was reported. Further reports of minor damage in small areas were received in 1937, 1938 and 1940, and in 1948 O. fasciculata became of major economic importance in an outbreak destroying large areas of improved pasture. The outbreak ended in 1950 and damage during 1951-1953 was restricted to local situations. However, an increase in the numbers of O. fasciculata in 1954 resulted in the insect again becoming of economic importance.

The larvae of O. fasciculata feed most actively during autumn and winter. They eat the herbage and dry feed left in the pasture from the year before, and thereby reduce the amount of food for the livestock. If the larvae are numerous enough they may consume the young growth as quickly as it appears. In this case the herbage may not make the usual "flush" of growth following the autumn rains, while the soil is still warm. Pastures receiving such a setback during autumn may not recover until the following spring, and when they do grow again they may contain a large proportion of winter growing annuals which may be a poor quality food for livestock.

There is a single generation of O. fasciculata each year. Moths fly and mate during the early spring (September-October) and eggs are laid on the ground, under pasture plants. Most larvae hatch during late October and early November; they shelter in colonies under silken webbing among surface debris for two to three weeks before making individual vertical tunnels in the soil. When feeding, a larva leaves its tunnel and crawls along a silken runway it has spun on the surface of the ground. A larva does not leave its runways and the area over which it may feed depends upon the number and length of these surface runways; one to three may extend outward from a tunnel and a runway may be up to eight inches in length. Although larvae are present from late October until July, evidence of their feeding does not become apparent until April-June, when the first substantial autumn rain causes annual clovers and grasses to germinate. At this time the larvae become more active and feed more. Prepupae appear during July-August and pupae during August-September; both stages remain in the tunnels.

So far as may be judged from reports the outbreak of 1948-50 began quite abruptly in 1948. But, for reasons stated in Section X, the absence of reports during 1940-47 may have been due to other causes and the start of the outbreak may not have been as abrupt as it appeared. The insect was being studied during the period that the outbreak ended; in 1950 O. fasciculata was a very serious pest while in 1951 only one small patch of damaged pasture was found. Field observations during 1950-1951 suggested that a marked change in climatic conditions, which coincided with the end of the outbreak, may have been responsible for the dramatic reduction in the numbers of the species.

Another prominent feature of the 1948-50 period was the pronounced shift in the outbreak area from well-drained soils to low-lying, poorly-drained soils during 1949-50, and preliminary studies indicated that this also may have been caused by the changes in weather. Field observations continued from 1950 to 1955 and information obtained was incorporated in field and laboratory experiments done to study the influence of environment on the distribution and abundance of _O. fasciculata_ in South Australia. The biology and behaviour of the insect (Madge 1954 a) also were studied and experiments were done on insecticidal control (Madge 1954 b).

II GENERAL DESCRIPTION OF THE AREA OF STUDY

In South Australia, O. fasciculata has been found only in County Grey, the southernmost county in the lower South-East. The South-East is the largest area in the state with an assured rainfall. However, other problems (low soil fertility, seasonal flooding, poor quality native grasses and clovers, deficiencies in trace elements in many of the soils) had to be overcome before large-scale agricultural development could proceed. Since World War II, development of the district has proceeded very rapidly, due mainly to the projects for the settlement of ex-servicemen.

County Grey is mainly an area of primary production. In earlier days, cereals were an important crop but the introduction of superphosphate and improved clovers and grasses caused a significant change from cereal growing to production based on improved pastures (wool, fat lambs, dairy products and beef cattle). Flax, potatoes and onions are grown on the better soils around Mt. Gambier and Kalangadoo. A large proportion of the poorer soils is being used to grow exotic softwoods.

(a) Climate

The lower South-East has a Mediterranean type of climate; effective rain falls from autumn to spring or early summer, summers are warm and sometimes humid and winters are mild. Rainfall is highest (34 inches annual average) in the centre of County Grey and is associated with higher land, but no part of the County receives less than 25 inches. Figure 1 shows the distribution of average annual rainfall in County Grey and also will serve as a locality plan for the paper as a whole.

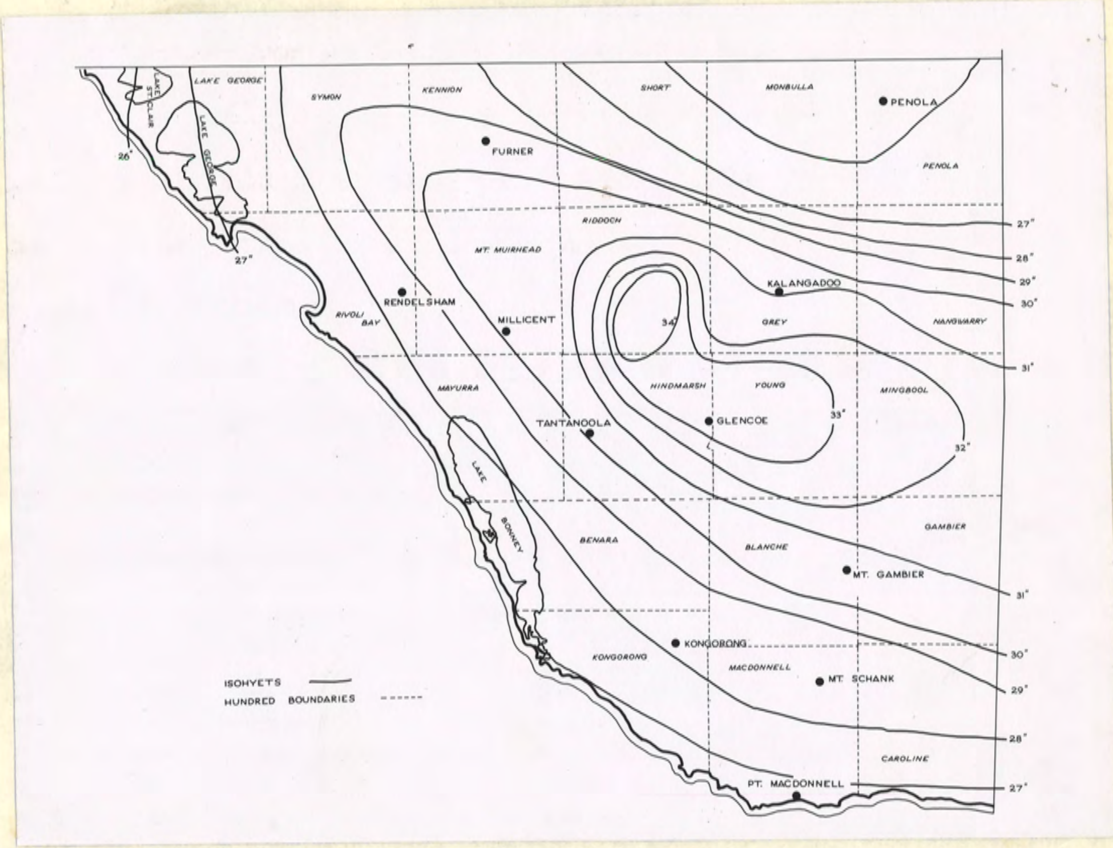

Fig. 1. Rainfall ischyets in County Grey. Also shown are the larger towns and Hundred boundaries. (After Sprigg, 1952)

One way in which the favourableness of climate may be measured is to consider the period of effective rain, i.e., the period when rainfall exceeds one-third the evaporation from a 36" evaporimeter (Trumble, 1948). This is the interval during which the top four inches of soil tend to remain above the wilting point for herbage plants. Most pastures in County Grey are developed around subterranean clover (_Trifolium subterraneum_) and most strains of this clover do best where the period of effective rain is 7.5 months or longer. Except for the northern edge of the County, where the period is between 8.5 and 9 months, all of County Grey has a period of effective rain of over 9 months. Although this method provides a measure of the length of the period favourable for the growth of herbage plants, this period does not necessarily coincide with the full growing season, because the growing season is modified by other factors, as temperature, soil drainage conditions, the composition of pastures and the ability of some species to use subsoil reserves of moisture.

The date of the "break" of the season (first substantial autumn rains) varies considerably from year to year and may come as early as March or as late as June. The date of the beginning of autumn rains is important because an early "break" with good following rains while the soil is still warm causes an early germination of clovers and annual grasses and an increased growth of perennial plants. Winter rains may continue into November or December or the dry period may start in September.

Mean daily temperatures for July, the coldest month, vary between 9.0°C at Kalangadoo and Penola and 10.5°C at Beachport, situated at the southern end of Lake George. Herbage plants continue to grow actively when the mean value for July is above 10.0°C; growth is checked when the value is below this temperature.

The main check to the growth of herbage plants during the summer is lack of moisture. When insufficient rain falls, annual plants are able to obtain additional moisture from about the top foot of soil but when these reserves are gone the plants die. The roots of perennial species extend deeper and these plants may continue to grow after the rainfall season has ended, and frequently grow actively following summer rains.

(b) Physiography and Soils

The lower South-East is essentially a subcoastal plain (Sprigg, 1952). The greater part is less than 300 feet above sea level and there are no prominent streams. Superimposed upon the subcoastal plain is a well-developed system of more or less parallel sand-dune ranges which are a series of successively younger beach deposits, mainly transverse to prevailing winds (Fig. 2). Sprigg (op. cit.) considered that they were formed from oscillations both in sea and land levels and described them as "stranded coastal dunes". These ranges consist of a solid backbone of limestone and calcareous cemented-sand covered by aeolian sand, now fixed by the native vegetation. The sand-dune ranges rarely are over 100 feet high or more than a few miles wide; the largest, Reedy Creek (Burleigh) Range, extends for more than 200 miles from Nelson in Victoria to the mouth of the Murray River.

Because of the old dune ranges, and the low fall of most of the country, natural drainage to the sea is prevented and marshes, swamps and lagoons are prominent features of the land between the ranges.

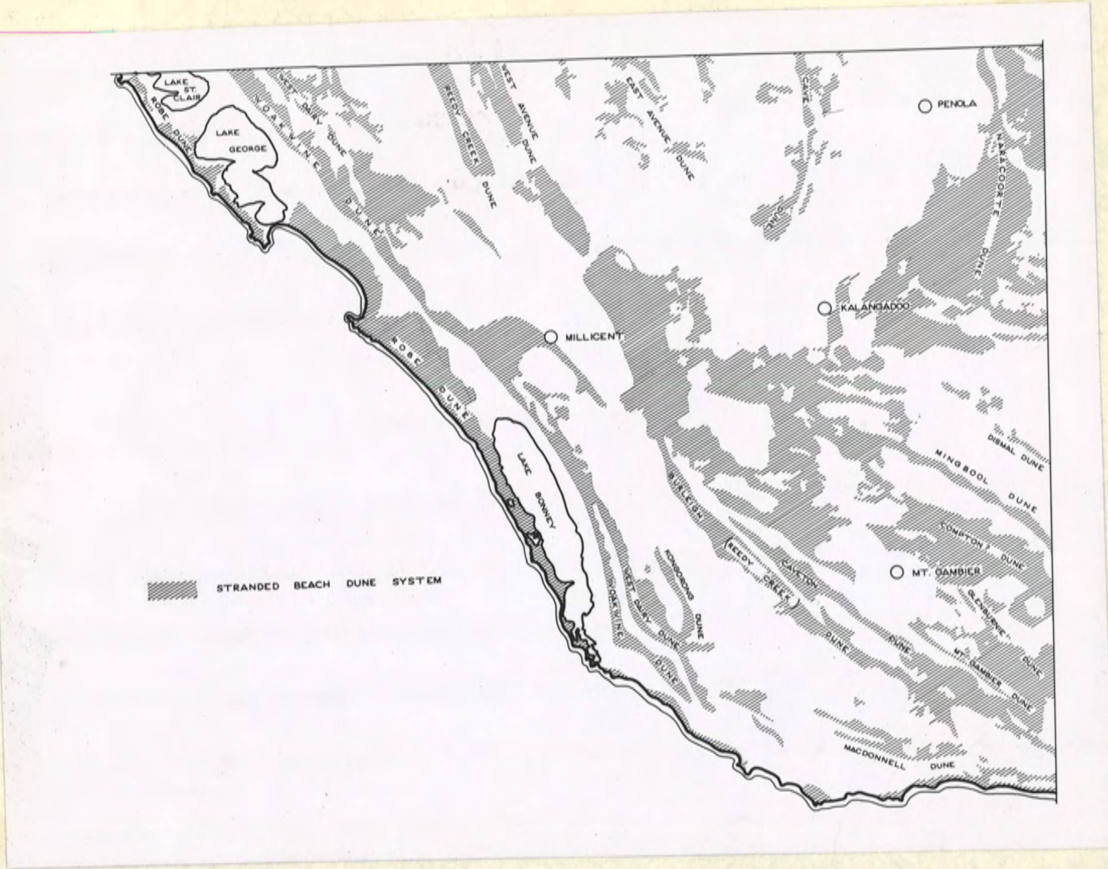

Fig. 2. Distribution of stranded coastal dunes in County Grey. (After Sprigg, 1952)

The relatively high winter rainfall, together with surface and underground water moving across from western Victoria, produces extensive seasonal flooding on the low-lying plains. Much of this land was too wet for agriculture until cuttings were made through the ranges; improved drainage, however, has made a large proportion of the plains available for farming.

Most of the lower South-East is underlain by very porous and cavernous limestone, and water flows rapidly in it; immense amounts of this water are discharged from the Port MacDonnell area. The water table is usually highest in September (end of winter) and lowest in April (close of summer); abnormal rains have a marked effect on the water table (Ward, 1941).

The most prominent landmarks in the lower South-East are the remnants of volcanic activity. The most conspicuous of these are Mt. Schank (520 feet) and Mt. Gambier (630 feet), both of which are shown in Figure 10, and the Mt. Burr Range (up to 802 feet).

Plains between the sand-dune ranges are composed mainly of rendzinas - dark grey or black soils, usually found over limestone. (The distribution of soil groups in County Grey is shown in Figure 3). They were first used for growing cereals (mainly barley) but now support large areas of sown pastures. Although O. fasciculata is present on some of these heavy clay soils, it has not been a serious pest because of the wet conditions.

Meadow podsols are found next to the rendzina plains and alongside some of the ranges; these soils are light-textured sand or sandy-loam overlying clay at depths of between one foot and three feet. Meadow podsols are an important group of soils in the lower South-East and pastures growing on them have been severely damaged by O. fasciculata, especially during dry years. In a wet year, larvae on these soils are likely to be drowned.

Terra rossa and volcanic soils occur as well-drained sandy loams, loams and clay loams and are highly fertile. In the Mt. Gambier-Kongorong district, terra rossa soils are developed over limestone

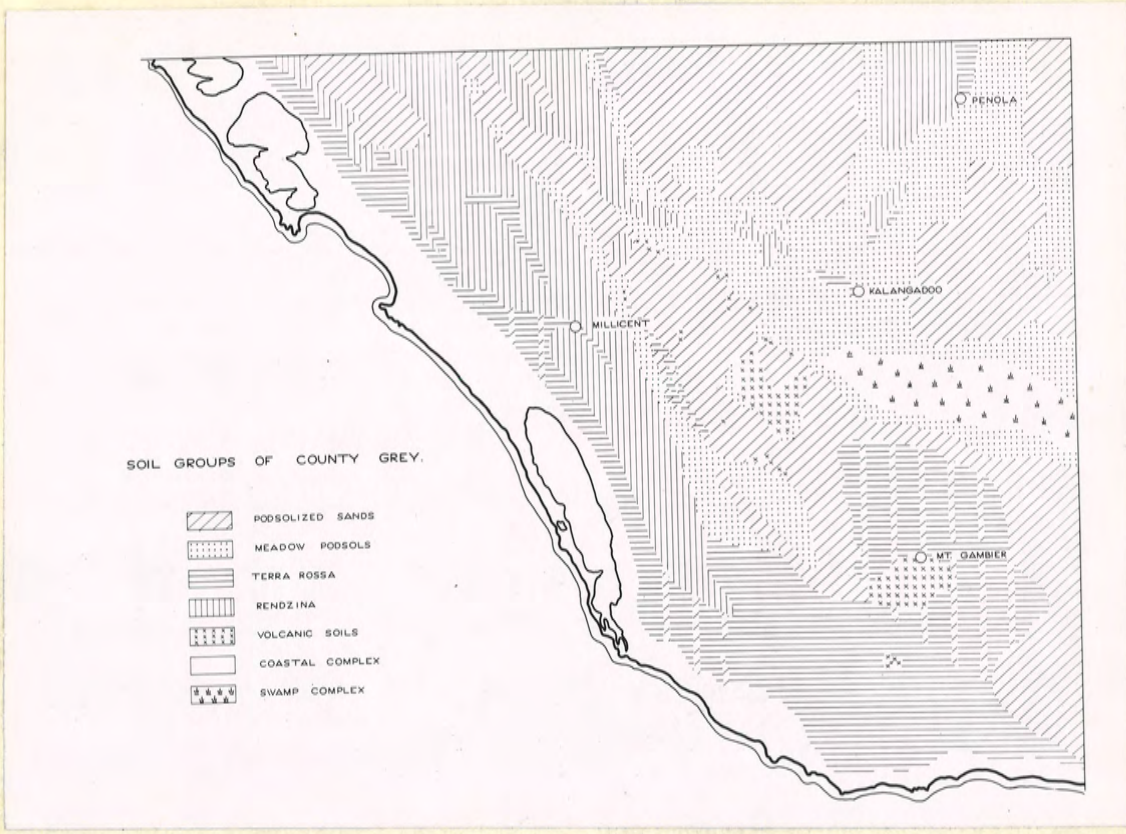

Fig. 3. Distribution of soil groups in County Grey. See text for descriptions of the soils. (Modified after Tiver and Crocker, 1951)

(Crocker, 1944) and have been used for agricultural purposes for many years. Volcanic soils are found to a limited extent around Mt. Gambier, Mt. Schank and the Mt. Burr Range and are mainly associated with the weathering of volcanic ash, tuff and basalt; they have a high P_2O_5 content (Prescott and Piper, 1929). Improved pastures on these soils were severely damaged by O. fasciculata during the 1948-50 outbreak.

Large areas of podsolized sands are found in the lower South-East; these are aeolian and their fertility is low. So far, O. *fasciculata* has not been a serious pest of pastures on these sands. The improvement of soil fertility, and thus of pastures, may make these areas favourable for the insect.

A description of the natural vegetation and pasture types is given in Section XII.

III FACTORS WHICH INFLUENCE THE SURVIVAL-RATE OF O. FASCICULATA

Other animals are associated with O. fasciculata in the pastures of the lower South-East but it was felt that little information on the distribution and numbers of this species could be obtained by studying only this aspect of its ecology. Andrewartha and Birch (1954, p.4) say: "The distribution and abundance of a species cannot be explained by studying only its relations with the plants and animals in its 'community'. There are certain other important components of environment which also require to be considered". This study on the influence of environment on O. fasciculata has dealt with the part played by weather, food, other animals and shelter (see Andrewartha and Birch, 1954, Ch. 2) in limiting the establishment and development of individuals of the species.

The main purpose of this study has been to find which components of the environment have the greatest influence on the numbers and distribution of the insect and, especially, what were the conditions which resulted in the recent outbreak. This information could enable future outbreaks to be anticipated and a means of natural control to be developed.

Studies on the biology of O. fasciculata revealed what appeared to be two critical periods during the life cycle of the insect. In one case the egg and young larva, being on the surface of the ground, might be exposed to dry conditions; this would be more likely to happen on the well-drained soils. The other critical period appeared to be during the mature larval, prepupal and pupal stages when the insect might be exposed to excess wetness during the winter if situated on the low-lying soils subject to flooding.

During the six years in which O. fasciculata was studied, predators were of very minor importance and no parasites were found. Most stages of the insect are found in sheltered situations which would offer a reasonable protection against natural enemies. Larvae live in silk-covered tunnels and feed mainly at night, and prepupae and pupae remain in tunnels closed with firm silken caps, and so would be safe from most enemies unless forced from their tunnels by unfavourable conditions, e.g., flooding. Adults would be exposed to predators while sheltering on the ground before the flight period and also during the brief flights. Also, eggs might be exposed to predators and parasites because of their relatively exposed position. Although young larvae are not living in tunnels they are sheltered under a protective cover of silken webbing. But I could not find any evidence that many of these stages were likely to be eaten by predators or attacked by parasites.

Starvation, under certain conditions, has had an influence on the survival-rate of O. fasciculata but I have considered this as being caused primarily by weather; the larvae died not so much because they were too numerous but rather because of unfavourable weather which delayed the growth of pasture plants.

As a result of these preliminary studies, most of the observations and experiments to be discussed in this paper have dealt with the influence of weather and the kinds of places in which the insects are living on the survival-rate of _O. fasciculata_; other components of the environment were considered to be of minor importance. This insect is found on two main types of soil; well drained soils and low-lying, poorly-drained soils. On the well-drained soils, exposure to desiccation was thought to be the main factor limiting the multiplication of _O. fasciculata_, and Sections V and VI deal with the studies on water relations. Exposure to extreme wetness was thought to be the limiting factor on the soils subject to waterlogging, and studies on this factor are described in Section VI.

IV FECUNDITY AND FERTILITY OF O. FASCICULATA

Eggs of O. fasciculata are extremely difficult to find in the field for they are small (0.71 mm long and 0.52 mm wide), are a dull black colour and are laid singly under herbage on the surface of the ground. Because of this difficulty, observations on the fecundity of the females could only be made in the laboratory. The procedure used was to collect fertilized females (see Madge, 1954 a for description of mating behaviour) and send them to Adelaide; there the moths were placed in individual pommade jars, together with any eggs laid during the trip, and all were placed in an incubator maintained at a favourable temperature.

There was a wide range in the number of eggs laid by the moths; the greatest number recorded was nearly 1,500, while some laid no eggs. It appeared, however, that at about 13°C a fertilized female laid about 1,000 eggs; more eggs might have been laid if the moths had been kept at a higher, though still favourable, temperature (Vance, 1949). Components of the environment other than temperature also would have an influence on the fecundity of the female.

The egg is creamy-white when laid but usually turns a dull black within a few hours. Occasionally eggs were found which remained creamy-white or did not change colour for many hours. To see whether these eggs differed from the others, creamy-white eggs were removed from the pommade jars and set aside at a favourable temperature and 100 per cent. relative humidity. A total of 84 eggs was set aside; of these, 32 became black, six grey, seven speckled-grey and 39 remained creamy-white. There was no embryonic development in these eggs. It seems that eggs which do not turn black within a few hours of being laid are infertile. Only black eggs were used in the experiments to be discussed but as they were collected at intervals of twelve hours, some could have been infertile. As will be seen later, some larvae did not emerge even when the eggs were at favourable temperatures and humidities, probably because the eggs were infertile.

V INFLUENCE OF TEMPERATURE AND MOISTURE ON SPEED OF DEVELOPMENT AND SURVIVAL-RATE OF THE EGGS

(a) Favourable Temperature Range

During the studies on O. fasciculata three experiments were done on the duration of the incubation period of the eggs at constant temperatures and 100 per cent. relative humidity, and the death-rate over a range of temperatures (6.3° to 31.6°C) also was obtained. The criterion for death was failure to hatch; this could have been caused by the influence of an unfavourable temperature or infertility of some of the eggs. There was a small amount of embryonic development at 6.3°C but no larvae hatched, and at 8°C 92 per cent. died. The favourable temperature range was between about 10°C and 22°C; the mortality ranged from 0 per cent. to 25 per cent. with a mean of 8 per cent. (18 observations). It is likely that most of the eggs which failed to hatch at these favourable temperatures were infertile.

At 26.7°C embryos had developed in most of the eggs and in some cases the larvae were fully formed. Some had tried without success to rupture their eggshells but only 39.5 per cent. of the eggs hatched. No larvae hatched at 31.6°C. The high death-rate at the higher temperatures may have been caused by injury to the developing embryo and possibly a change in the texture of the eggshell which prevented eclosion.

In the field, eggs would be exposed to unfavourably low temperatures (mean daily temperature at Mt. Gambier for September is 11.7°C) but these temperatures would not last long enough to injure the developing embryos, and they are not likely to be exposed to harmful high temperatures.

(b) Speed of Development at Constant Temperatures

The first laboratory experiment with the eggs of O. fasciculata was done to determine the incubation period of the eggs at constant temperatures. This information was needed before further studies could be done on the influence of moisture on survival-rate. The first incubation experiment was done in 1950 and others were done in 1952 and 1953. These latter experiments were done to see if there was any difference in the incubation period at any one temperature from year to year, as a large variation could have an influence on the results of the more important experiments which were to be done. Also, in 1952, eggs were used from Mil Lel and Kalangadoo (eggs for the other experiments were from Mil Lel), to see if there was any difference in the incubation period of eggs from different localities. Mil Lel is located on a well-drained, terra rossa soil and Kalangadoo on a low-lying, meadow podsol soil; these two places are 19 miles apart.

In these experiments, eggs were of a uniform age (0-12 hours) and were selected at random from the pooled eggs of the female moths. Eggs were distributed among the temperatures used and at each temperature the eggs were grouped in batches, usually of 100 eggs each. Each batch of eggs was placed on moist blotting paper in a petri dish, as previous work had shown that few larvae emerged when eggs were not kept moist.

The petri dishes were placed on stands in air-tight glass jars containing distilled water and the jars were placed in incubators maintained at the required temperature. Temperature readings (to 0.1°C) were taken at 9 a.m. each day and the temperature of each incubator was calculated as the arithmetic mean of a large number of these readings. Temperatures inside the petri dishes containing the eggs would not have fluctuated as much as the air inside the incubator, shown in parenthesis after the temperature readings in Table I (Appendix).

At the completion of each experiment the mean duration of the incubation period, the mean per cent. development per day and the per cent. mortality were computed for each temperature.

In the analysis of the comparison of duration of incubation period for different years and with eggs from different localities, figures for mean duration at each temperature were transformed to log (mean duration -10) to give a linear relationship of duration with temperature and to make the calculations less laborious. Temperature was the independent variate (x) and duration of the incubation period in hours, was the dependent variate (y). The four regressions on temperature were then compared, i.e., a test was made of the agreement of the four regression coefficients by an analysis of variance. Transformed figures, temperatures used and data for the analysis of variance are given in the Appendix; the analysis of variance and the regression coefficients and their standard deviations are shown in Table 1. This analysis showed that there was no significant difference between the regression coefficients; in other words, the incubation period of eggs at any one

TABLE 1

ANALYSIS OF VARIANCE OF DURATION OF INCUBATION PERIOD

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Total	20	9.4801			
Regressions	4	9.3335	2.3334		0.1%
Combined Regressions	1	9.2902	9.2902		
Difference between Regressions	3	0.0433	0.0144	1.58	NS
Deviations from Separate Regressions	16	0.1466	0.0091625		

1950 (Mil Lel) regression coefficient (b)	= -0.1088 ±0.0032
1952 (Mil Lel)	= -0.1196 ±0.0086
1952 (Kalangadoo)	= -0.1204 ±0.0080
1953 (Mil Lel)	= -0.1019 ±0.0029

temperature (within the temperature ranges of the experiments) was the same for the three years and the two localities. Therefore eggs and larvae used in the experiments to be described later may be considered as samples from a homogeneous population, although they were present in different years and were from two different localities.

The combined regression coefficient was -0.1133 (±0.0036) and was highly significant; the duration decreased by 2.72 hours for each degree Centigrade increase in temperature. The 24 observations of percentage development per day (untransformed) plotted against temperature are shown in Figure 4 and a freehand sigmoid curve has been drawn through the points.

No attempt was made to determine precisely the incubation

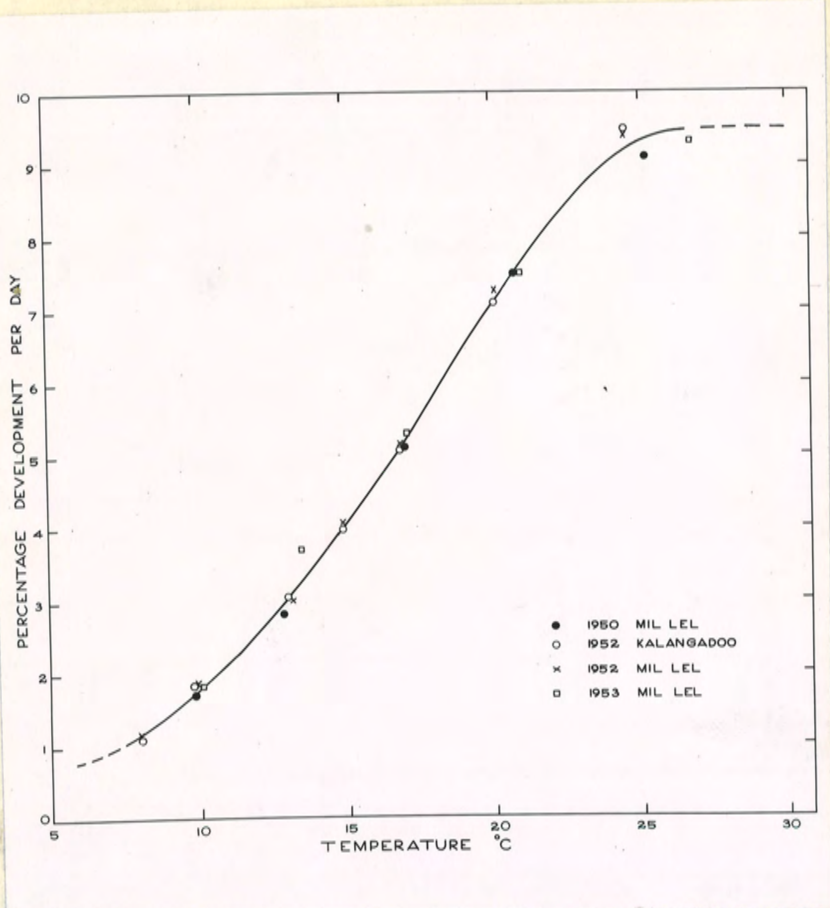

Fig. 4. Percentage development per day for eggs of O. fasciculata at constant temperatures and 100 per cent. relative humidity.

period of eggs under natural conditions, but as the eggs do not enter diapause it would be reasonable to assume that the incubation period at constant temperatures would be about equivalent to the incubation period when there were brief changes in temperature within the favourable range (Birch, 1942). Thus it was estimated that the incubation period of eggs in the field was about three to five weeks.

The speed of development of O. fasciculata eggs at constant temperatures is quite different from that of O. intricata in Tasmania.

At 21.2°C and 100 per cent. relative humidity, the mean incubation period of O. fasciculata eggs was thirteen days while O. intricata eggs at the same temperature and moisture level took 63 days; at 24°C the former eggs took eleven days to hatch and the latter 71 days (Data for eggs of O. intricata are from Martyn, unpublished report). The differences in speed of development appear to be adaptations by which the two species are able to survive the dry summer period. Eggs of O. fasciculata are laid early in the spring and the larvae hatch and become established in tunnels before the summer. If their speed of development were the same as O. intricata, larvae would appear in early summer and would be more exposed to unfavourable weather than older larvae. On the other hand, eggs of O. intricata are laid during mid- to late-summer and the larvae do not hatch until mid-autumn; with a more rapid speed of development larvae would appear during late summer, when weather would be much more severe than in mid-autumn.

(c) Field Observations and Experiment

During the period that eggs of O. fasciculata are in the field, the top few inches of soil tend to be above the wilting point for pasture plants and these are growing rapidly as a result of the warmer weather. Late October to late November is the ideal time to cut herbage for ensilage or hay, although this often is done later in the year. In September there is a low dense mat of clover and grass on the improved and grazed pastures, together with taller dead growth remaining from the previous year. The growth of pastures during September-

November depends largely on seasonal conditions. A long spell of warm weather results in the grasses growing rapidly and setting seed, thus producing a tall growth. Cooler conditions produce a slower growth of grasses and the plants are more compact.

During their incubation period, eggs are resting on, or just above, the soil and in an improved pasture would be covered with both a layer of surface litter and a mat of pasture. Under these conditions the eggs and young larvae would be reasonably well protected against dry conditions - the danger of exposure, of course, would be determined largely by the amount and spread of rain and dew during the time that these stages were present.

On unimproved pastures there would be much less clover, grasses would be more spindly and there would be a large proportion of bare ground. In these situations the eggs and young larvae would not have the protection afforded by improved pastures and would be more exposed to dry conditions.

In 1951 a field experiment was done to study the influence of "cover" on the survival-rate of the eggs and young larvae. A split-plot factorial experiment was designed because it was desired to study at the same time the influence of both the number of eggs per unit area (density) and the way in which the eggs were distributed (spread evenly over the plot or placed in evenly spaced clumps) on the chance of survival of the larvae under different sorts of "cover". Each replicate was divided into two main blocks for density (50 and 1,000 eggs per square yard), each block was divided into two plots for method of distribution and each plot was divided into four sub-plots for type of "cover". There were three replicates in the experiment and all sub-divisions of each replicate were distributed randomly.

The four types of cover were made by modifying the herbage on the experimental area. Type 1 was untouched herbage and provided a high, dense cover. In Type 2 the herbage was "thinned" by eliminating the dicotyledons with a hormone-type weed killer; this provided a high, sparse cover. Herbage in Type 3 was "mown" by clipping it closely with hedge clippers, providing a low, dense cover, and herbage in Type 4 was "thinned" and "mown", providing a low, sparse cover.

This experiment was set out in a paddock near Mt. Schank; the soil was a terra rossa and the pasture was composed mainly of subterranean clover and Wimmera rye-grass (Lolium rigidum). Sub-plots were one square yard in size and were separated by metal strips which were pressed into the ground and extended three inches above the surface. Both sides of the strips were painted with creosote; these treated strips served as barriers to prevent the movement of larvae from one sub-plot to another.

Eggs were obtained from moths collected in the field and were counted into groups of 50 and kept in pillboxes until the experiment began. When the barrier strips were in place and the four types of cover had been prepared, the eggs were distributed. In the treatment requiring 50 eggs per sub-plot in which the eggs were clumped, eggs were placed in the centre of the sub-plot on the surface of the ground under herbage. This was to duplicate as nearly as possible the habit of the ovipositing female. For sub-plots where the 50 eggs were scattered the method was to spread the eggs evenly over the sub-plot. In the treatment requiring 1,000 eggs per sub-plot in which the eggs were clumped, the eggs were placed on the sub-plot in twenty groups of 50 eggs each, and for the scattered treatment the 1,000 eggs were scattered evenly over the sub-plot; in each case the eggs were placed on the ground under herbage.

The experimental area (48 square yards) was covered with hessian during the flight period in 1951 to prevent the entry of gravid females; this cover slowed down the growth of the pasture plants and probably was favourable for the eggs because it would have helped to prevent the loss of moisture from the area.

This field experiment was sampled in January, 1952, when larvae had become established in individual vertical tunnels in the soil. Under field conditions it was impossible to determine the death-rate among eggs and the criterion for survival of the eggs was the proportion of larvae which survived to become established in tunnels. The sampling technique used was that which was developed during studies on the insecticidal control of O. fasciculata (Madge, 1954 b). Surface growth was removed from the sub-plots and shellacked cardboard covers were placed on the cleared area and left for 24 hours. During this period larvae rebuilt the damaged silken covers of their tunnels and when the cardboard covers were removed the entrance of each vertical tunnel in the sub-plot could easily be seen.

For the analysis of the data, counts of larvae in each treatment were expressed as a proportion surviving from the eggs put on each sub-plot (zero counts were replaced by 0.25) and the angular transformation was used to replace proportions by angular values (the analysis of variance is given in Table II of the Appendix). The transformation of proportions to angles is necessary because it is assumed in the analysis of variance that each datum is subject to the same variance; this is not so where data are in proportions, for each proportion is determined with a different precision (Mather, 1951). Transformed data are given in Table 2.

There was a high death-rate on all sub-plots of this experiment; the largest proportion surviving was 22 per cent. on one of the untouched pasture sub-plots where eggs were scattered. No larvae were found on eight of the sub-plots which received 50 eggs each and there were no larvae on two of the sub-plots receiving 1,000 eggs each. In seven of these ten sub-plots the pasture had been mown and thinned.

The most important information obtained from this experiment was that there were more larvae on the untouched sub-plots (high dense cover) than on any of the other types of pasture (P = 1%). Also, there were more larvae on unmown and thinned sub-plots than on mown and thinned sub-plots (P = 1%). These results confirmed the statement, based on field observations, that the type of pasture in a paddock where <u>O. fasciculata</u> was situated probably had an influence on the survival-rate of the eggs and young larvae.

An unimproved pasture may be considered as unfavourable for the egg and young larvae while an improved pasture may be considered as

TABLE 2

MEAN SURVIVAL-RATE OF EGGS UNDER VARIOUS TYPES OF PASTURE, EGG LEVELS AND METHODS OF APPLICATION

(DATA IN DEGREES)

	50 Eggs/sub-plot			1,000 Eggs/sub-plot			
Pasture	Grouped	Scattered	Pasture Mean	Grouped	Scattered	Pasture Mean	Total Pasture Mean
Not changed	13.84	19.53	16.69	11.52	12.25	11.89	14.28
Unmown and thinned	9.92	13.84	11.88	5.49	7.75	6.62	9.25
Mown	5.41	12.03	8.72	3.30	8.19	5.75	7.24
Mown and thinned	4.05	8.18	6.12	3.09	4.33	3.71	4.91
Method mean	8.31	13.40	10.85	5.85	8.13	6.99	

Total Grouped mean = 7.08 ; Total Scattered mean = 10.77

Min. Diff. for significance	5% level	1% level
Between 2 total pasture means	2.87	3.88
" 2 pasture means at same egg level	4.06	5.50
" 2 pasture means at same method	4.06	5.50
" 2 method means at same egg level	3.41	4.99
" 2 method means at same pasture	3.74	5.06

favourable. However, the removal of cover from an improved pasture just before or during the early part of the period when eggs and young larvae are present (September-November) would make this situation unfavourable; the proper timing of cutting herbage for hay (and the prompt removal of the cuttings), or heavy grazing by sheep would cause such a change.

The analysis showed that there was no significant difference between the survival-rate of 50 eggs per square yard and 1,000 per square yard, i.e., the same proportion survived at the higher density as at the lower.

Contrary to expectation, there was a higher survival-rate when eggs were scattered than when they were grouped. This was unexpected because the female lays most of her eggs in groups. After mating, the female crawls under the pasture and comes to rest on the surface of the ground. After fluttering about briefly she settles down and starts ovipositing; most of the eggs are then laid. The higher survival-rate of scattered eggs in this experiment suggests that it is not to the advantage of the species, living as it does today in modern pastures, to lay eggs in groups. It is not known what additional hazards beset a larva that is living as one of a group. Under natural conditions, emerging larvae establish themselves in colonies under silken webbing among surface debris and live in these colonies for several weeks before constructing individual vertical tunnels in the soil. The silken webbing should provide extra protection for the larvae, but on the other hand, cannibalism may reduce their numbers. No evidence of cannibalism among young larvae was found in the laboratory but this does not mean that it does not occur in the field.

It may be that laying eggs in large clumps was an adaption which resulted in a higher survival-rate in native pastures. This could be so, because native pastures are composed mainly of grasses having a tussocky growth and there is a great deal of bare ground between the tussocks. After mating, the female would crawl under a tussock to seek shelter and there would lay her eggs. If eggs had been scattered over the ground most would have come to rest in unfavourable situations. Today, however, improved pastures provide large areas of favourable cover and it would be expected that eggs scattered over such an area would have a good chance to survive, but the species seems not yet to have become adapted to this change in its environment.

(d) Laboratory Experiments

The place where O. fasciculata eggs were laid appeared to have an influence on the survival-rate of this insect and it was considered that the amount of pasture growth was important because this cover helped to protect the eggs against loss of moisture. The next step was to do some laboratory experiments with the eggs to study their ability to survive under various conditions of dryness.

(i) Preliminary Experiment on the Survival-rate of Eggs when Exposed to Dryness

Very little was known about the survival-rate of O. fasciculata eggs when they were exposed to dry conditions and this experiment was considered as a preliminary to work to be done later. The two temperatures used (20.1° and 13.0°C) were within the favourable range of the eggs; the higher temperature is about the mean daily temperature in the field during the egg stage. Temperature was controlled to ±0.4° at 20.1°C and ±0.2° at 13.0°C. Eggs were exposed for 20 per cent. of their incubation period at each temperature; this was 3.0 days at 20.1°C and 6.75 days at 13.0°C. There were six levels of evaporation at each temperature and saturation deficits were arranged so that, at any one level of evaporation, eggs would be exposed to the same amount of evaporation at each of the two temperatures, i.e., the product of saturation deficit (mm Hg) and length of exposure (days), the total evaporating power of the air, would be the same. Air movement would have been constant at all the treatments for the lids were not removed from the glass jars during the periods of exposure. The mean daily saturation deficit at Mt. Gambier for the September-November period is 4 mm Hg, and at 20.1°C three of the levels of evaporation were below and three were above this point; the six levels at 13.0°C were then selected to give the same product of saturation deficit and length of exposure at each level of evaporation. In this way the eggs at any one level of evaporation were exposed to the same amount of evaporation for the same proportion of their incubation period. The layout of the experiment is shown in Table 3b.

There were 100 eggs for each treatment. Eggs were placed in scooped-out recesses in a disc of plaster of Paris, the discs were placed on glass tripods in airtight glass jars and the jars were placed in incubators. Atmospheric humidity in the jars was controlled by means of sulphuric acid solutions. Samplings of the twelve solutions at the end of the experiment showed that there was a very slight change in their specific gravities, resulting in an average increase of 0.9 per cent. relative humidity in each treatment. As the change in humidity was in the same direction for all treatments it was not considered to have influenced the results of the experiment. When their period of exposure was finished, eggs were removed from the jars and placed on moist blotting paper in the bottom of a petri dish, and the dishes were placed in incubators at the same temperature as when the eggs were exposed to evaporation. A record was kept of the emergence of larvae.

This experiment was done three times; in the first series, eggs were exposed when one-third of their embryonic development had been completed, in the second series eggs were exposed when one-half developed, and in the third series when three-quarters developed.

The proportion of larvae which emerged at each treatment was replaced by an angular value and Table 3 gives these transformed values and minimum differences for significance. The analysis of variance is shown in Table III in the Appendix. This analysis shows that there were no significant differences between the survival-rate of eggs at the two temperatures or at the six levels of evaporation. However, differences between egg stages were highly significant; the table of means shows that very few larvae emerged from eggs which were exposed to dry conditions when most of the embryonic development had been completed. The percentage emergence of larvae in this stage (III)

TABLE 3

TRANSFORMED PERCENTAGES OF LARVAE WHICH EMERGED FROM EGGS EXPOSED TO EVAPORATION

		Levels of Evaporation						
Temp.	Stage	1	2	3	4	5	6	Σ
20.1°C	I	65.65	64.90	66.42	62.72	75.82	68.87	404.38
	II	58.69	61.34	56.17	57.42	60.00	56.17	349.79
	III	40.40	56.17	43.28	51.35	38.65	43.28	273.13
	Σ	164.74	182.41	165.87	171.49	174.47	168.32	1027.30
13.0°C	I	50.77	50.18	66.42	52.53	57.42	58.69	336.01
	II	63.44	64.90	51.35	52.53	64.16	64.90	361.28
	III	42.71	53.13	46.72	41.55	47.29	33.83	265.23
	Σ	156.92	168.21	164.49	146.61	168.87	157.42	962.52
TOTAL	I	116.42	115.08	132.84	115.25	133.24	127.56	740.39
	II	122.13	126.24	107.52	109.95	124.16	121.07	711.07
	III	83.11	109.30	90.00	92.90	85.94	77.11	538.36
	Σ	321.66	350.62	330.36	318.10	343.34	325.74	1989.82

TABLE 3a

TABLE OF MEANS : TEMPERATURE x EGG STAGE

	Egg Stage		
Temperature	I	II	III
20.1°C	67.40	58.30	45.52
13.0°C	56.00	60.21	44.21
$\bar{x}$	61.70	59.26	44.86

Min. diff. for significance:

5% level	6.59
1% level	9.36
0.1% level	13.55

TABLE 3b

DESIGN OF LABORATORY EXPERIMENT, 1952

		Levels of Evaporation						
Temperature	S.D.	1	2	3	4	5	6	Length of Exposure (days)
20.1°C	mm Hg	1.50	3.00	3.75	4.50	5.25	6.75	3.00
13.0°C		0.67	1.34	1.67	2.00	2.33	3.00	6.75

was 49.8, compared with 75.6 per cent. emergence when eggs were exposed when one-half developed (stage II) and 77.5 per cent. when eggs were exposed when one-third developed (stage I). Stages I and II differed significantly only at the higher temperature and this increase in death-rate, plus the very great increase in death-rate at stage III, indicates that the ability of the egg to survive dry conditions decreases as the embryo develops.

Failure to obtain significant differences between survival-rates at the six levels of evaporation must have been because the amount of exposure (SD x time) was not severe enough at the drier levels. However, some information was obtained for later experiments.

(ii) Influence of Water-loss on Survival-rate of the Eggs

This experiment was similar to the preceding one and it was designed to elaborate the information already obtained. There were two favourable temperatures (16.9° and 13.4°C) and at each temperature were six levels of evaporation plus one level in which eggs were in a nearly saturated atmosphere. Compared with the previous experiment, the period of exposure was increased from 20 per cent. to 48 per cent. of the incubation period of the eggs at each temperature (9.1 days at 16.9°C and 14.9 days at 13.4°C) and the air was drier. The same method was used in which the total evaporating power of the air (as indicated by the product of saturation deficit and length of exposure) was the same at any one level of evaporation at the two temperatures. The experiment started when the eggs had completed eight per cent. of their embryonic development. Each treatment contained four groups of 25 eggs, each group was in a separate wire-gauze cage (eggs were spread evenly over the bottom of the cage) and the cages were placed on a wire support resting on a glass tripod in a jar. Atmospheric humidity inside the jars was controlled with sulphuric acid solutions. For the control treatments, moist blotting paper was placed on the wire supports holding the wire-gauze cages and there were 100 ml of water in the bottom of the jar. When their period of exposure was completed, the groups of eggs were placed on moist blotting paper in individual petri dishes and a record was kept of the number of larvae that emerged and of their incubation period.

Plans had been made to record the weight of each egg before and after exposure to dryness but because of the light weight of the eggs (ca. 0.09 mg for a turgid egg) and the inaccuracy of the torsion balance, only group weighings could be done. Each group was weighed before and after exposure and 48 hours after the eggs had been placed on moist blotting paper. The latter weighings were done to find if the eggs were able to regain water they had lost. Four other groups of 25 eggs each were weighed and oven-dried to obtain the weight of dry matter.

An analysis of variance was done on the weights of the groups of eggs before the experiment as well as on the loss of weight and percentage emergence and these data are given in the Appendix (Tables IVa, b, c). For some unknown reason there were significant differences among the weights of the groups before they were exposed to dry conditions. Eggs for any one group were taken at random from a large number and the same weighing techniques were used.

Weighings done at the end of the treatment showed that eggs in the controls (0 level) lost a slight amount of weight but this loss was very much less than at levels one to six. Although eggs in the controls were resting over water they were not actually in contact with it and this probably is why they lost a slight amount of weight. Loss of weight at the other levels was closely associated with dryness; the drier the air, the greater was the loss of weight.

Analysis of the percentage emergence of larvae (data transformed to degrees) showed that the only significant differences between the means of levels of evaporation were between levels three and four and between five and six. This was rather puzzling, because the mean losses of weight of the other groups differed significantly, i.e., the amount of water lost did not appear to be associated with survival-rate. Also, temperature had an influence on the survival-rate (more larvae emerged at the higher temperature) but not on the amount of water that the eggs lost.

Because of the conflicting results of the three analyses of variance it was decided to test the data by fitting them to a partial regression of the form $Y_1 = a + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4$, where Y_1 refers to the survival-rate expressed in degrees. The four independent variates were original weight (x_1), loss of weight (x_2), specific gravity of the acid solutions (x_3) and temperature (x_4). Specific gravities of the acid solutions were included to see whether the acid itself had any influence on the developing eggs, e.g., harmful effect of fuming. The coefficients (b) paired with the independent variates measure the association of Y_1 with their respective variates, independent of any relationship between Y_1 and a particular variate and any other variate, i.e., b_1 measures the association of Y_1 and x_1 independently of any relationship between Y_1 and x_2, x_3 and x_4. A second dependent variate, duration of incubation period in days (Y_2), was included so that the influence of the four independent variates on it could be examined. There were 55 observations and the sums of squares and products of the variates are given in Table 4.

The first analysis by partial regression showed that original weight and specific gravity of the acid solutions had no influence on survival-rate, independently of loss of weight and temperature, and were discarded. Results of the second partial regression of Y_1 on x_2 and x_4 are shown in Table 5. This partial regression was significant ($P = 0.1\%$) and accounted for 58 per cent. of the variance of Y_1; the remainder of the variance would have been due to random sampling error and factors other than loss of weight and temperature. The influence of loss of weight was very great and, within the temperature range of this experiment, for each 0.1 mg of weight lost by a group the survival-rate decreased by about six per cent. Temperature also was closely related to survival-rate and there was a 2.5 per cent. increase in survival for each degree Centigrade increase in temperature.

With the more sensitive analysis by partial regression it was possible to demonstrate that the number of larvae which emerged at any one level of evaporation was closely associated with the amount

TABLE 4

SUMS OF SQUARES OF VARIATES SELECTED
FOR THE PARTIAL REGRESSIONS

Variate	$(x - \bar{\bar{x}})^2$
x_1	0.7506
x_2	2.5926
x_3	0.6768
x_4	54.9800
$x_1\ x_2$	0.4994
$x_1\ x_3$	0.0483
$x_1\ x_4$	- 0.2400
$x_2\ x_3$	1.0913
$x_2\ x_4$	- 0.4825
$x_3\ x_4$	- 0.9076
$x_1\ Y_1$	- 36.5950
$x_2\ Y_1$	- 140.3320
$x_3\ Y_1$	- 60.9923
$x_4\ Y_1$	- 210.6364
$x_1\ Y_2$	1.4370
$x_2\ Y_2$	14.0256
$x_3\ Y_2$	3.2467
$x_4\ Y_2$	291.6327
Y_1	14411.0073
Y_2	1693.6811
$Y_1\ Y_2$	-2305.6145

TABLE 5

PARTIAL REGRESSION OF SURVIVAL-RATE (DEGREES) ON LOSS OF WEIGHT (x_2) AND TEMPERATURE (x_4)

Variate	Regression Coefficient	S.E.	t	P.
x_2	- 54.92431	6.5620	8.370	0.1%
x_4	- 4.30861	1.4247	3.025	1%

Analysis of Variance

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Regression	2	8615.1863	4307.5931	38.65	0.1%
Residual	53	5795.8210	111.4581		
Total	54	14411.0073			

TABLE 6

PARTIAL REGRESSION OF DURATION OF INCUBATION PERIOD (DAYS) ON x_2, x_3 AND x_4

Variate	Regression Coefficient	S.E.	t	P.
x_2	4.11877	0.91829	4.485	0.1%
x_3	5.45497	1.81615	3.004	1%
x_4	5.42861	0.11429	47.499	0.1%

Analysis of Variance

Source of Variation	Degrees of Freedom	S.S.	P.
Regression	3	1658.6391	0.1%
Residual	51	35.0420	
Total	54	1693.6811	

of water lost from the eggs (independent of temperature). Survival-rate also was closely associated with temperature, independent of loss of weight, as also was shown in the analysis of variance.

The first partial regression of duration of incubation period (Y_2) on the four independent variates showed that original weight (x_1) contributed practically nothing to the variance of Y_2 and so was discarded. Results from the second analysis are shown in Table 6.

The analysis of variance shows that the regressions were very significant and accounted for 98 per cent. of the total variance of Y_2; only two per cent. of the variance of the dependent variate could be attributed to "error". Temperature was clearly the most important independent variate and for each degree Centigrade increase in temperature (within the temperature range of the experiment) the incubation period decreased by three days. The amount of water that the eggs lost also had an influence on the speed of development; for each 0.1 mg lost by a group, the incubation period was increased by one hour. When _O. fasciculata_ eggs were exposed to different amounts of evaporation it was found that larvae emerged last at the driest level, probably because the lowering of the water content of the eggs reduced the rate of metabolism and so retarded development (Wigglesworth, 1950). Increased speed of development associated with increased temperature was expected and will be discussed later.

Two other experiments were done at the same time as the previous experiment (2a). One was done to find whether eggs from Kalangadoo differed from those from Mil Lel (used in Experiment 2a) in their ability to survive dry conditions. There were not many eggs from Kalangadoo and only one temperature (16.9°C) was used. There were five levels of evaporation and a control level, and at each level were four groups of 25 eggs each. The experiment started when the eggs were at the same stage of development as in Experiment 2a, the eggs were exposed for the same length of time as those at 16.9°C in the other experiment and the same methods of exposure were used.

In order to study the relationship between the influence of dryness and the stage of development of the eggs, the third experiment was done with eggs which had completed 45 per cent. of their embryonic development. Three temperatures (20.1°, 16.8° and 13.4°C) were used and there were four levels of evaporation and a control level at each temperature. The total evaporating power of the air was the same at any one level at each of the temperatures. Each treatment contained four groups of 25 eggs each, from Mil Lel, and the same method of exposure was used as in Experiment 2a.

Each of these three experiments (Experiment 2a - eggs from Mil Lel which had completed eight per cent. of their embryonic development; 2b - eggs from Kalangadoo at the same stage of development; 2c - eggs from Mil Lel which had completed 45 per cent. of their development) was analysed separately by probit analysis. The relationship between the amount of evaporation to which the eggs were exposed (measured as saturation deficit times length of exposure) and survival-rate was sigmoid and there was a different curve for each temperature. This relationship has been shown by other workers and is discussed by Andrewartha and

Birch (1954, p. 265). As the "dosage-mortality" curve was sigmoid and approximated that derived from a normal distribution, it was permissible to analyse the data by probit analysis; with this analysis the sigmoid curve becomes a straight line (Finney, 1947).

As a first step, data from each temperature were taken in pairs and the estimates of LD 50 and b were compared. For example, tests of parallelism showed that regression lines for the two temperatures in Experiment 2a were parallel and the values for LD 50 did not differ significantly. Also, regression lines for the two lower temperatures of Experiment 2c were parallel but their values for LD 50 differed significantly. Both the regression coefficient and value for LD 50 at 20.1°C differed from those for 13.4° and 16.9°C. Moreover, a further test of parallelism showed that the regression line for 16.9°C of Experiment 2a did not differ from the one for Experiment 2b and so it was decided to combine the data from all of the temperatures but 20.1°C of Experiment 2c (see Finney 1947, Chapter five). In this way it would be possible to study the ability of eggs in different stages of development and from different places to survive at a given level of evaporation, and their response to small and large amounts of water-loss; in other words, to see if there were significant differences between the values for LD 50 or the regression coefficients (b).

Results of the combined probit analysis are given in Table 7 and the probit regression lines are shown in Figure 5. The test of parallelism showed that the regression coefficient, which determines the slope of the line, was the same for each temperature. This value was

TABLE 7

COMBINED PROBIT ANALYSIS FOR LABORATORY EXPERIMENTS

2a, b AND c

2a						2b		
13.4°C			16.9°C			16.9°C		
Evaporation*	Death-rate %	Probit	Evaporation	Death-rate %	Probit	Evaporation	Death-rate %	Probit
83.26	78	5.77	80.90	85	6.04	90.14	70	5.52
71.91	45	4.87	69.34	29	4.45	85.52	83	5.95
60.55	28	4.42	57.78	17	4.05	78.59	35	4.61
45.42	2	2.95	46.23	7	3.52	64.72	27	4.39
34.06	1	2.67	34.67	4	3.25	60.10	17	4.05
22.71	5	3.36						
b	0.0704 ±0.0063			0.0704 ±0.0063			0.0704 ±0.0063	
LD 50	74.5176 ±1.2117			74.5176 ±1.2117			74.5176 ±1.2117	

* As indicated by the product of saturation deficit (mm Hg) and length of exposure.

Analysis of x^2 for Test of Parallelism

	d.f.	S.S.	M.S.	P.
Parallelism of Regressions	4	8.7106	2.1777	NS
Residual heterogeneity	13	39.7618***	3.0586	
Total	17	48.4724		

2c								
13.4°C			16.9°C			20.1°C		
Evaporation	Death-rate %	Probit	Evaporation	Death-rate %	Probit	Evaporation	Death-rate %	Probit
82.68	96	6.75	60.32	67	5.44	61.16	100	
72.83	71	5.55	45.85	18	4.08	45.44	92	6.41
61.02	51	5.05	33.78	2	2.95	34.08	39	4.72
45.28	9	3.66						
0.0704 ±0.0063 59.9986 ±1.4716			0.0704 ±0.0063 59.9986 ±1.4716			0.1476 ±0.0213 35.97 ±0.806		

Fiducial Limits

Differences Between:	M	P.
1a 16.9° and 1b 16.9°C	6.3260 ±3.0085	NS
1a 16.9° + 1b 16.9° and 1a 13.4°C	3.6916 ±2.6432	NS
1a 13.4° and 1c 13.4°C	9.6140 ±2.9472	5%
1a 16.9° + 1b 16.9° and 1c 16.9°C	18.9893 ±2.7759	5%
1c 13.4° and 1c 16.9°C	5.6837 ±3.1916	NS
1a 13.4° + 1a 16.9° + 1b 16.9° and 1c 13.4° + 1c 16.9°C	14.5190 ±1.9059	5%

small, indicating a rather wide range between the amount of evaporation needed to kill a few eggs and to kill most of them. The position of the lines for 2a 13.4°, 16.9°C and 2b 16.9°C, in relation to the ability of the eggs to survive loss of water (values for LD 50), did not differ and so only one line was needed for the three temperatures. Although the regression coefficient for 2c 13.4° and 16.9°C was the same as for the previous three temperatures, the eggs were more susceptible to dryness and the value for mean tolerance (LD 50) differed significantly from the LD 50 for the other temperatures. However, the values of LD 50 for these two temperatures did not differ between themselves and the one regression line shows the relationship between exposure and the probit of kill. The value of the regression coefficient for 2c 20.1°C was much larger than for any of the other temperatures and so the regression line for that temperature has a steeper slope.

The positions of the three regression lines show that eggs in which only eight per cent. of embryogenesis had occurred (whether from Mil Lel or Kalangadoo) were much more resistant to water-loss than were eggs in which 45 per cent. of embryogenesis was completed; however, the lethal influence of short and long exposures to dryness was the same and so the lines are parallel. Also, eggs at 2c 20.1°C differed in their response to short and long exposures and were more susceptible to dryness, and the regression line for this temperature has a lower value of LD 50 and a steeper slope than any of the other temperatures.

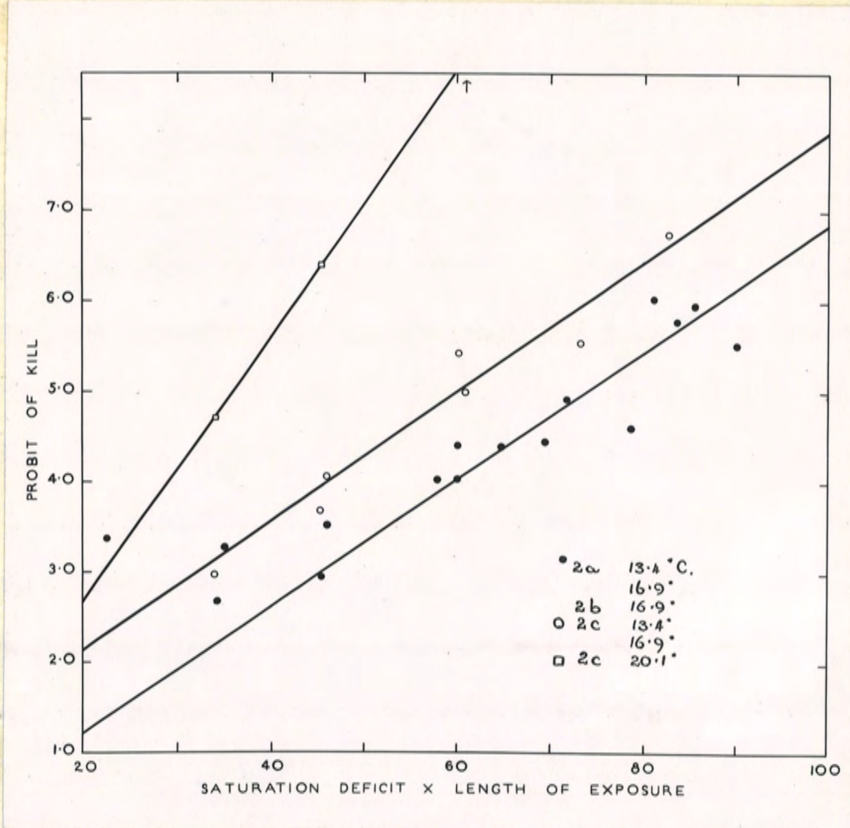

Fig. 5. Probit regression lines showing relationship between probit of kill and amount of evaporation to which O. fasciculata eggs were exposed.

(iii) Survival-rate of Eggs when Different Proportions of Water are Lost

The previous experiments showed that there was a close relationship between loss of water from O. fasciculata eggs and the numbers of larvae which emerged, and this experiment was done to study more precisely the relationship between the amount of water lost and survival-rate of the eggs. Ten groups of 200 eggs each were selected at random from eggs that had completed 15 per cent. of their embryogenesis.

One group was weighed and then oven-dried to obtain the moisture content, which was found to be 61.6 per cent. of the total weight of the eggs. Eight of the remaining groups were weighed and placed in individual wire-gauze cages in a desiccator in which the air was maintained at a relative humidity of 65 per cent. and the desiccator was placed in an incubator at 13.4°C. This combination of relative humidity and temperature gave a saturation deficit of 4.06 mm of mercury. The remaining group was weighed and eggs were put in a wire-gauze cage resting on a stand in an airtight jar containing water. Having the original weights of the groups, and an estimate of the amount of water in each, it was possible to determine how much weight any one group should lose to correspond to a proportional loss of water, e.g., one group weighed 19.43 mg before exposure, of which 11.97 mg were water. A loss in weight of 3 mg, then, would correspond to a 25 per cent. loss of water.

It was not known how much water the eggs could lose without damaging the developing embryos but from the work done on the eggs of other insects it was expected that few larvae would emerge when half the water content of the eggs was removed; the amount of water lost from the eggs in this experiment ranged from seven to fifty per cent. of their water content before desiccation. The method used was to weigh the groups at intervals and when the eggs in any one group had lost a certain proportion of their water they were placed on moist blotting paper in a petri dish and the dish was returned to 13.4°C.

Eggs used in this experiment were from Mil Lel and the same sort of experiment also was done with eggs from Kalangadoo; five groups of 100 eggs each were exposed to water-loss, one group remained in nearly saturated air and one group was oven-dried. The experiment started when the same amount of embryonic development had occurred as with the Mil Lel eggs (15 per cent.), eggs were at the same temperature, and the same method of exposure was used.

The number of larvae that emerged from each group of exposed eggs was recorded and data for the two lots of eggs were analysed separately by probits. Values for LD 50 and b were almost the same for eggs from Mil Lel and Kalangadoo and so a combined probit analysis was done; results are given in Table 8 and the probit regression line is shown in Figure 6. A 43 per cent. loss of water resulted in a fifty per cent. mortality and the small value for b shows that there was a rather wide range between the level where few larvae emerged and where most emerged.

(iv) Influence of Rate of Evaporation on Survival-rate

The rate at which O. fasciculata eggs lose water may have an influence on their ability to survive dry conditions, and this experiment was designed to study the survival-rate of eggs when exposed to the same amount of evaporation but when the rate at which the water was lost differed. There were seven rates of evaporation, and one lot of eggs, the controls, were kept at nearly 100 per cent. relative humidity. Four groups of 25 eggs each were at every level and all were at 13.4°C. The seven rates of evaporation with their lengths of exposure, saturation deficits and other data are given in Table 9.

TABLE 8

COMBINED PROBIT ANALYSIS FOR LABORATORY EXPERIMENT DONE TO STUDY INFLUENCE OF THE PROPORTION OF WATER LOST ON SURVIVAL-RATE OF EGGS

Eggs from Mil Lel			Eggs from Kalangadoo		
Water Lost (%)	Death-rate		Water Lost (%)	Death-rate	
	%	Probit		%	Probit
50	64	5.36	61.5	88	6.18
45	61	5.28	47.5	84	5.99
35	27	4.39	39.5	29	4.45
30	19	4.12	35.5	14	3.92
25	8	3.59			
20	6	3.44			
10	4	3.25			
7	5	3.36			
	b	0.0692 ±0.0091			
	LD 50	43.1980 ±0.9834			

Analysis of x^2 for Test of Parallelism

	Degrees of Freedom	S.S.	M.S.	P.
Parallelism of regressions	1	6.5928	6.5928	NS
Residual heterogeneity	8	43.3445***	5.4181	
Total	9	49.9373		

TABLE 9

INFLUENCE OF RATE OF EVAPORATION ON SURVIVAL-RATE OF THE EGG

Level of dryness (in the order of rate of evaporation)	Saturation deficit (mm Hg)	Relative humidity (%)	Length of exposure (days)	Mean emergence (Percentage emergence transformed to degrees)
0	-	100	33	76.8
1	2.29	80	32	65.1
2	2.79	77	26	54.2
3	3.56	70	20	48.3
4	4.06	64	18	40.7
5	5.08	56	14	42.9
6	8.89	22	8	21.1
7	10.41	8	7	26.4

Least significant difference between means of levels of evaporation

5% level	5.05
1%	6.84
0.1%	9.17

This Table shows that the intensity of treatment ranged from a long exposure to a high humidity (100 per cent.) to a short exposure to low humidity (8 per cent.).

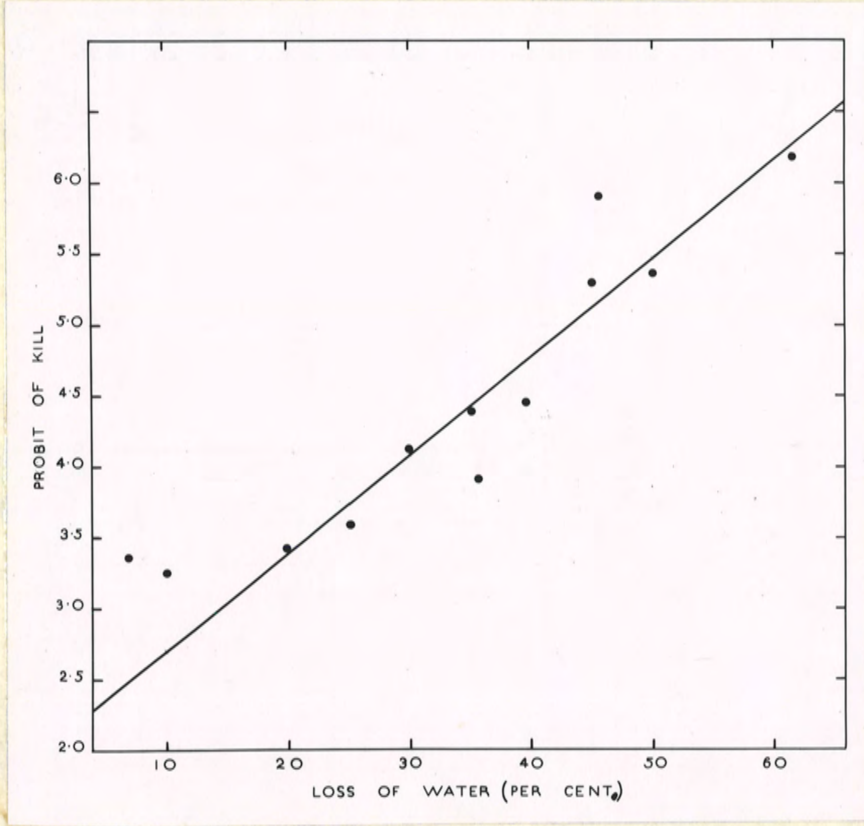

Fig. 6. Probit regression line showing relationship between probit of kill and proportion of water lost by the eggs.

Eggs were placed in wire-gauze cages over sulphuric acid solutions in airtight glass jars and at the end of treatment were removed and placed on moist blotting paper. The eggs had completed 15 per cent. of their development at the beginning of the experiment.

A record was kept of the number of larvae which emerged from each group and the mean emergence (in degrees) is given in Table 9.

The rate of evaporation had a significant influence on the number of larvae which emerged ($P = 0.1\%$)(see Table V in the Appendix), although the amount of evaporation was practically the same at rates 1 - 7; as the intensity of evaporation increased fewer larvae emerged. The only inconsistencies were between the mean survival-rates of 4 and 5, which did not differ significantly, and rates 6 and 7, where more larvae emerged at the higher rate of evaporation (just significant at $P = 5\%$).

In other words, most larvae emerged from eggs that were at a moist level for a long time, and as the rate of evaporation increased fewer larvae emerged, although all groups were exposed to the same amount of evaporation. However, it is not possible from this experiment to say precisely what caused fewer larvae to emerge as the rate of evaporation increased. This could have been;(1) damage to the developing embryos and as the rate of water loss increased more died; (2) eggs at the driest level were exposed for a small proportion of their embryonic period while eggs at the wettest level were exposed for a large proportion of their embryonic period and the difference in the stages of development could have had an influence on survival-rate; (3) as the air became drier the chorion of the eggs may have changed in texture so that even healthy larvae could not break through.

One way in which the influence of these factors might be separated would be to do the experiment at a temperature where there was little or no embryonic development and where the levels of evaporation were arranged so that the eggs would be exposed for only a short time. Also, eggs would be weighed individually before and after exposure to find how much water was lost. Where no larvae emerged, eggs would be examined to see if there had been any development and whether there were healthy larvae which had been unable to break through the chorion. With this design the eggs would be exposed during the same stages of embryogenesis to about the same amount of dryness and the intensity of dryness (rate of loss) would be the variable. The weighings would show what proportion of water was lost at the various levels of dryness. Another design would be similar to this but each egg would be removed after it had lost a definite amount of water (say 20 per cent. of the average moisture content of the eggs). With this design the eggs would be exposed to different amounts of dryness but the water-loss would be the same. Further experiments to study the influence of rate of water-loss on survival-rate of _O. fasciculata_ eggs were not done because no balance was available for weighing individual eggs accurately.

In all of the experiments where groups of eggs were weighed, after the eggs were removed from exposure to evaporation they were weighed, placed on moist blotting paper and then weighed 48 hours later to find if they had taken up any water. In no case was there any evidence that the eggs were able to replace water lost during exposure. A few groups out of a total of 155 used in the experiments increased very slightly in weight and it was thought that in these few cases not all of the external water had been removed from the eggs before they were weighed. For weighings done to study water uptake, eggs were taken from the moist blotting paper and were not weighed until the surface film of water had evaporated - this could be determined easily, for the eggs with the film of water were shiny black while those without the water were a dull black.

Results from the laboratory experiments with eggs of O. *fasciculata* described in section (d) suggest that under natural conditions there would probably be a higher survival-rate among eggs laid early in September than in October. Eggs laid at the start of the flight season would develop while the environment was relatively moist, and when older and more susceptible to water-loss, would be in the field during late September and early October. Eggs laid at the end of the flight season would develop while the environment was becoming increasingly unfavourable (dry) and when older would be in the field during late November.

Eggs which are not in contact with free water may be expected to lose water (this loss cannot be regained when free water becomes available) and such a loss has an important influence on the survival-rate of the eggs. It would seem that eggs located under a mat of herbage stand less chance of losing water than eggs not in such a protected situation. Also, if eggs under the herbage should be exposed to evaporation, it is very likely that the rate at which water was lost would be lower than with more exposed eggs, and so there would be a higher survival-rate among the sheltered eggs.

VI INFLUENCE OF TEMPERATURE AND MOISTURE ON SURVIVAL-RATE OF THE LARVAE

(a) Field Observations and Experiments

Most eggs of O. fasciculata are laid under pasture, and for a fortnight to three weeks larvae live among surface debris and often are found under a communal network of silken webbing. The extent of the unfavourable weather to which they may be exposed seems to depend largely on the quantity and type of pasture and surface debris; conditions unfavourable for the egg should be unfavourable for the young larva. The field experiment described in V (c) showed that there was a higher survival-rate of O. fasciculata where there was more pasture, and the conclusion formed was that the thicker pasture acted as a buffer to protect the insect against unfavourable temperatures and dryness.

After several weeks on the surface of the ground, the larva makes a subterranean burrow with a silken cover which would provide some protection against unfavourable weather. From early summer until the end of the feeding stage the tunnel is increased in depth, providing the larva with increased protection against unfavourable weather. But from the time tunnelling starts until early summer the larva is within one inch of the surface and might be exposed to dry conditions or unfavourable temperatures.

(i) Influence of Surface Cover and Insect Density on Survival-rate of the Larvae

At the same time as the field experiment described in V (c) a similar experiment was done to study the ability of larvae to survive from the time they started tunnelling until they were fully grown. There were two types of pasture (untouched and mown), five levels of insect density (ranging from 50 to 1,000 eggs per square yard), and four replicates. The experimental area was covered with hessian until larvae were established in tunnels to provide them with additional protection against evaporation while on the surface of the ground. Analysis of the data obtained from sampling done in June 1952, when larvae were fully grown, showed that there were no significant differences between survival-rates at the two types of pasture or the five levels of density. Although there were more larvae in the untouched plots than the mown plots, this could not be attributed to any difference in the amount or type of pasture cover on the plots (see Table VI in the Appendix).

The spring and summer of 1951-52 were very dry and it was considered that part, at least, of the failure to obtain significant results from this experiment was due to the high death-rate among larvae; the mean survival-rate on unmown plots was eight per cent. and was five per cent. on mown plots. Also, the number of replicates (4) may not have been sufficient for this type of field experiment.

Another experiment, similar to the preceding one, was done in 1952 to study the survival-rate of larvae established in tunnels in the field. It was set out adjacent to the previous one and the same general technique was used; there were two types of pasture (untouched and mown), four levels of insect density (ranging from 150 to 600 eggs per square yard), and seven replicates. Analysis of the data obtained from sampling in June, 1953, showed that the only significant main effect was type of pasture ($P = <2\% >1\%$); there were more larvae on the untreated plots than on the treated ones (see Table VII in the Appendix).

Because of the high over-all death-rate in the 1951 experiment an attempt was made in this experiment to provide more favourable conditions for the larvae by watering the plots in mid-January. More watering would have been done but for the fact that the experiment was located 300 miles from the Waite Institute laboratory and frequent trips could not be taken. There was a slight increase in the amount and spread of rain during the spring and summer of 1952-53 as compared with the previous year but in the district where this experiment was carried out the weather was considered to have been just as unfavourable for *O. fasciculata* during this year as it had been the year before. Even with additional watering in January there was a high death-rate in all plots of the experiment; the mean survival-rate on untreated plots was 11 per cent. (8 per cent. in 1951) and 5.5 per cent. on treated plots (5 per cent. in 1951).

Results from this experiment indicate that the type of pasture in which *O. fasciculata* larvae are living has an influence on their survival-rate. As with the eggs and larvae on the surface of the ground, larvae established in subterranean tunnels seem to have a better chance to survive where the ground is covered with a fairly dense mat of pasture. The herbage in this case would serve mainly as a buffer between larvae and the heat and dryness outside, and partly as food.

In the field experiments described here the only case where there was any evidence of deaths caused by starvation was in the highest level of the first experiment. Even if deaths here had been caused by overcrowding, analysis of the data showed that the survival-rate at all levels was the same, i.e., the same proportion of larvae survived where there were 1,000 per square yard as where there were only 50 per square yard.

(ii) Influence of Moisture and Type of Food on Growth and Activity of Larvae

Although O. fasciculata larvae are in the field from about October to July (spring-winter), field observations suggest that for much of this time they are relatively inactive. From the time the larva becomes established in its tunnel (ca. mid-November) until about April, there is a slow, steady increase in growth and a corresponding increase in the depth and width of the tunnel but the growth during this, the warmest part of the year, is very little compared to the rapid growth which occurs from about April onwards, when the temperature is much lower. This very great increase in the growth of the larva appears to be related to the break of the season. At this time several important changes occur in the environment of the larvae. The soil becomes moist and this in turn causes a rapid germination and growth of annual grasses and clovers, providing green food for the larvae. Also, the air becomes more humid and as autumn progresses the temperature falls and the days become shorter. It is not known exactly how these changes stimulate the larvae to greater activity, or which are more important, but the experiments described below throw some light on this problem.

A series of field experiments was done during the autumn of 1954 to study the influence of moisture and food on the growth and activity of O. fasciculata larvae. The general procedure was that larvae were dug up, weighed, desiccated, reweighed to find how much water was lost, replaced in individual tunnels in the paddock, given one of several treatments of moisture and food supply, removed after a period and reweighed to find if weight had been gained or lost during the treatment.

This work was done in the autumn so that larvae would be easy to find in the field and large enough to handle without difficulty. Also, it had been hoped to "tease" larvae from their tunnels with a piece of straw, and, after desiccation, return them to their original tunnels. However, "teasing" was a failure (too slow) and larvae had to be dug out and later returned to artificial tunnels in the soil. Twenty larvae were used for each treatment and each larva was placed in a cellophane container, weighed on a torsion balance (to 0.01 mg) and the container was then placed on a hook in the lid of a glass jar containing a sulphuric acid solution. Preliminary weighings showed that an exposure of about four hours was needed to reduce the weight of the larva by about 20 per cent. and this loss of weight would not be harmful. Air inside the glass jars was circulated by pumping a rubber syringe attached to the lid of the jar as soon as larvae were placed in the jar and at regular intervals afterward. After desiccation, each larva was reweighed, together with its faeces. Larvae were then removed from their cellophane containers and placed in vertical holes in a cleared portion of the paddock. The holes, made with a steel rod, were the same depth and diameter as actual O. fasciculata tunnels. The location of each larva was recorded with a small numbered peg and the group of larvae then received one of the treatments to be described later. After one or two nights in the tunnels, larvae were removed, placed in individual cellophane containers and weighed; this last weighing showed whether the larvae had lost or gained weight during the time they were in the tunnels and exposed to a particular condition of moisture and food supply.

Thirteen groups of larvae were treated during a period of almost three weeks but the only ones to be discussed in detail here are the eight in which significant results were obtained. Heavy rains fell midway through this work and so it was possible to compare the activity and growth of larvae before and after this break of season. The treatments were done on a well-drained terra rossa soil at Mil Lel and on a low-lying meadow podsol soil north-west of Kalangadoo. A record of temperature and relative humidity during these studies was obtained from a thermo-hygrograph placed in the paddock alongside the treatment areas.

Treatment 1. (Mil Lel)

Because larvae were removed from tunnels and, after desiccation, were placed in artificial tunnels, there would be a certain amount of silk spinning activity while the larvae re-established themselves. Treatment 1 was done to find how much weight larvae lost because of this disturbance so that a "correction factor" could be applied to the other treatments. Twenty larvae were dug up, weighed, and placed in individual tunnels in the soil, from which surface growth had been removed. Over the entrance to each tunnel was placed a leaflet of subterranean clover to prevent the larvae from leaving their tunnels in search of food. A double thickness of hessian bags was then placed over the area containing the larvae. Forty-eight hours later the bags were removed, the amount of clover leaflet eaten by each larva recorded, and the larvae were dug up and weighed; three larvae had left their tunnels and so were discarded. After adjustments were made for the amount of food eaten by each larva, a "t" test was done to determine the significance of the mean change in weight of the group and Table 10 (this table includes pertinent data of the eight treatments to be discussed) shows that larvae lost, on the average, 8.1 per cent. of their weight during

TABLE 10

DATA FROM FIELD EXPERIMENT ON INFLUENCE OF MOISTURE AND FOOD ON GROWTH AND ACTIVITY OF THE LARVA

Treatment	n	$\bar{\bar{x}}$ (per cent. loss or gain in weight)	$\Sigma(x-\bar{x})^2$	$\frac{S_2}{n}$	t	P.
1	17	- 8.10	1079.85	3.97	4.07	0.1%
2	14	- 9.25	735.85	8.01	3.27	1%
3	15	-10.85	463.23	6.18	4.36	0.1%
4	16	- 6.59	1282.16	9.31	2.16	5%
5	6	22.74	506.54	20.85	4.97	1%
6	15	14.25	847.41	8.00	5.04	0.1%
7	10	10.97	434.78	8.80	3.70	1%
8	16	7.54	1073.93	8.44	2.60	2%

the forty-eight hours of exposure; this was clearly a significant loss and must be attributed largely to the activity of larvae in establishing themselves in the new tunnels.

The results were used as a correction for the results of later experiments. The mean loss of weight associated with activity (silk spinning, establishing new tunnels) was subtracted from the gross loss or gain of weight determined in the later experiments and the variance was added to the variance of the other treatments.

The two nights that larvae were in tunnels were mild (lowest temperature recorded was 16.5°C) and without rain but there had been a heavy dew. The hessian bags prevented the deposition of dew near the tunnel entrances; the soil was damp but there was no evidence of free water on the area when the bags were lifted early next morning.

Treatment 2. (Nil Lel)

Larvae in this group were placed in tunnels over which was placed a layer of straw and four layers of hessian bags. The straw was used to prevent too much surface movement of the larvae and the bags were to prevent any dew which might form from becoming available to the larvae. Under these conditions the only moisture available to the larvae would have been atmospheric or in the straw. The mean loss of weight during desiccation was 19.77 per cent. Larvae were placed in tunnels one afternoon and were dug up the following morning. All of the remaining larvae (14) had lost further weight; the mean loss was 9.25 per cent. of their weight before being placed in the tunnels, and this loss was significant at P = 1%. The night when this group was exposed was cool and windy; the lowest temperature reading was 11°C, the highest humidity reading was 88 per cent. relative humidity and no dew fell. Under these conditions larvae continued to lose weight while in the tunnels.

This treatment was repeated at Kalangadoo and larvae were left for two nights instead of one; here also they lost weight while in the tunnels but the mean loss, 3.0 per cent. of their weight before treatment, was not significant (P = 20%). The two nights that larvae were in tunnels were foggy and there were heavy dews.

Although the Kalangadoo treatment was inconclusive, larvae did continue to lose weight and this, together with the significant results from Mil Lel, does indicate that _O. fasciculata_ larvae probably cannot absorb water from vapour in the air, as do some insects (Wigglesworth, 1948) and, more important, during dry periods when no green feed is available, larvae might run the risk of using up their moisture reserves if they are too active.

Treatment 3. (Mil Lel)

Larvae in this group received no moisture in the form of free water but were given green herbage to eat. After desiccation, larvae were placed in tunnels in the soil and the tunnel entrances were covered with freshly cut subterranean clover and Wimmera rye-grass, and the area covered with bags. Of the twenty larvae which were dug up, three escaped from their cellophane cages while being desiccated and two were lost from their tunnels. The larvae were left overnight in their tunnels and were dug up and weighed the following morning. Although fresh green feed had been available, larvae lost an average of 10.85 per cent. of their weight during the treatment and this loss was significant (P = 0.1%). It appears that green food alone is not sufficient to cause greater activity and feeding among the larvae. The night when larvae in Treatment 3 were in tunnels was mild (minimum temperature 13°C) and a slight amount of rain fell but it did not penetrate the bags and so would not have been available to the larvae.

Treatment 4. (Kalangadoo)

Larvae in this group received the same treatment as in 3; after being desiccated in the glass jar, when they lost an average of 13.58 per cent. of their weight, larvae were placed in tunnels in the soil and the area was covered with freshly cut clover and rye-grass and bags. This group was left for two nights before being dug up and weighed. Here, also, larvae lost weight, even though fresh green food had been available for two nights; the grass and clover were still moist and green at the end of the treatment. During the time in the tunnels, larvae lost an average of 6.59 per cent. of their weight, and this was significant (P = 5%).

Heavy dew formed on each of the nights that the larvae were in tunnels but it did not penetrate the bags; the nights were cool and the lowest temperature recorded was 10°C.

Results from this treatment were the same as in 3; when abundant green feed, but no water, was available larvae continued to lose weight while in the tunnels.

Treatment 5. (Mil Lel)

Because larvae in the previous two treatments continued to lose weight even when green feed was available, the treatment was repeated in 5 but the area containing larvae in tunnels was not covered with bags so that larvae might have access to water in the form of rain or dew. After desiccation, fifteen larvae were placed in tunnels, green feed was provided and the following morning nine were dug up and weighed; the mean weight of the larvae had not changed significantly during the time they were in the tunnels. The remaining six larvae were not dug up until the second morning and these had gained a significant amount of weight during their 48 hours in the tunnels; the mean increase in weight was 22.74 per cent. and this was significant at the one per cent. level.

During the first night of exposure there was no rain or dew and weighings showed that the larvae did not change significantly in weight. During the second night, when only six larvae were left of the group, a light rain fell, and as the treatment area was not covered, this rain would have fallen onto the area. The six larvae gained significantly in weight, and it is considered that the moisture encouraged greater activity and thus a greater uptake of water and food.

Treatment 6. (Mil Lel)

The results from Treatment 5 showed that water seemed to have an influence on the activity and change of weight of _O. fasciculata_ larvae. Therefore, in Treatment 6, larvae were desiccated in the glass jar, losing 11.81 per cent. of their weight, placed in tunnels, provided with a covering of straw, and then the treatment area was watered with a knapsack spray. Larvae were left in the tunnels overnight and then were dug up and weighed; this weighing showed that when larvae were provided with straw from dead grass and moisture they increased significantly in weight. The mean increase was 14.25 per cent. and this was significant at the 0.1 per cent. level. It appeared that the presence of moisture caused increased larval activity and feeding and thus an increase in weight. The night that larvae were in the tunnels was cold (minimum temperature reading was 6°C) and there was no rain of dew.

The treatments described so far were done during early April, before any substantial amount of rain had fallen. The surface soil was below the wilting point for herbage plants and although there had been some germination of subterranean clover in March this growth had not persisted because there was no following rain. In mid-April there was a heavy fall of rain (184 points in two days) which caused a very rapid germination and growth of annual clovers and grasses. Later in the year, when rainfall records were examined, the mid-April rains were recognised as the break of the 1954 season. The two treatments to be discussed now were done after the fall of rain, when the environment would have been very favourable for the larvae; the soil was moist and there was abundant green feed.

Treatment 7. (Kalangadoo)

After exposure to desiccation over the acid solution in the jar, when the mean loss of weight was 19.88 per cent, fourteen larvae were placed in tunnels in the soil and the treatment area was covered with a layer of straw from dead grass. After a few showers of rain had fallen on the area it was covered with bags. Larvae were left overnight and dug up the following morning; six had been lost during the desiccating and four were lost during the digging. Each of the ten larvae remaining had gained weight overnight; the mean was a 10.97 per cent. increase and this was significant (P = 1%). This result was the same as in Treatment 6, where the treatment area was watered with a knapsack spray. The moist conditions caused an increase in weight, even though there was no green feed.

Treatment 8. (Mil Lel)

Larvae in this group lost an average of 15.89 per cent. of their weight during desiccation. They were then placed in tunnels and the treatment area was covered with fresh, green grass and clover which were wet from recent rains, and then with bags. After 48 hours the sixteen larvae remaining were dug up and weighed. All but two had gained weight during this treatment; the mean increase was 7.54 per cent., which was significant (P = 2%). This result was the opposite of those obtained from Treatments 3 and 4; with green feed only, larvae continued to lose weight, but with green feed and free water they increased significantly in weight.

Another group was set out in which larvae, after losing a mean of 15.93 per cent. of their weight over the acid solution, were placed in tunnels, given a treatment of green feed but no free water and the treatment area was covered with bags. Larvae were dug up 48 hours later and weighing showed that their average weight had increased by 4.72 per cent.; this increase, however, was not significant ($P < 20\% > 10\%$). There had been an over-all gain in weight, however, as compared with a significant loss of weight when larvae received the same treatment before the rains.

It would appear from these experiments that during the autumn period, before substantial rains produce a growth of annual grasses and clovers, O. fasciculata larvae remain relatively inactive, probably because of the hot, dry conditions and the absence of green feed. When they are disturbed and have to construct new tunnels and/or webbing, a considerable amount of weight may be lost and, in this experiment, the loss was attributed mainly to silk-spinning (Treatment 1). During a dry period it would not be to the advantage of larvae to feed, for such activity, when only dead growth is available, probably would cause a loss rather than a gain in weight (Treatment 2). Even when green feed is available but the soil surface is dry and there is no free water, larvae could be expected to remain fairly inactive (Treatments 3 and 4). However, after a rain, or possibly a heavy dew, larvae become active and do more feeding because of the moist conditions. This increased activity occurs if green feed is available (Treatments 5 and 8) or if there is only dead growth (Treatments 6 and 7).

The results from Treatments 2, 3 and 4 seem to indicate that feeding of O. fasciculata larvae is controlled by moisture and that they remain relatively inactive during dry periods. This is a reasonable statement when it is noted that all twelve species of this genus in Australia are restricted to the wetter areas and probably are not adapted to living in dry situations. If O. fasciculata were so adapted, it might be expected that the larvae would behave as do some insects found in deserts, which obtain water by eating dead vegetation that has absorbed water from the atmosphere during the night (Buxton, 1924). Or they might eat large amounts of food, much of which is excreted undigested, to obtain the water it contains. But O. fasciculata would seem to do none of these things. Larvae remain relatively inactive in their burrows during summer and resume activity only after the soil has been wetted. The species persists in the area where it is found because the autumn rains are relatively reliable.

(iii) Studies on the Micro-environment Within a Larval Tunnel

At the same time as the experiments described in section (ii), studies were made of the micro-environment inside the tunnel of an O. fasciculata larva. Tunnels are covered with silk, to which are attached bits of herbage and soil, and it was thought that this cover, plus the fact that soil beneath the surface would be moister than on the surface, might keep the air inside the tunnel moister than the outside air. The amount of moisture in the air in the tunnel was determined by inserting a piece of paper treated with cobalt thiocyanate

(Solomon, 1945). The procedure used was to remove carefully the silken cover from a tunnel, remove the larva, insert a strip of treated paper, replace the cover, and after a time remove the paper, drop it in liquid paraffin to preserve the colour and obtain an estimate of the relative humidity of the air by comparing the colour of the paper with a series of standards. A larva was removed from its tunnel by inserting a small piece of straw which the larva grasped in its mandibles and then could be lifted out. The time needed for the papers to reach equilibrium depended on the temperature and humidity of the air in the tunnel and in this work the paper strips were exposed for at least thirty minutes. Cobalt thiocyanate papers are suitable for work above 50 per cent. relative humidity and standards were made for the 50 - 100 per cent. range, at intervals of 5 per cent. At the lower end of the range the treated papers are blue with a trace of red. From 60 to 75 per cent. relative humidity the colours are blue-lilac, from 75 to 90 per cent. they are red-lilac and from 90 to 100 per cent. light red, although there still is a trace of blue. By interpolation it is possible to estimate the relative humidity to one per cent.

In order to obtain a comparison of moisture conditions inside the tunnel and on the surface of the ground, treated papers were placed in three situations for each observation - in the tunnel (paper strips were two inches long), on the ground under pasture and exposed on the surface. Papers on the surface were held in place with paper clips attached to corks. Tests were made near a thermohygrograph set out in the field and readings were taken from it at the end of each exposure period; readings from the exposed paper and the thermohygrograph should be nearly the same.

TABLE 11

RESULTS FROM STUDIES WITH PAPERS TREATED WITH COBALT THIOCYANATE

(Figures are % R.H.)

Date		Time	Tunnel*	Sheltered	Exposed	Thermohygrograph
March	31	5.45-6.45 p.m.	85-95	83	81	-
"	31	7.45-8.15 p.m.	88-92	92	88	90
April	1	6.45-8.45 a.m.	85-92	65	58	69
"	1	10.45-11.30 a.m.	60-96	-	-	49
"	1	2.50-3.20 p.m.	55-97	-	-	44
"	2	11.15-11.45 a.m.	80-97	-	-	70
"	2	4.00-5.00 p.m.	83-97	82	72	78
"	3	7.15-8.00 a.m.	-	100	98	99
"	5	11.45-12.30 p.m.	90-97	65	53	54
"	9	1.15-2.45 p.m.	98 full length	81	79	80
"	10	1.45-3.15 p.m.	88-98	78	65	68
"	11	1.15-2.00 p.m.	80-98	65	58	59
"	11	5.00-5.30 p.m.	95-98	87	83	74
"	12	2.15-3.00 p.m.	77-98	76	<50	42

* The first figure is the reading at the tunnel entrance and the second figure is the reading near the bottom of the tunnel.

Results from a series of tests, given in Table 11, show that in all but three cases, readings obtained from treated papers on the surface of the ground were very close to readings obtained from the thermohygrograph; figures from the former method were slightly lower than those from the latter. This close relationship shows that the treated papers may be considered to give a reliable indication of relative humidity.

The driest air in the tunnel was at the entrance and the wettest was at the bottom; there was a steady increase in moisture down the tunnel. Tunnels were slightly more than two inches long and larvae averaged 0.9 inch in length so that when in the lower inch of its tunnel a larva would be surrounded by air nearly saturated with water vapour. Air under the pasture was drier than at the tunnel entrance (except for the evening observation on March 31), although in some cases this difference was slight. As would be expected, air in exposed positions was drier than air under the pasture.

(b) Laboratory Experiments

Field observations had suggested that unfavourable hot or dry weather during the time that the young larvae are exposed on the surface of the soil might prove harmful to them. In 1950 two small laboratory experiments were done with newly-emerged larvae to study the influence of temperature on the survival-rate of starving larvae.

In the first experiment, larvae were kept individually in 0.5 inch diameter glass tubes four inches long. In the bottom of each tube was a layer of plaster of Paris 0.5 inch thick, and above this was 0.5 inch of soil (a terra rossa from Mil Lel). The tubes were placed upright in moist sand, and soil in the tubes was kept moist by the movement of water from the sand through the plaster of Paris. In this way water did not have to be applied to the soil from above. After a larva was placed in a rearing tube, the open end of the tube was closed with a cotton wool plug. The trays of sand containing the tubes were placed in incubators; temperatures used were 25.2°, 20.8°, 16.9°, 12.8° and 6.0°C. Larvae were examined every eight hours and any deaths were recorded. The lowest temperature had to be discarded because soil in the tubes became too wet and all of the larvae were drowned; there had been no deaths at this temperature up to this time, which was after all larvae at the other four temperatures had died.

The mean survival period (in hours) for the four temperatures were: 25.2° (38.4), 20.8° (43.2), 16.9° (52.8), 12.8°C (73.6). The time at 12.8°C was longer than at any other temperature in the experiment ($P = 0.1\%$), and larvae lived longer at 16.9° than at 25.2°C ($P = 5\%$). Data are given in Table VIII in the Appendix. Thus, under the conditions of this experiment, an increase in temperature caused a reduction in the mean length of life of larvae. Even at the lowest temperature the length of life was very short and probably was caused by starvation; larvae were not exposed to dry conditions for they were living in damp soil, and the air in the tubes must have been nearly saturated with water vapour.

What may have happened in this experiment was that higher temperatures caused a greater activity of larvae, and, as no food was available, a corresponding reduction in the time before their sources of energy were exhausted. This suggests that under natural conditions there might be a high death-rate among newly-emerged larvae if the weather encouraged greater activity (warm and moist) and they did not obtain food within about two to three days.

In the second experiment newly-emerged larvae were placed on moist blotting paper in the bottom of a petri dish and the covered dishes were placed over water in desiccators standing in incubators. The same temperatures were used as in the previous experiment, in addition to 9.8°C. The mean survival periods (in hours) for the five temperatures were: 25.2°(23.2), 20.8° (38.7), 16.9° (49.8), 12.8° (67.9), 9.8°C (77.7). Significant differences between the means are given in Table IX in the Appendix.

At any one temperature larvae lived longer in the petri dishes than in the rearing tubes of the previous experiment. It was thought that this time would be shorter in the petri dishes for larvae were more exposed than in the tubes and the impression was that they were more active in the dishes. However, the over-all results of the two experiments were the same; as the temperature increased, the mean survival period decreased. The decrease is attributed more to starvation than to the harmful effect of temperature, although this conclusion cannot be proven from the results of the experiments.

(i) Influence of Temperature and Dryness on Survival-rate of Unfed, First-instar Larvae

In this experiment, a study was made on the influence of temperature and dryness on the survival-rate of unfed, first-instar larvae, because in nature, newly-emerged larvae might experience unfavourable temperatures and dryness while on the surface of the soil. Three temperatures were used (25.2°, 20.8° and 12.8°C) and at each temperature were four levels of evaporation, measured as saturation deficit (0.51 mm, 1.78 mm, 2.79 mm and 3.56 mm Hg). The wettest level was considered favourable for larvae.

Larvae were placed in individual cellophane tubes 0.5 inch long and the ends were plugged with cotton-wool. Tubes were placed in a wire-mesh basket resting on a glass stand over a sulphuric acid solution in an airtight glass jar which was placed in an incubator kept at the required temperature. Larvae were examined every eight hours and any deaths recorded; a larva was considered to be dead if it did not move when touched. The experiment was done in four parts because there were not enough larvae on any one day to provide sufficient replication. Larvae in all cases came from the same group of eggs. Groups 1 and 2 were separated by one day, Groups 2 and 3 by thirteen days and Groups 3 and 4 by one day. There were 25 larvae at each treatment in Group 1, 40 in Group 2, 20 in Group 3 and 20 in Group 4, i.e., a total of 105 larvae at each treatment. Table 12 gives the mean length of life (log hours) of larvae in the treatments and the analysis of the data are given in Table X in the Appendix.

Temperature had a very great influence on the length of life of larvae in this experiment; as in the two previous experiments, larvae lived longer at the lower temperatures. Significant differences between temperature means were: $12.8^{\circ} > 20.8^{\circ}C$ ($P = 0.1\%$), $20.8^{\circ} > 25.2^{\circ}C$ (2%).

The variance contributed by Groups also was significant and was caused by the longer life of larvae in Group 1; the mean of this Group was very much greater then the means of the other three Groups ($P = 0.1\%$), but the mean values of Groups 2, 3 and 4 did not differ significantly. No explanation can be given for this result. Any expected difference would have been between the first two and the last two Groups, because larvae in the latter Groups emerged about a fortnight

TABLE 12

MEAN LENGTH OF LIFE OF LARVAE WHEN EXPOSED TO DRYNESS

(Data are in logs)

Temperature (°C)	Length of Life		Mean Length of Life
25.2	18.1002		1.1313
20.8	19.4271		1.2142
12.8	22.8246		1.4265
	Min. diff. for signif.:	5%	0.0622
		1%	0.0852
		0.1%	0.1160
Groups			
I	17.0683		1.4224
II	14.4625		1.2052
III	14.1913		1.1826
IV	14.6298		1.2191
Levels of Evaporation			
0.51	15.4226		1.2852
1.78	15.6049		1.3004
2.79	14.7834		1.2319
3.56	14.5410		1.2117
	Min. diff. for signif.:	5%	0.0716
		1%	0.0982
		0.1%	0.1337

after those in the first Groups. Group 2 was started one day after Group 1, the same technique was used and larvae came from the same pool of eggs and yet larvae in Group 1 lived much longer than larvae in Group 2. There was no valid reason for discarding the data from Group 1 so they were retained.

The four levels of saturation deficit contributed little to the total variance in this experiment and the differences associated with this treatment could be expected to happen by chance five or six times in 100 trials. The five per cent. level of probability usually is taken as the minimum value for judging the results of experiments and as the value for saturation deficit was only very slightly beyond this point, a test of significance was done to find how the mean values of the four levels differed among themselves. This test showed that larvae lived longer at the wettest level than at the driest, and they lived longer at the second wettest level than at the two driest levels. Although the mean length of life was shorter at the wettest than the second wettest level, this difference was not significant. The influence of dryness was not as significant as the other two main effects but the results do suggest that as the air in which the larvae were living became drier the length of life became shorter.

The only significant interaction was that of temperature with Group. This means that the larvae in the Groups were not equally affected by temperature, while the non-significance of Groups with Saturation Deficit shows that larvae in the Groups responded in the same way to dryness.

A subdivision of the sums of squares contributed by the temperature x Group interaction showed that irregularities in the responses of larvae in Groups 2 and 4 caused this interaction to be significant, *i.e.*, their behaviour was significantly different from the behaviour of the four Groups combined. The temperature x (Group 2 vs. the other 3) interaction was significant at P = 1% and Group 4 was significant at P = 5%. The average response of larvae to increasing temperature was a decrease in longevity, but in Group 2 there was a significant *increase* in the survival period between 20.8° and 25.2°C. In Group 4 there was a very marked decrease in survival period between 20.8° and 25.2°C - much more than would have been expected. Just as it was not possible to explain the significant differences in longevity observed among the four groups, so no obvious explanation can be found for the unusual behaviour of the groups of larvae in relation to temperature, unless it was entirely fortuitous.

Results from this experiment suggest that an increase in saturation deficit caused a decrease in the longevity of the larvae, and at any one level of saturation deficit there was a decrease in the survival period as the temperature increased. The decrease associated with rising temperature may have been caused by the harmful effects of temperature alone (injury to larvae), by the warmer conditions causing an increase in the rate of respiration which would mean that larvae would use up their water reserves more quickly, or by temperature causing an increase in the activity of the larvae so that they would starve to death sooner. The two previous experiments showed that even when unfed, first-instar larvae were kept in a moist atmosphere and on a moist surface there was a decrease in length of life associated with increasing temperature. It would appear, then, that in this experiment the reduction in survival-period associated with increasing temperature was caused by starvation or actual injury to larvae, but the influence of these two factors cannot be separated.

(ii) <u>Influence of Water-loss on Unfed, First-instar Larvae</u>

Earlier experiments had shown that there probably would be a high death-rate among unfed, first-instar larvae if they were exposed to dry conditions or unfavourably high temperatures. In these experiments, however, larvae were exposed to a particular treatment until all were dead, and this is not a very precise method of determining the influence of unfavourable conditions on survival-rate. The experiment to be discussed in this section was designed to be analysed with probits, because the transformation to probits makes it possible to estimate the amount of evaporation needed to kill any particular proportion of the larvae.

At each of two temperatures (16.9° and 20.2°C) were four levels of evaporation, and a control treatment at 100 per cent. relative humidity. There were fifty larvae at each treatment and each larva was in an individual cellophane cage - the same technique was used as in the last experiment. Larvae were examined at intervals and when it appeared that about half the larvae had died at the mid-level of evaporation at each temperature all the larvae were removed from that temperature and placed in a moist environment at the same temperature in which they had been exposed. (At 16.9°C the length of exposure was 23 hours, and was 22 hours at 20.2°C) It was then possible to obtain counts of the number of larvae which did not survive at each treatment. The measure of each treatment was the product of saturation deficit to which larvae were exposed and the length of exposure. Separate analysès of data for the two temperatures showed that the slopes of the regression lines were almost the same, as were values for LD 50, and so a combined probit analysis was done; results of this analysis are given in Table 13 and the probit regression lines are shown in Figure 7. The lines were

TABLE 13

COMBINED PROBIT ANALYSIS OF DATA FROM LABORATORY EXPERIMENT ON UNFED, FIRST-INSTAR LARVAE

16.9°C			20.2°C		
Evaporation*	Death-rate		Evaporation	Death-rate	
	%	Probit		%	Probit
12.17	93	6.48	16.29	100	∞
9.24	57	5.18	12.10	95	6.64
6.81	45	4.87	9.08	70	5.52
			6.04	47	4.92
b		0.2825 ±0.0399			
LD 50		7.1324 ±0.5326			

* As indicated by product of saturation deficit (mm Hg) and length of exposure

Analysis of x^2 for Test of Parallelism	Degrees of Freedom	S.S.	P.	Fiducial Limits M.	P.
Parallelism of regressions	1	0.003	NS	1.0913 ±0.6729	NS
Residual heterogeneity	3	3.495	NS		
Total	4	3.498			

parallel and the value of the regression coefficient was large, showing that there was a rather narrow range between the exposure where few larvae were killed and where most were killed at each temperature. The value for LD 50 was very small when compared with the LD 50 for eggs exposed at the same temperatures, which suggests that larvae are much more susceptible to water-loss than are the eggs.

It was not possible to do laboratory experiments with later stages of the larvae because they are extremely difficult to rear in the laboratory. Various techniques were used but none was successful -

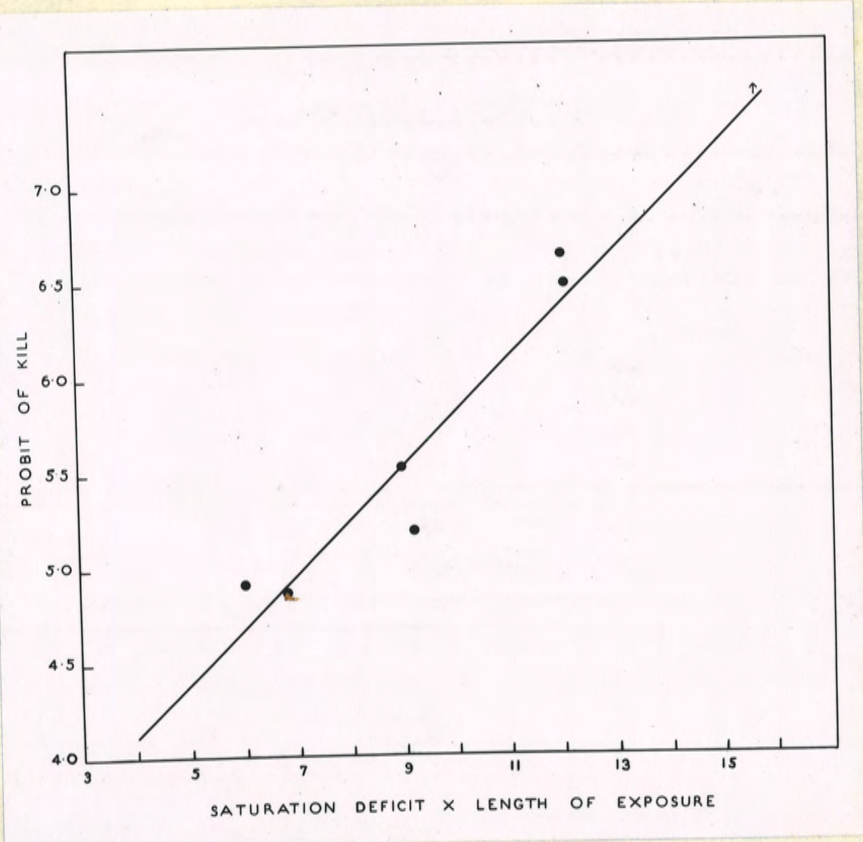

Fig. 7. Probit regression line showing the relationship between exposure to evaporation and probit of kill.

most larvae died during the second ecdysis. Plots of herbage containing larvae were taken to the laboratory from the South-East but in these cases most larvae died because there was no suitable way to protect them against the unfavourable weather (hot and dry) of the Adelaide plain.

(c) <u>Influence of Excess Moisture</u>

As the soil becomes soaked following a rain, the larva remains in its subterranean tunnel even when the tunnel is filled with water.

After about 24 hours the larva is forced out to escape drowning. If the surface of the ground is not covered with water the larva shelters in its covered runway and returns to its tunnel when the water has drained away. When the ground surface is covered with water the larva is able to escape drowning by crawling upward into vegetation extending above the water; if this sort of vegetation is not available the larva remains on the surface under the water and is drowned. A larva will not recover if it has been under water for 48 hours or longer. After the larva has been forced from its tunnel and covered runway the surface water may drain away before the insect has drowned; however, it then has to construct a new tunnel and until it is underground once again the larva is exposed to predators, of which birds are most important. Also, the larva would be weakened by the extreme wetness and might die from this exposure or it might be infected by pathogenic organisms which would be favoured by the wet conditions. Although no epizootics were seen, Martyn (unpublished report) found an outbreak of a fungal disease of _O. intricata_ in Tasmania and thought it was caused by the unusually wet season.

The first time during this study that _O. fasciculata_ larvae were found drowned was in late August, 1950, on a property near Kalangadoo. The soil here is a meadow podsol with a layer of clay about one to three feet under the surface, and the pasture was composed mainly of subterranean clover and Yorkshire fog. There had been severe damage by _O. fasciculata_ in the district during 1950 and in many places all of the herbage was eaten. The break of the season was late that year and rainfall during June and July was below average. However, rain during August was slightly above average and 109 points fell on the 29th and 30th. The Kalangadoo district was visited the following day and it was evident that a large proportion of the larvae living in the lower areas had been killed. Dead larvae, prepupae and pupae were found in pools of water on the surface of the ground as well as in areas where the water had drained away. Sampling of the area which had been flooded showed that there were no larvae still in tunnels - all had been forced to the surface by the water. Larvae on some of the higher land nearby were still established in their tunnels and had not been disturbed by the rain.

Two days later, following further rain (85 points), the property was examined again and similar conditions were seen. Land that had not been flooded on the 31st was very wet or under water and there were large numbers of larvae, prepupae and pupae on the surface of the ground. Magpies (Gymnorhina tibicen leuconota) and crows (Corvus spp.) were seen feeding in the flooded area and an examination of faeces showed large numbers of larval head capsules.

In this particular situation there was no vegetation extending above the water and larvae had no chance to escape the extreme wetness. After being forced from their tunnels, larvae which survived drowning sheltered under whatever cover was available but were unable to build new tunnels because the soil was too wet. From the number of birds seen, and the amount of their faeces on the ground, it would seem that a large proportion of these larvae were eaten.

Another example of wet conditions causing a high death-rate among larvae was seen at Eight Mile Creek the same year. This district runs parallel to the coast east of Port MacDonnell and formerly was swamp-land, but by 1950 was drained sufficiently to enable soldier settlers to take over their blocks of land. Before the land was settled it was cleared and pasture was sown. The soil is peaty and the pasture was mainly cocksfoot (Dactylis glomerata) and strawberry clover (Trifolium fragiferum). In 1950, O. fasciculata caused severe damage to pastures in the Eight Mile Creek settlement in only a few areas. Rain during August caused considerable flooding in the district, forcing larvae from their tunnels, and many were drowned or eaten by seagulls (Larus spp.).

This situation differed from the one at Kalangadoo in that there was vegetation extending above the water, enabling larvae to crawl upwards away from the water. The paddock in which the observation was made had not been grazed for some time after the pasture was sown and the cocksfoot had developed a large tussocky growth (Figure 8). Some larvae were living in these tussocks and their runways extended upwards into the growth instead of horizontally along the surface of the ground. As the water rose and forced these larvae from their tunnels they were able to crawl up into the cocksfoot tussocks, while most of the larvae living away from the tussocks were drowned or eaten by the seagulls. The paddock was gently undulating and in some cases larvae which were not living in the tussocks were not disturbed by the wetness because the water did not reach them.

Fig. 8. Tussocky growth of cocksfoot in a paddock at Eight Mile Creek. Larvae living in the tussocks have a better chance to escape drowning than those between the tussocks.

In 1951, five cases were seen in which the numbers of O. fasciculata were greatly influenced by wet conditions. The first substantial rain came in May of that year; there were 626 points in May, compared with the average of 348 points. June was dry but July and August were very wet and the examples were seen late in July, as compared with late August - early September of the previous year.

Wattle Range is a small settlement about eighteen miles west of Penola. The soil here is a relatively infertile podsolized sand, and the terrain is quite flat and subject to extensive flooding in the winter. Wattle Range appears to be the northern boundary of

O. fasciculata in South Australia and the insect is found here in small numbers. On 20th July the district was visited and one place was found where larvae had been drowned. Only those larvae living in the higher ground escaped drowning; and these were only a small proportion of the original population.

The property near Kalangadoo mentioned earlier was examined the next day and many larvae were found dead under water on the surface of the ground. In one flooded area two larvae were found which had climbed up into a tussock of reeds and had not been drowned. There were few larvae on this property in 1951 and a large porportion were drowned during the July rains.

The heavy black soils around Millicent are very wet in the winter and dry out and crack in the summer. O. fasciculata has not been found here in large numbers, probably because of the wet conditions. In 1950, however, a very small infestation was found in a paddock two miles north-west of Millicent. This property was visited in July, 1951, to see whether larvae had survived the unusually wet weather. Much of the paddock was under water and most of the larvae had drowned. This was a well managed pasture with no tussocky growth and that, together with the flatness of the land, would have meant that very few, if any, larvae would have survived the flooding.

About one mile north-west of Port MacDonnel is a very small area of heavy, black soil. This land usually is very wet and so has not been developed agriculturally; it carries an inferior pasture with no tussocky growth. O. fasciculata had bored some of this land in 1951 but in late July the infested area was under water and most of the larvae were drowned. Seagulls and white ibis (*Threskiornis molucca strictipennis*) were seen feeding on larvae which were exposed on the surface of the ground.

Wet conditions also limited the distribution and numbers of *O. fasciculata* at Eight Mile Creek in 1951. In July, larvae were restricted mainly to the lower portions of the paddocks (dry conditions earlier in the year had apparently reduced the numbers on the higher land) and flooding which occurred that month resulted in a high death-rate among larvae. The management of some of the paddocks had improved since the previous year and there were very few cocksfoot plants with a tussocky growth. Larvae in the lower areas of these paddocks had a smaller chance of escaping drowning than did those in the same situations in the previous year.

Further examples of wet conditions reducing the numbers of *O. fasciculata* were seen in 1952. These were: Kalangadoo, where many larvae were drowned and others which had been forced out of their tunnels were eaten by crows and magpies; Dismal Swamp, north of Mt. Gambier, where a large flock of white ibis was seen feeding on larvae; Kaladbro, just across the border in Victoria, where larvae were drowned and crows and magpies ate many larvae which might have escaped drowning. The Kaladbro district is very similar to the country around Kalangadoo and much of it could not be examined because it was too wet. The extreme wetness must have caused a very high death-rate among the larvae in this district.

VII INFLUENCE OF OTHER FACTORS ON SURVIVAL-RATE OF THE LARVAE

(a) Predation and Parasitism

While young larvae are on the surface of the ground they might be exposed to predators, but this was not seen. It may be that the profuse webbing spun by the larvae protects them from roaming predators. Except for the examples mentioned in VI (c), where unfavourable weather forced larvae from their tunnels and exposed them to birds, predators appeared to be of minor importance in limiting the distribution and abundance of this insect in County Grey. Many hundreds of soil samples were taken during experiments with insecticides, yearly surveys and general field observations and in only a very few of these were other animals found to be attacking the larvae. At Mil Lel an adult carabid (*Morphros bestii*) was seen feeding on a larva and at Mt. Schank larvae of another carabid (*Scaraphites crenaticolles*) were found attacking *O. fasciculata*. Predators also were found by D.C. Swan in 1949 and were associated with *O. fasciculata* larvae. These predators were so few that they would have had practically no influence on the numbers of *O. fasciculata*. Predators might be expected to be of more importance when there are few *O. fasciculata* than when there are many, *i.e.*, with few larvae, there would be a greater chance of any one larva being found by a predator than when there were many larvae. There were very few larvae during 1951-53 but there were also very few predators and it is considered that these other animals had very little influence on the numbers of larvae.

Although a careful search was made for parasites of O. *fasciculata* during this study, none was found. Evans (1941) reared two species of Tachinids from O. *intricata* in Tasmania but these were not identified and may have been general parasites of caterpillars. Martyn (unpublished report) dissected a number of O. *intricata* prepupae and found small dipterous larvae in two of them; he thought that they may have been specimens of the Tachinids mentioned by Evans. Cameron (1950a, 1950b) described a parasite (*Ichneumon suspiciosus*) which destroys about ten to seventeen per cent. of the population of *Hepialus lupulinus* in England. This parasite seeks out its prey in their tunnels. *Porina* spp. (*Hepialidae*) are parasitised by Tachinid flies in New Zealand and some of these parasites were sent to Australia in the early 1930's to be liberated against species of *Oncopera*. Females of *Hystricia lupina* deposit larvae on turf infested by *Porina*. The larva is very active and on finding the tunnel of a *Porina* larva it crawls inside and enters the host caterpillar. *Porina* usually survives until the pupal stage (Anon., 1931). Tachinids of the genus *Hexamera* were liberated in Tasmania, Victoria and around Canberra but apparently did not become established because none was found in 1935 (Anon., 1936).

It would appear that in Australia there are no specific parasites of *Oncopera* and the few examples of parasitism may have been by general parasites. Because of its underground habit, an O. *fasciculata* larva must be reasonably well protected against all but specific parasites and as none was found it is concluded that parasites had very little or no influence on the numbers of this insect during the study.

(b) Observations on Food and on the Kinds of Places in which O. fasciculata Lives

(i) Type of Pasture

Small areas still may be found in County Grey in which the pasture has not been improved by the addition of adequate superphosphate and introduced clovers and grasses. This land usually is associated with large holdings; few sheep can be carried per acre but with a large acreage a good income may be obtained with relatively little work. The same sort of vegetation is found alongside roads and on stock routes. The composition of native vegetation is discussed in detail in Section XII and all that needs to be said here is that there are few or no clovers and the grasses are mainly species of Danthonia (wallaby grass), other perennials and annuals.

A striking feature of the 1948-50 outbreak was that O. fasciculata larvae rarely damaged these undeveloped pastures. A typical example of this was seen in the district north-west of Kongorong. A small portion of a large property was bought by the State Government after World War II to be subdivided into blocks for returned servicemen. The blocks were fenced off and given liberal dressings of superphosphate and sown with subterranean clover and grasses. During the outbreak severe damage was done to improved pastures on the blocks while the adjoining undeveloped land was lightly infested.

In 1950 many cases were seen where there was a dense population of larvae in a paddock of improved pasture while there were few or no larvae in the area between the paddock fence and the road. Some properties which were heavily-infested in 1950 had stock routes running through them and almost invariably there was little damage to vegetation on the stock routes. What appeared to be exceptions were seen but in each case an examination revealed that native growth had been replaced by clovers and introduced grasses. One such case was found at Mil Lel. A stock route ran along a strip of land between two low, parallel rises; cocksfoot had become established in part of the lowest portion of the stock route and _O. fasciculata_ larvae were there in large numbers, as well as in the paddock alongside. Where there was no cocksfoot on the stock route there were few or no larvae.

Results from the field and laboratory experiments help to provide an answer to the question of why larvae are not seen in large numbers on unimproved pastures. Vegetation usually is upright and sparse and there is a large proportion of bare ground. Under these conditions it would be expected that, from the eggs laid, there would be few larvae the following winter. This would be because both the eggs and larvae would be exposed to unfavourable dry conditions and high temperatures. Also, the food supply for larvae would be poor because there would be little or no clover and only poor quality grasses.

Evans (_op. cit._) said that _Oncopera_ species in Tasmania had been found damaging lucerne, wheat, onions, carrots, strawberry plants and potato tubers. Martyn (unpublished report) added pea vines and tomato seedlings to this list. Martyn said that in the cases he saw, the reason for damage to crops was that _Oncopera_ larvae were living among grasses and weeds between the rows and when cultivation destroyed this food supply larvae started feeding on the crop. Damage to cultivated crops has not been reported or seen in County Grey, probably because proper cultivation keeps down the weedy growth between the rows and O. fasciculata cannot become established. A young lucerne paddock was found to be very lightly infested with larvae but this plant has not been damaged after it has become established. This may be because older lucerne plants have an erect habit and there is little or no green growth on the ground under them. In this situation it would be expected that O. fasciculata eggs and larvae would be exposed to unfavourable weather and larvae to starvation.

(ii) Interaction of Type of Pasture with Weather

Although larvae were numerous in 1950, only a few places were found in which all of the pasture had been eaten and where it appeared that the amount of food available depended on the number of larvae. One example was on a property (Kaladbro) north-east of Mt. Gambier, in Victoria. The manager estimated that about 3,000 acres were severely damaged by O. fasciculata larvae, and when the property was visited in July this large area carried very little herbage. Digging revealed larvae, prepupae and pupae but there were not many, considering the amount of damage. It appeared that an enormous number of eggs had been laid here the previous spring and that enough larvae survived to practically eliminate the food supply. Starvation must have killed most of these larvae, because there were few in July.

One way of explaining this could be to say that the high death-rate was caused by the large numbers of larvae that ate all of the food, and only those which emerged earlier or developed faster survived. It is true that the shortage of food can only be expressed relative to the numbers of larvae. However, I believe that there would have been enough food for these larvae if the weather had been favourable. It would therefore seem more realistic to attribute the high death-rate and the consequent small population surviving at the end of the season to shortage of food. The shortage of food may be explained in terms of an interaction between weather and type of pasture. Kaladbro is in typical red-gum country; a low-lying meadow-podsol soil subject to extensive flooding during the winter and spring (the owner uses an amphibious jeep for transport during part of this period). The winter of 1950 was very dry (as was 1949) and parts of the property which normally would be under water were driven over in a vehicle. Even in situations where there had not been many larvae, the growth of pasture was poor because of the very late break and insufficient following rain. Also, these pastures were composed of annual grasses and clovers and there were no perennial plants. The combination of a dry autumn and winter and a pasture composed of annuals meant that there would have been little food for the larvae, and as this food was eaten there would have been very little regrowth. If there had been more rain (enough to promote pasture growth but not enough to expose larvae to drowning) there probably would not have been a problem of starvation, for there would have been enough food for the larvae to complete their development.

Kalangadoo is red-gum country similar to that at Kaladbro and

O. fasciculata did severe damage to pasture there in 1950. Larvae at Kalangadoo, however, were not exposed to the same degree of starvation because there was a better quality pasture (some perennial grasses) and there had been more rain than at Kaladbro.

VIII INFLUENCE OF ENVIRONMENT ON SURVIVAL-RATE OF THE PREPUPAE AND PUPAE

The larva stops feeding about July (mid-winter) and plugs the entrance to its tunnel with a firm silken cap. Shortly afterward it enters the prepupal stage, and after about a fortnight becomes a pupa. Both the prepupa and pupa are active and move up and down inside the tunnel.

It would appear that a larva which survives to become a prepupa stands a good chance of emerging as an adult. Food and dryness, which have a great influence on the survival-rate of the egg and larva, play no part in limiting the development of the prepupa and pupa. Because they are protected, these latter stages would not be exposed to parasites or surface-roaming predators, although they might be attacked by underground predators, as carabid adults and larvae.

Temperature does not appear to have an unfavourable influence on the numbers of prepupae and pupae. These stages are found in the field during the winter and early spring and so would not be exposed to high temperatures; they remain in tunnels about five to six inches below the surface of the ground and so would not be exposed to low temperatures which might occur at the surface.

The main danger to which prepupae and pupae may be exposed seems to be extreme wetness. As with the larvae, this would only occur on the low-lying flats and plains, and in the examples described in Section VI (c), prepupae and pupae also were forced from their tunnels by the water. Prepupae can crawl, and some could move upward into tussocks, if these were available, but pupae would not be able to escape. Individuals which were not under water long enough to be drowned would remain on the surface of the ground and would be exposed to unfavourable weather and birds and other predators. It is doubtful whether any adults emerge from prepupae or pupae forced from their tunnels by wet conditions. In August, 1950, waterlogging forced large numbers of larvae, prepupae and pupae from their tunnels on the property near Kalangadoo. By September-October none could be found and apparently no moths emerged from the flooded land, for no empty pupal cases or moths were found.

IX INFLUENCE OF ENVIRONMENT ON THE ADULTS

Adults of O. fasciculata do not feed and probably live no longer than two or three days. Most moths emerge during the afternoon in early spring and shelter under surface cover until dusk, when they take part in a brief flight. The first flight appears to be one of dispersal, for the moths rise twenty to thirty feet into the air and then fly away for some distance. This is quite distinct from the mating flight, when moths fly rapidly back and forth one to two feet above the pasture. Mating flights take place over areas where there is upright pasture and /or stubble and moths usually mate on this upright growth, although, less often, mating has been observed on bracken fern (Pteridium aquilinum) and on the ground. The flight lasts for about fifteen minutes and then the moths alight and crawl under herbage, where they shelter until dusk the following evening.

Unfavourable weather (heavy rain or strong wind) may restrict flights of moths but appears to have little influence on their numbers; nor does food. Temperatures would be mild during the afternoons but the adults might be exposed to cold while sheltering under herbage during the night. There was no evidence from field observations that the temperature was ever low enough to kill many adults. Although birds may feed on the moths, it was considered that they played an insignificant part in reducing the numbers of the insect. Magpies appeared to be the most important predator of the moths and have been seen searching for them under pasture. Also, during a flight of moths, magpies were seen making short flights to catch "dispersing" moths but did not attempt to catch those flying just above the pasture. Very few moths in flight were captured by the magpies because most of the birds had stopped searching for food when the moths appeared. In one paddock domestic ducks were seen feeding on moths, and these and other domestic fowl may reduce the numbers of moths in the pastures around farm buildings.

The sort of place in which moths shelter between flights does not have much influence on their numbers but is of great importance in determining how many moths will emerge from these situations in the next generation. If the gravid female shelters (and lays her eggs) in dense herbage, the eggs and larvae have a good chance of surviving unfavourable weather, but if only sparse pasture is available, there may be a high death-rate among the immature stages. Also, if the female shelters under herbage in the lower areas of poorly-drained soils, the larvae, prepupae and pupae may be exposed to extremely wet conditions.

It would appear that most adults which emerge survive to take part in the mating flight and most gravid females survive to lay their eggs. The important contribution the female makes is to shelter under herbage, for this behaviour has a direct bearing on the survival-rate of her progeny.

X DESCRIPTION OF THE DISTRIBUTION AND NUMBERS OF O. FASCICULATA DURING 1948-54

Larvae of the genus Oncopera have been considered serious pests of pastures for many years. Descriptions of the insects and damage done in Victoria, New South Wales and Tasmania appeared in the early 1900's. In 1921, another species was reported from the Atherton Tableland in Queensland, where pastures were being severely damaged.

Apparently O. fasciculata was known as a minor pest of pastures in County Grey in the 1920's, for Hill (1929) visited the Mt. Gambier district in search of specimens. The first year that O. fasciculata caused concern among land owners was in 1935, and Swan (1937) reported pastures damaged at Glencoe as well as in the area immediately around Mt. Gambier. In 1937-38 and 1940 minor damage was done around Mt. Gambier and Glencoe but only a few graziers suffered economic loss.

Although no damage was reported from 1940-47, it seems quite certain that the insect must have been increasing in numbers during part of that time for it to appear in plague proportions in 1948. Larvae were scarce at Glencoe in 1944 (Andrewartha, personal communication). The absence of reports during 1940-47 probably was due to the combined effects of the following: (1) The pasture cockchafer (Aphodius howitti) did considerable damage to pastures in the south-eastern portion of the State during 1940-45, and some of the damage attributed to this insect may have been done by O. fasciculata; (2) Rainfall during 1946-47 was unusually high and the resulting abundant growth of pasture may have masked damage being done by the larvae; (3) A large area infested in 1948 was in the process of being developed by the State government for closer settlement by returned servicemen and was mainly ungrazed and not under close supervision during 1946-47.

No thorough survey was made during 1948-49 of the distribution of O. fasciculata in the South-East but enough information was obtained from other members of the Entomology Department, departmental records, farmers in the district and somewhat unreliable newspaper reports to enable a reasonably accurate map to be drawn of the distribution and numbers of the insect for these two years. It would be reasonable to assume that O. fasciculata was more widely spread over County Grey than is indicated on these maps.

During 1950-55 frequent trips were made to the South-East to make observations of the insect in the field and to record the places where it was living and its abundance. The main survey was done each year when larvae were fully-grown (July-August) so that they would be easy to find and also so that observations could be make on the amount of damage that had been done. The method used was to travel along the road and stop about every two miles and make a tour of the field, during which the number of tunnels in several square-foot samples was recorded, as well as the amount of damage. At the start, samples were dug up and larvae counted, but it was found that counting the number of tunnels was sufficient. Larvae were classified as being scarce (very low numbers and no evidence of damage), few (small numbers and slight damage), moderate numbers, and large numbers (larvae very numerous and causing severe damage to pastures). Damage to pastures alone could not be used as a criterion of the number of larvae in a field because the amount of growth also was dependent on weather. In some years a good season meant that there could be many larvae attacking a pasture but the growth would be able to "keep ahead" of this feeding; during a bad season, the same number of larvae in the same paddock could cause severe damage and eat most of the herbage.

A survey in May, 1950, showed that it would be a waste of time to make a thorough examination of the numbers of larvae in such places as pine plantations, coastal sand-dunes, dense wood or scrub or other places where there was no herbage. As no larvae were found in these situations in May, and as it is very unlikely that they would be found here, the survey in July, 1950, as well as in the other years, was restricted to natural grassland and developed pastures. A key map of County Grey was drawn showing the stranded dune system, forest reserves, lakes and other places extremely unfavourable for the insect and this portion of the County is shown unhatched on the survey maps for each year. The rest of the County is mainly under natural grassland or developed pastures and on the maps this land has been divided into poorly-drained and well-drained soils. The insect is not distributed over all of this land because portions of the poorly-drained soils still are much too wet for it to become established, nor would it be found where cultivated crops are grown. Some parts of the County could not be visited because there were no roads, and it was assumed that in these undeveloped areas O. fasciculata was rare or absent.

TABLE 14

KEY TO TOWNS SHOWN IN THE MAPS

FR	Furner	MT	Millicent
KG	Kongorong	PA	Penola
KO	Kalangadoo	PM	Port MacDonnell
MG	Mount Gambier	TA	Tantanoola
ML	Mil Lel	WR	Wattle Range Settlement

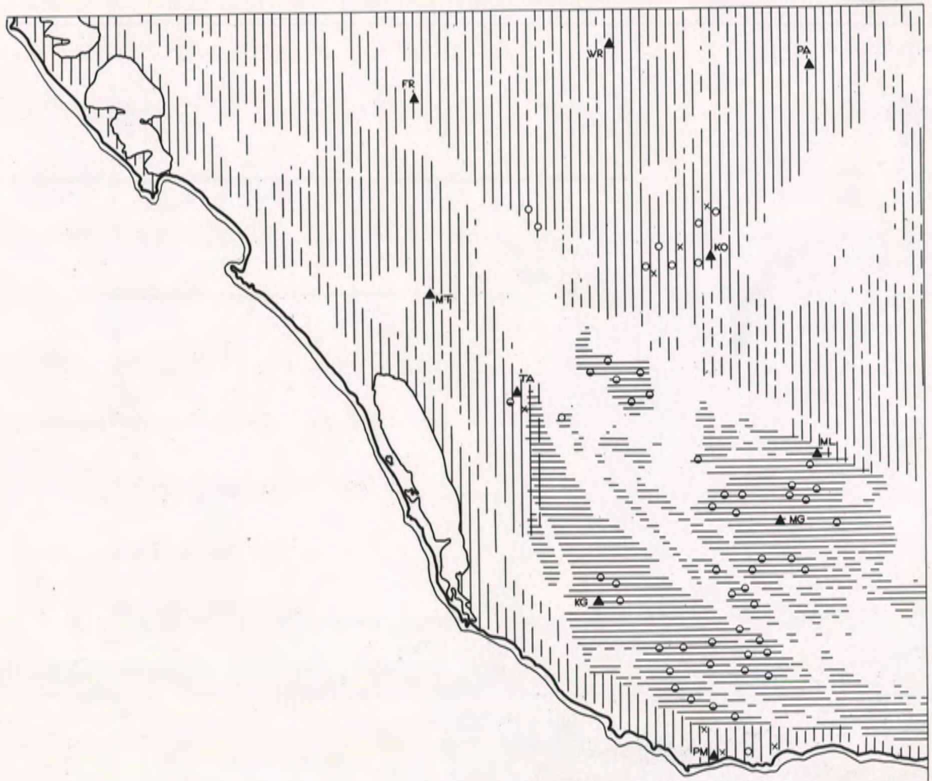

Fig. 9. Distribution of O. fasciculata in 1948. Poorly-drained soils are shown by vertical hatching and well-drained soils by horizontal hatching. Clear areas are places where O. fasciculata is not likely to survive, as schlerophyll forests, pine plantations, sand dunes, etc. O. fasciculata is shown as being scarce, • ; few, ×; moderate numbers, O; large numbers, Ꝋ. Severe damage was done to pastures on the well-drained soils.

Fig. 10. An example of pastures severely damaged in 1948. Darker portions of the paddock are where _O. fasciculata_ larvae have eaten all of the herbage and have left the surface exposed. Lighter areas are where only old, dead vegetation is left. Mt. Schank is in the middle distance with Mt. Gambier in the background. (D.C. Swan)

(a) 1948

By mid-year _O. fasciculata_ had reached plague proportions in the area around Mt. Gambier and Mt. Schank and thousands of acres of pastures were severely damaged (Figure 9). The worst damage was seen between Mt. Gambier and Port MacDonnell (Figure 10) but pastures north of Mt. Gambier and at Kongorong and Glencoe also were severely attacked. Some farmers lost so much herbage that they were forced to sell some or all of their livestock. Larvae were less numerous on the poorly-drained soils and appeared to be restricted mainly to the higher land.

(b) 1949

Larvae again caused severe damage to pastures in the Mt. Gambier-Mt. Schank area (Figure 11). A small area south of Tantanoola and at Eight Mile Creek was heavily infested (Figure 12) and minor damage was done at Kalangadoo, where the insect appeared to be restricted to the higher, better drained land (Browning, personal communication). In 1948 and 1949 larvae were numerous where there were well established pastures, and some of the most severe damage was seen where land was being developed for soldier settlement.

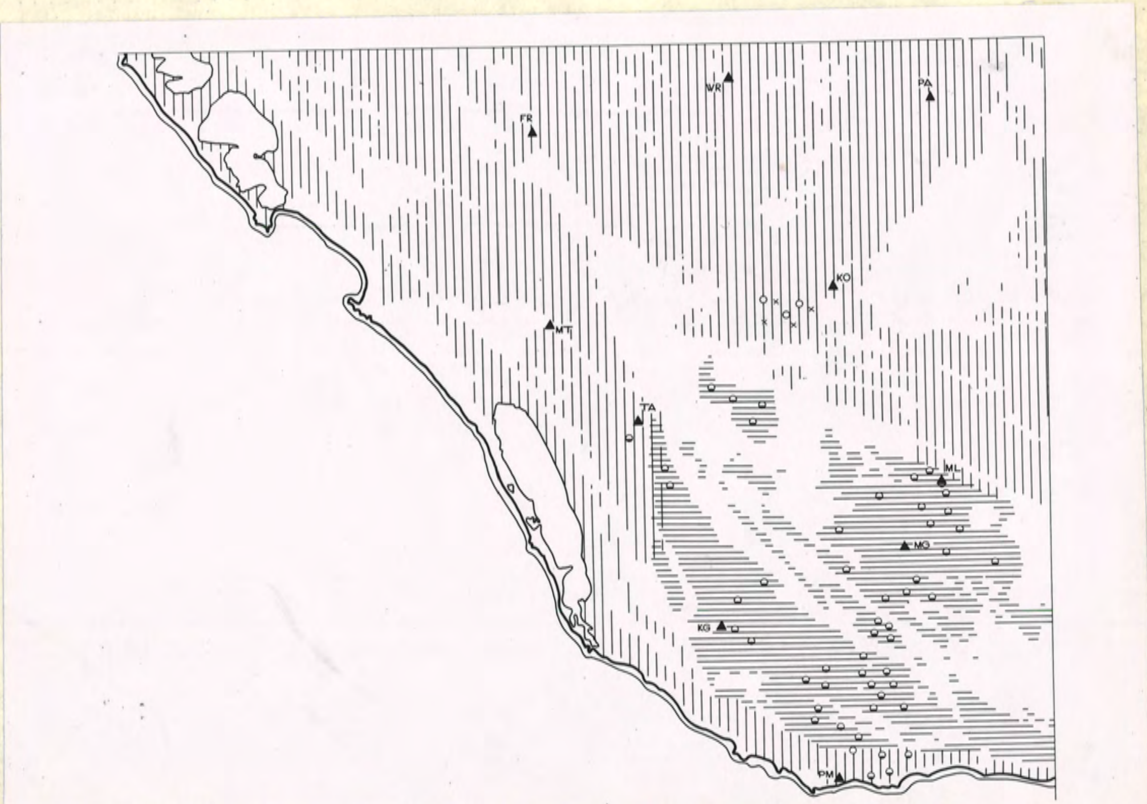

Fig. 11. Distribution of O. fasciculata in 1949. Damage was restricted mainly to pastures on the well-drained soils. Symbols as in Figure 9.

Fig. 12. Portion of a paddock at Eight Mile Creek severely damaged by O. fasciculata in 1949. The lighter patch in the centre has been caused by larvae eating all of the green herbage. (D.C. Swan).

(c) 1950

This was the first year in which a detailed study was made of the distribution and numbers of O. fasciculata in the South-East. The first sampling was done in April, and larvae were found to be abundant in the southern half of County Grey as well as in the Kalangadoo district. The largest number found in a sample (one square foot) was 28 at Kalangadoo. Slight damage to pastures was seen here and near Mt. Schank. By May it was evident that pastures were being severely damaged at these two places; larvae already had bared some of this land. This was the first time that a large infestation was found in the Kalangadoo district and was so severe in May that some graziers were forced to rent additional land because they did not have enough feed for their livestock. This also was the first time that <u>O. fasciculata</u> had been found at Wattle Range.

The area severely damaged by larvae increased during June, and by July larvae had destroyed a large proportion of the pastures to the north of Kalangadoo and, to a lesser extent, pastures to the south of Mt. Gambier (Figure 13). Much of the damage at Kalangadoo was on the lower portions of the paddocks, although larvae were easy to find on the higher banks (<u>ca.</u> two to three per sample). Larvae also caused severe damage to pastures on sandy soil at the soldier settlement of Pleasant Park, several miles south-east of Kalangadoo. Directly east of this area, in Victoria, and in much of the rest of the western district of that State, many thousands of acres of improved pasture were devastated. Larvae were found in most of the rest of the County where soils were poorly-drained, and were found in plague numbers south of Tantanoola and at Port MacDonnell. The soil at Tantanoola is a black clay, as at Millicent, and <u>O. fasciculata</u> had not previously been found in this district. At Eight Mile Creek, pastures on a peat soil were severely damaged.

There were fewer larvae on the well-drained soils north-east of Mt. Gambier and around Mt. Schank than in 1949 and the largest numbers appeared to be on the lower land. Only a few places were found where larvae were numerous enough (<u>ca.</u> ten to twelve per sample) to cause economic loss.

A survey was make of County Robe, north of Grey, but larvae were not found. A large proportion of the cleared land in Robe is extremely wet in the winter and this may restrict the establishment of the insect in that region.

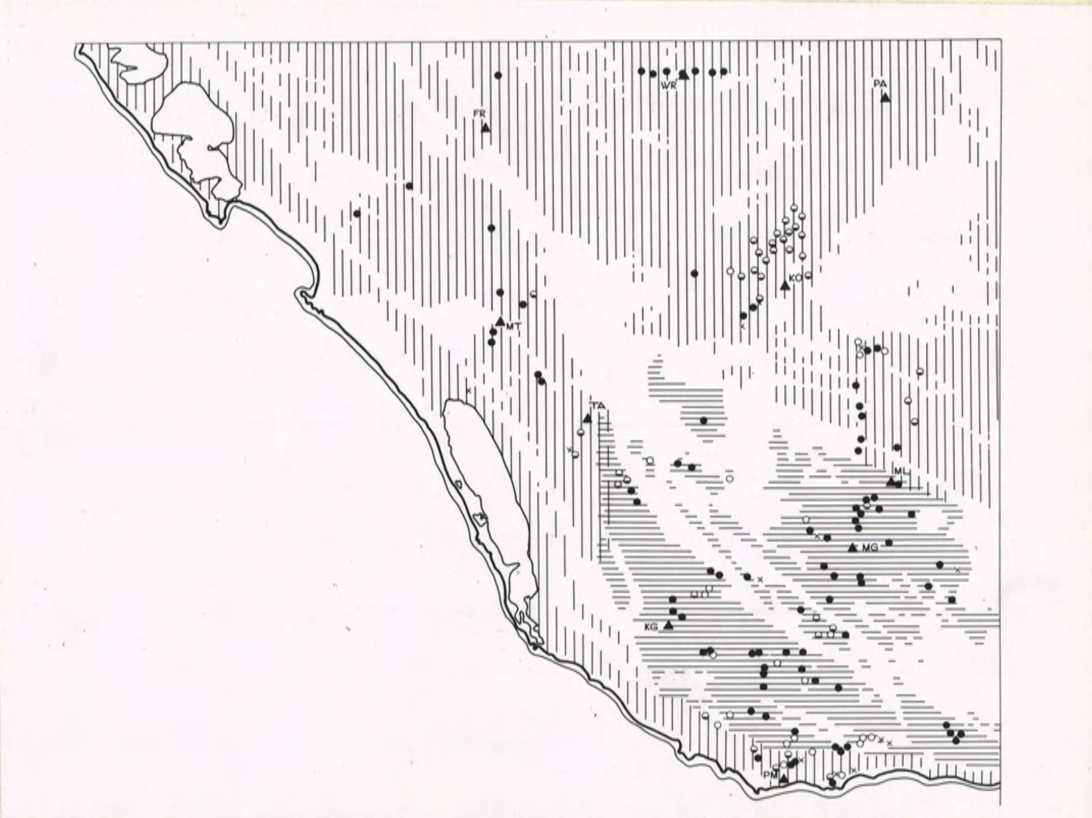

Fig. 13. Distribution of O. fasciculata in July, 1950. Larvae were numerous on the poorly-drained soils and caused severe damage to pastures near Kalangadoo; less damage was done on the well-drained soils. Note that the distribution is almost the opposite of that shown for 1948 and 1949. Symbols as before.

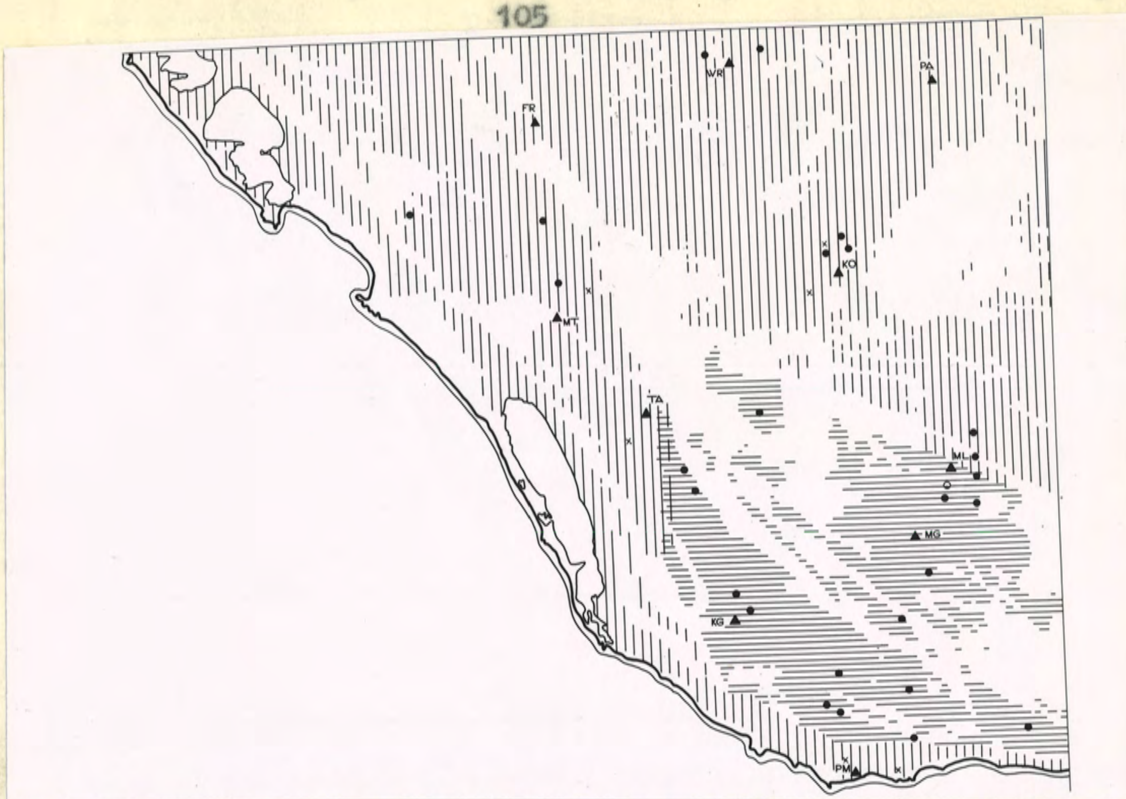

Fig. 14. Distribution of O. fasciculata in July, 1951. Larvae were very scarce and only one place was found where they were in numbers large enough to cause economic loss to pastures. Symbols as before.

(d) 1951

A survey of County Grey in January showed that there were not many larvae around Mt. Gambier and Mt. Schank and it looked as though the only area in which there might be damage later in the year was at Kalangadoo. Although large flights of moths had been seen the previous September on a property near Mil Lel, very few larvae could be found and those which were found were situated in the lower portion of the paddocks. At Kalangadoo, larvae were numerous where there were dense stands of herbage. There were few larvae in those parts of the paddocks where most of the growth had been eaten the previous year.

The damaged areas contained little herbage in January because sheep concentrated their feeding on the new growth which was easier to get here than under the stubble.

The picture did not change much during the following three months; larvae could be found in most of the well-established pastures but were in small numbers and there was no evidence of damage. The first obvious sign of feeding by larvae was seen in May at Kalangadoo. Even here the damage was very restricted and consisted of small patches, about five to six inches across, where there were four or more larvae feeding. Where larvae were fewer the damage could not be seen unless the upright growth was parted, revealing a slightly bared patch where one larva was situated. No damage was seen elsewhere in the County except a small area near Mil Lel.

The survey in July, at the end of the feeding period (Figure 14), showed that the only place where larvae were numerous enough to cause economic loss (<u>ca</u>. ten per sample) was in a small paddock at Mil Lel; larvae had eaten most of the dead pasture and new growth on two-thirds of this land. There was no visible damage done to pasture in the paddock at Mil Lel where large flights of moths were seen the previous year. Sampling showed that there were few larvae in the paddock (mean of fifteen random square-foot samples was slightly more than one larva per square foot). The distribution of larvae in the southern portion of the County was much the same as in this paddock. Larvae could be found but were in such small numbers that they did not cause any economic loss to farmers. Larvae were more numerous in the Kalangadoo district but there were only a few small patches where there were enough to cause obvious damage. Some of the lower land around Kalangadoo was flooded in 1951, causing a high death-rate among larvae, prepupae and pupae.

(c) 1952

Larvae were much harder to find during the early part of this year than they were in 1951. Results from surveys done during the first four months indicated that larvae were most numerous in the Kalangadoo district and might cause damage during the winter. In most of the rest of the County there were few larvae, even where there were dense stands of herbage. The exceptions were at Eight Mile Creek and Mil Lel, where larvae were few or moderate in numbers in some of the lower (wetter) situations.

Much the same sort of result was obtained from a survey done early in August (Figure 15). Larvae were scarce in most parts of the County, there were a few local situations where moderate damage was done and only a small area near Kalangadoo where there was economic loss. In one pasture near Mil Lel which was grazed only occasionally by a few dairy cows, larvae did moderate damage. A paddock at Eight Mile Creek had been moderately infested with larvae and most of the damage was restricted to the lower areas; many larvae in these situations were drowned.

Several acres of a property north of Kalangadoo were found to contain many larvae doing considerable damage to herbage. This paddock had been understocked in 1951 and carried a heavy growth of Yorkshire fog. The owner said that the lower portion of the infested area had been under water in July and he had seen many larvae on the surface of the ground, and ibis, crows and magpies feeding on them. In the rest of the Kalangadoo district larvae were scarce or few in numbers.

At Wattle Range, livestock had been kept off a paddock during the spring so that the herbage could be cut and baled for hay later in the year; it was not cut, however, and O. fasciculata larvae were in large enough numbers to cause moderate damage.

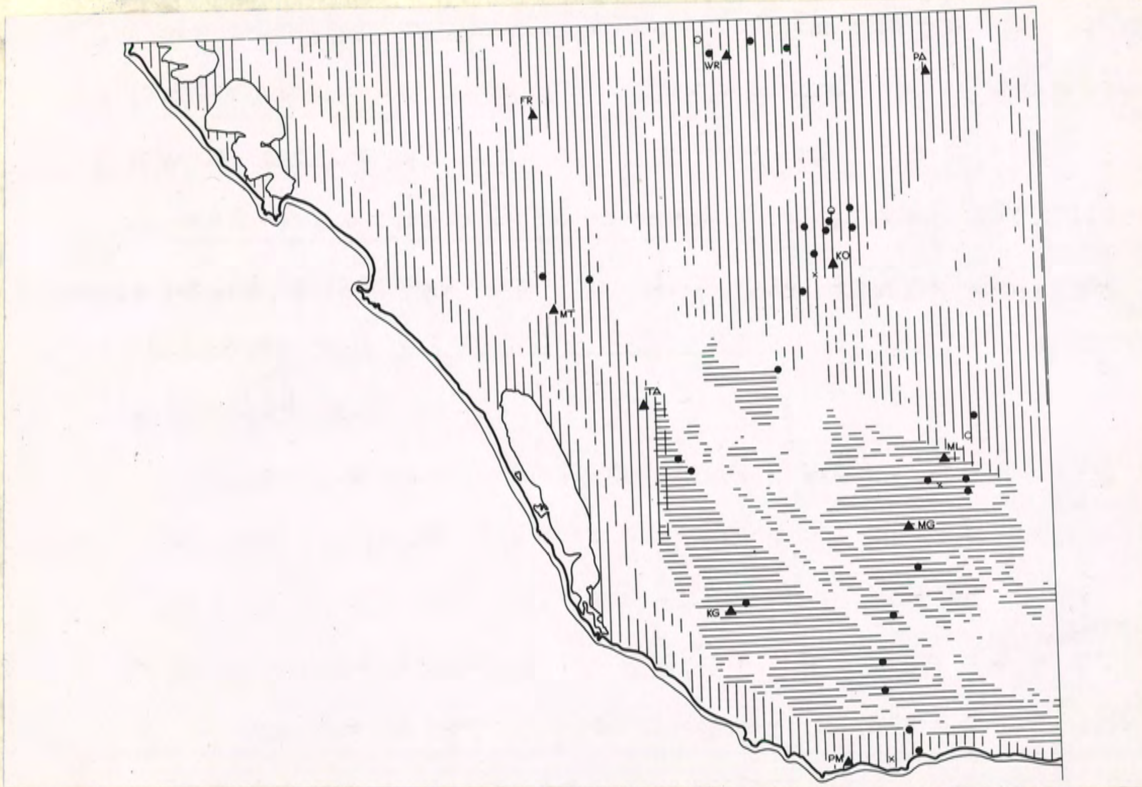

Fig. 15. Distribution of O. fasciculata in August, 1952. The species was slightly more abundant on the poorly-drained soils. Symbols as before.

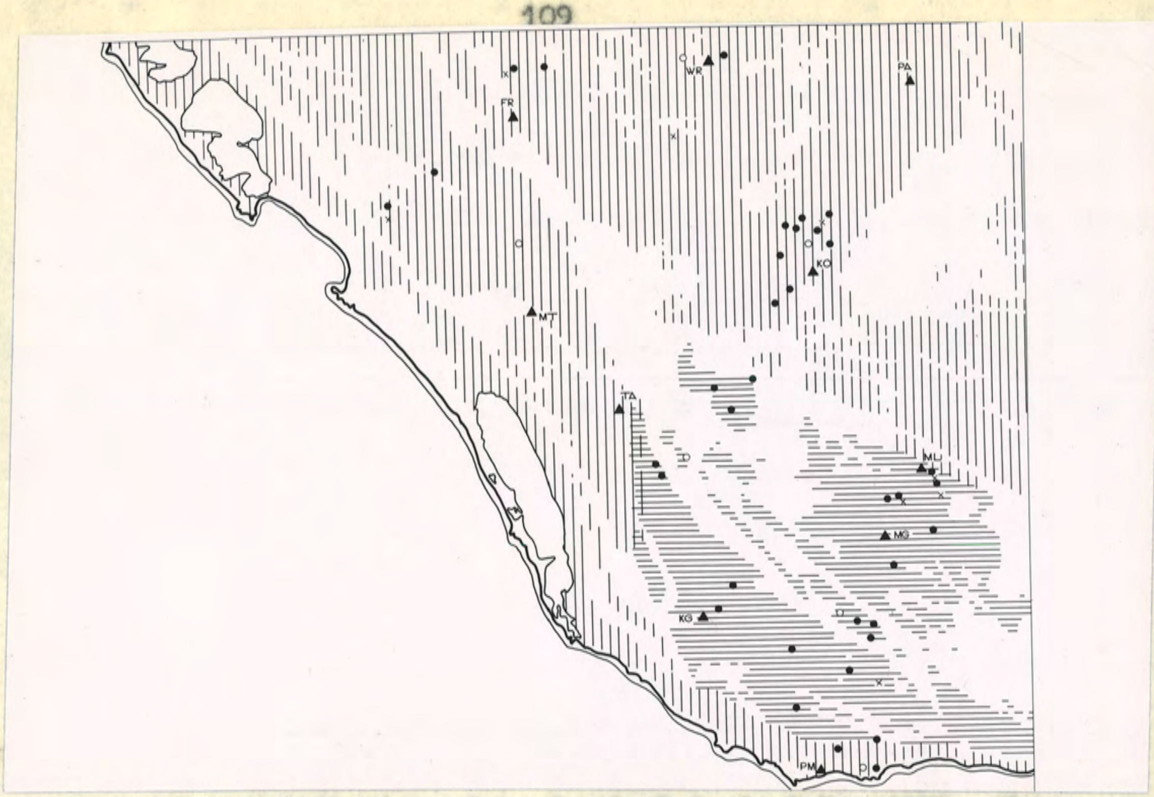

Fig. 16. Distribution of O. fasciculata in July, 1953. There had been a higher survival-rate on both the poorly-drained and well-drained soils. Symbols as before.

(f) 1953

The general impression obtained from surveys done early in the year was that larvae were more numerous on both the well-drained and low-lying soils. Whereas larvae had been difficult to find at the same time of year in 1951-52, they were much easier to locate this year, although they were not extremely numerous in any one situation. The main survey in July (Figure 16) showed that larvae were more abundant than they had been since 1950. Minor damage was done to herbage on the well-drained soils at Mil Lel and Mt. Schank and also on the low-lying soils at Kalangadoo, Wattle Range and near Millicent. Three paddocks were found at Mil Lel where larvae were in fairly large numbers but there were not enough in any one small area to cause severe damage. Even though there were few obvious signs of feeding, herbage in these paddocks must have been greatly depleted by the larvae. In the Mt. Schank district the picture was much the same; although there were moderate numbers of larvae in some situations, their feeding was not sufficient to cause bare patches in the pasture.

The property north of Kalangadoo that had contained large numbers of larvae the previous year had very few in 1953. The suggestion had been made to the owner that he try to have as little pasture cover as possible during the spring, which he had done. One large paddock had been cut for hay and the cuttings removed by November. Livestock had been concentrated in the remaining paddocks and had kept the pasture grazed rather low in comparison with nearby paddocks on other properties where heavy grazing was not done. In this one instance it did appear that proper management of the property, in relation to the requirements of O. fasciculata, had helped to prevent what could have been a serious loss of feed during the winter.

Other pastures around Kalangadoo contained about the same number of larvae as in 1952; in some places larvae were more numerous but no severe damage was done. Larvae were not so widespread at Wattle Range as they had been the previous year but there were enough in one paddock to cause moderate damage. A minor infestation was found on a black clay soil north of Furner.

Two locations on this map have been recorded as having few to moderate numbers of larvae, although they were not visited during the survey in July. Because fairly severe damage was done to pastures at these two places in 1954, and owners recalled having seen minor damage in 1953, they have been included. The one location was north-west of Kalangadoo and east of Furner, where the soil is very sandy and subject to extensive winter flooding, and the other was north of Millicent.

(g) 1954

Observations made early in April indicated that larvae were more plentiful than they had been the previous year, especially on the well-drained soil in the Mt. Gambier-Mt. Schank district. By July several places were found where there was economic loss, both on well-drained and low-lying soils (Figure 17). There were four paddocks at

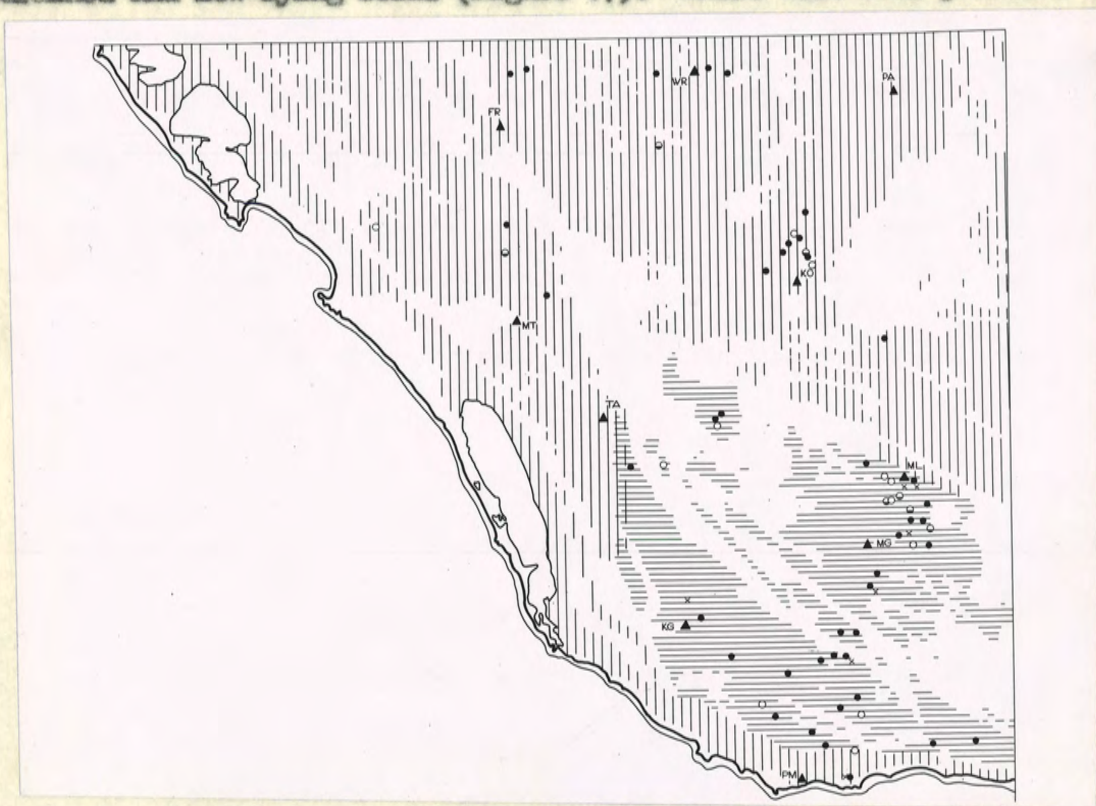

Fig. 17. Distribution of O. fasciculata in July, 1954. Numbers continued to increase on both types of soil and severe damage was done to improved pastures near Kalangadoo and at Mil Lel. Symbols as before.

Mil Lel where most of the herbage had been eaten; in the same district were several places where larvae were numerous but were not causing severe damage.

Samplings done in the area between Mt. Gambier and Port MacDonnell showed that there was a wider distribution of larvae than in the previous year and there were larger numbers in some local situations. The distribution in the Kalangadoo district was much the same as in 1953 but larvae were found mainly on the higher land and one paddock on this land was heavily infested. Another paddock near Kalangadoo had been closed for hay and was cut in December but the cuttings were not removed. There were many larvae in this paddock and much of it had been eaten bare. On a nearby property one paddock had been cut for hay in November, and the hay baled and removed soon after, and all of the remaining paddocks but one had been closely grazed. There were few larvae on the mown and heavily-grazed land but there were large numbers on the remaining paddock that had carried only a few sheep during the spring.

A property about midway between Kalangadoo and Furner was heavily infested and about 150 acres had been severely damaged by the larvae. This district is similar to that at Wattle Range except that the surface is more uneven and there are many banks of higher land. Damage to herbage was restricted to this higher land, where larvae probably would not be exposed to extreme wetness except during very wet winters.

A paddock north of Millicent contained large numbers of larvae and much of it had been severely damaged; the owner said that he had seen some damage on the higher portion of the paddock in 1953. During the spring of 1953 it had been closed for hay but the herbage had not been cut.

(h) 1955

A survey of the distribution and abundance of O. fasciculata was done in July and results are shown in Figure 17a. The largest

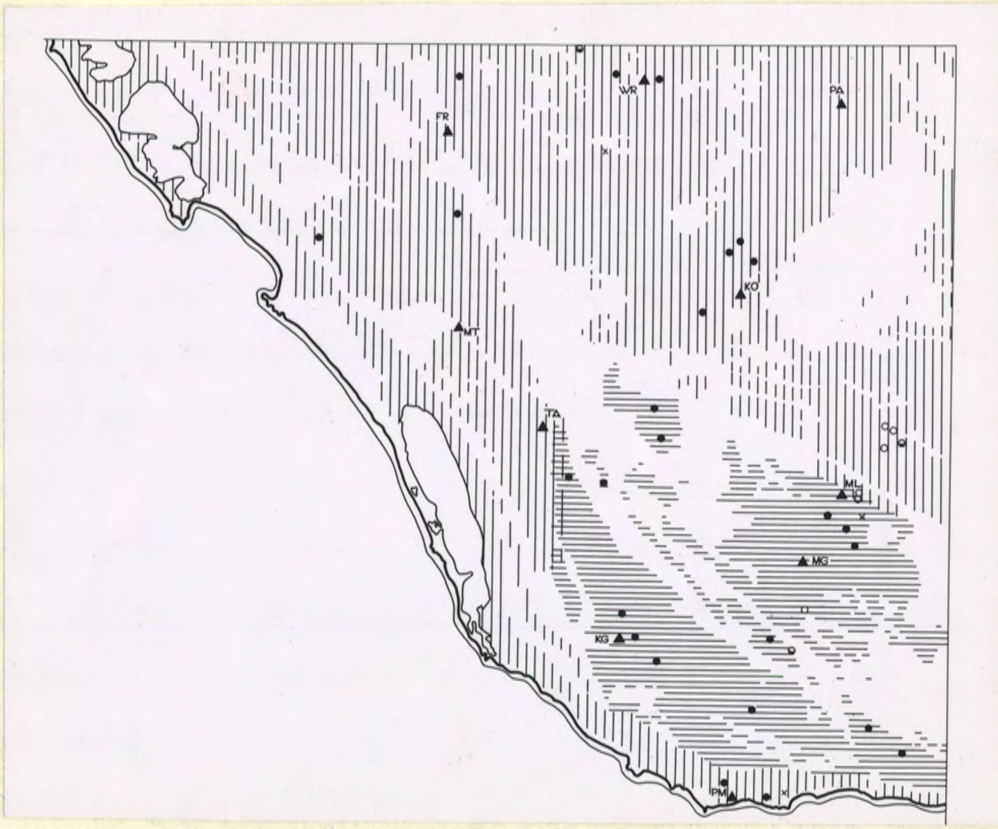

Fig. 17a. Distribution of O. fasciculata in July, 1955. The insect was less abundant than in 1954 and the largest numbers were found in the low-lying areas of both the well-drained and poorly-drained soils. Symbols as before.

numbers of the species were found in low-lying areas of both the well-drained and poorly-drained soils. In other areas of County Grey the distribution of O. fasciculata was much the same as in 1954, but larvae were less numerous.

A paddock near Mt. Schank had been closed for hay production during the spring of 1954 but the herbage was not cut. This paddock was heavily-infested in 1955. Similar conditions were found in a property north of Wattle Range. There had been an abundant growth of grasses and clover during the previous spring and this herbage had been only lightly grazed. In July, larvae of O. fasciculata were in large numbers on the lower area of a paddock. The owner said that this lower area was usually under water in July, but this had not happened in 1955 and O. fasciculata had not been exposed to extreme wetness.

North-east of Mil Lel a portion of a paddock had been ploughed in 1953, left fallow and ploughed again in 1954. It was sown with clover and grasses soon after and the whole paddock was lightly grazed during 1954. In September, 1954, the newly-sown portion of the paddock carried a low, dense growth of clover and grasses while the unploughed area carried a high, dense growth of Yorkshire fog (Holcus lanatus) and clover. During the spring and summer of 1955 the paddock was lightly stocked with sheep and cattle. Larvae of O. fasciculata were very abundant in July, 1955, but were restricted to that portion of the paddock which had carried the tall, dense growth of Yorkshire fog. The contrast between the sorts of cover can be seen in Figure 17b. The area in the foreground was sown with clover and grasses and the growth is short and dense. In the background is the unploughed area, carrying a dense growth of Yorkshire fog. Ten random, square-foot samples were taken from each situation. The numbers of O. fasciculata in the high, dense growth ranged from two to nine per square foot, with a mean of 3.9, while no larvae were found in ten samples from the low, dense growth. No O. fasciculata was found in this situation after intensive searching.

Fig. 17b. Scene showing the influence of surface growth on the abundance of O. fasciculata. Herbage in the foreground is low and dense and no larvae were found. In the background the growth is tall and dense and larvae were in large enough numbers to do severe damage. For further explanation see text.

XI ANALYSIS OF THE ENVIRONMENT OF O. FASCICULATA : ITS INFLUENCE ON THE DISTRIBUTION AND ABUNDANCE OF THE SPECIES

(a) Weather

The twelve species of Oncopera recorded in Australia appear to be adapted to living in situations where they would not be exposed to dry conditions. Four species are found near Cairns in Queensland and the other species are found in the south-eastern area of the continent from Brisbane southward to the south-east of South Australia, and Tasmania.

Preliminary studies on O. fasciculata indicated that unfavourable weather, in the form of dryness during the egg and early larval stages, might be the main factor in limiting the development of this insect in South Australia. It was thought that these stages would be more exposed to the lethal influence of dryness than other stages of the life cycle because they are found on the surface of the ground in the late spring and early summer when the environment is becoming increasingly dry.

Results from field observations had suggested that the sort of herbage-growth where eggs and larvae were situated might have an influence on their survival-rate, because high, dense cover appeared to be commonly associated with later damage to pastures. The results of the experiments recorded in Section V (c) confirm this. With these stages there was a higher survival-rate where the herbage remained tall and dense and thus would shelter the eggs and larvae from heat and dryness (see Geiger, 1950, Chapter 28). Under natural conditions this sort of growth would be found in paddocks where the improved pastures had not been heavily grazed or cut for hay, and several examples were given in Section X of paddocks which had been closed for hay but the herbage had not been cut, and severe damage had been done by _O. fasciculata_ larvae.

Few eggs and larvae survived in the field experiments when they were under herbage that had been cut or thinned (the cutting treatment simulated a mown paddock and the thinning treatment a natural pasture, where the growth is sparse). These two treatments did not provide sufficient cover for the insect and there was a high death-rate caused by exposure to unfavourable weather. This would help to explain why _O. fasciculata_ seldom is found in large numbers in natural pastures, or paddocks that have been heavily grazed or mown during the early spring. In these field experiments there was a high death-rate (_ca_. 90 per cent.) even where the eggs and larvae were under dense herbage, probably caused by the unusually dry conditions during 1951-53; in other words, weather was so unfavourable that most individuals died even when they were in the most favourable situations.

Further confirmation for this hypothesis can be drawn from the results of the laboratory experiments described in Sections V (d) and VI (b). There it was shown that eggs and young larvae were easily killed by dryness and lost water at a rapid rate when exposed to desiccation. It seems quite certain from these results that as the embryo develops it becomes more susceptible to water-loss, and newly-emerged larvae are much more susceptible to water-loss than are the eggs.

Results from weighings of _O. fasciculata_ eggs showed that the eggs lost water readily through the cuticle but there was no water-uptake. This is unusual behaviour for an insect that appears to be adapted for living in moist places; the eggs lose water when exposed to dryness and yet they cannot take up water when it becomes available. This behaviour is quite different from that of other insects which live in moist places. Many ticks lose water rapidly in dry air, but are able to replace it by absorbing water from the air; one species can do this when the relative humidity is 82 per cent. or more (Lees, 1946).

Further experiments showed that in the autumn, larvae remain relatively inactive during spells of dry weather but become active and feed during wet periods; such feeding probably would continue until the environment again became too dry. The greatest and most prolonged period of feeding would be expected after the end of the summer drought, when the soil remains moist and there is a continued growth of annuals. Although these field experiments may indicate the feeding behaviour of _O. fasciculata_ larvae during the autumn, it does not necessarily follow that they behave in the same way during the late spring and summer. However, field observations substantiate the belief that larvae grow slowly during the drought period and then increase rapidly in size following the break of the season. If increase in length is taken as a measure of growth, larvae collected in the field during 1950 showed an increase of 26 per cent. in growth from January to February, a 45 per cent. increase from February to April, a 28 per cent. increase from April to May, a 55 per cent. increase from May to June and a 51 per cent.

increase from June to July. In other words, larvae increased in length by about one-quarter each month during the dry summer-autumn period and by one-half after the drought ended, which was very late that year. It would seem that exposure to dry conditions not only kills many larvae but also has an influence on the speed of development of those which survive.

Studies of moisture conditions inside an O. fasciculata tunnel in the autumn showed that a larva sheltering in the lower portion of its tunnel would not be exposed to the dryness on the surface of the ground during a hot, dry day. However, the larva would probably lose water when in the upper portion of the tunnel or on one of its surface runways. Activity during a hot day would cause the spiracles to open more often, which would increase the water-loss. At night, with a falling temperature and rising relative humidity, a larva might be able to leave its tunnel without being exposed to dryness.

Another point which was considered was the moisture content of the soil in which larvae were living. Soil samples were obtained from three depths at Mil Lel on 12th April. Weather during March was drier but cooler than normal while the first eleven days of April were dry and hot. Twenty points of rain fell during the fortnight preceding sampling - the largest fall, seventeen points, was recorded on the sixth. Soil samples were taken from 0.5 - 1 inch, 2.5 - 3.5 inches and 3.5 - 4.5 inches. The first depth corresponded to the upper portion of the tunnels, the second depth to the lower portion and beneath the tunnels and the third depth to soil beneath the tunnels. Soil near the surface contained 13.4 per cent moisture while soil at the other two depths contained 17.5 per cent. and 17.9 per cent. moisture. These figures indicate that as the larva increases the depth of its tunnel it enters a moister and thus a more favourable zone.

The field studies were done in April, before the break of the season. Weather in April should be more favourable for the species than the summer months because it is cooler and wetter. (Meteorological data for the three summer months and April at Mt. Gambier are given in Table 15). Also, larvae are living closer to the surface of the ground during the summer and so would be more exposed to heat and dryness.

TABLE 15

METEOROLOGICAL DATA FOR SUMMER MONTHS AND APRIL, MT. GAMBIER

Month	Mean Daily Temperature (°F)	Mean Daily Rel. Humidity (%)	Mean Daily Saturation Deficit (in. Hg)	Mean Daily Rainfall (points)
December	62.0	61	.247	166
January	64.8	58	.286	133
February	65.8	60	.274	107
April	58.1	75	.128	231

Except for the first two or three weeks of its life an _O. fasciculata_ larva lives in a subterranean tunnel and usually emerges only to feed. Having a subterranean habit, the larva would be exposed to excess wetness if the place in which it is living should become waterlogged. Waterlogging has not been seen on the well-drained soils of County Grey but is of great importance in limiting the numbers of the insect on the low-lying soils which may be flooded for part of the year (Section VI (c)). Little rain falls during the summer and it usually is not until late winter or early spring that the water table rises to the surface of the ground. In some situations the land may be under water for several weeks or more but usually the surface water drains away and the length of time that this land would be under water would depend on the amount and spread of the rain. Even when the surface water has drained away the soil may remain very wet and the larva would not be able to remain underground for long because there would be water in its tunnel.

Unfavourably wet conditions may cause a high death-rate among larvae, prepupae and pupae in two ways: indirectly by forcing individuals from their tunnels and exposing them to predators, and weakening them and making them more subject to attacks of virus, bacterial and fungal diseases; directly by drowning or exposure.

An examination of daily rainfall records for Mt. Gambier (typical of the well-drained soils) indicated that changes in the numbers of _O. fasciculata_ were closely associated with the number of "wet" and "dry" days during October-December. A day was counted as wet if one point or more of rain fell. During the late spring there are many days when the sky is overcast and there is a mist or occasional light fall of rain. Only a point or two of rain would be recorded on such a day but it was felt that eggs and larvae under herbage would be exposed to little or no evaporation. Figure 18 shows the fluctuations in the number of dry days during October-December at Mt. Gambier for the period 1933-54. This figure shows the close agreement between the relative numbers of _O. fasciculata_ and the weather during the late spring; a higher survival-rate could be expected when there were few dry days.

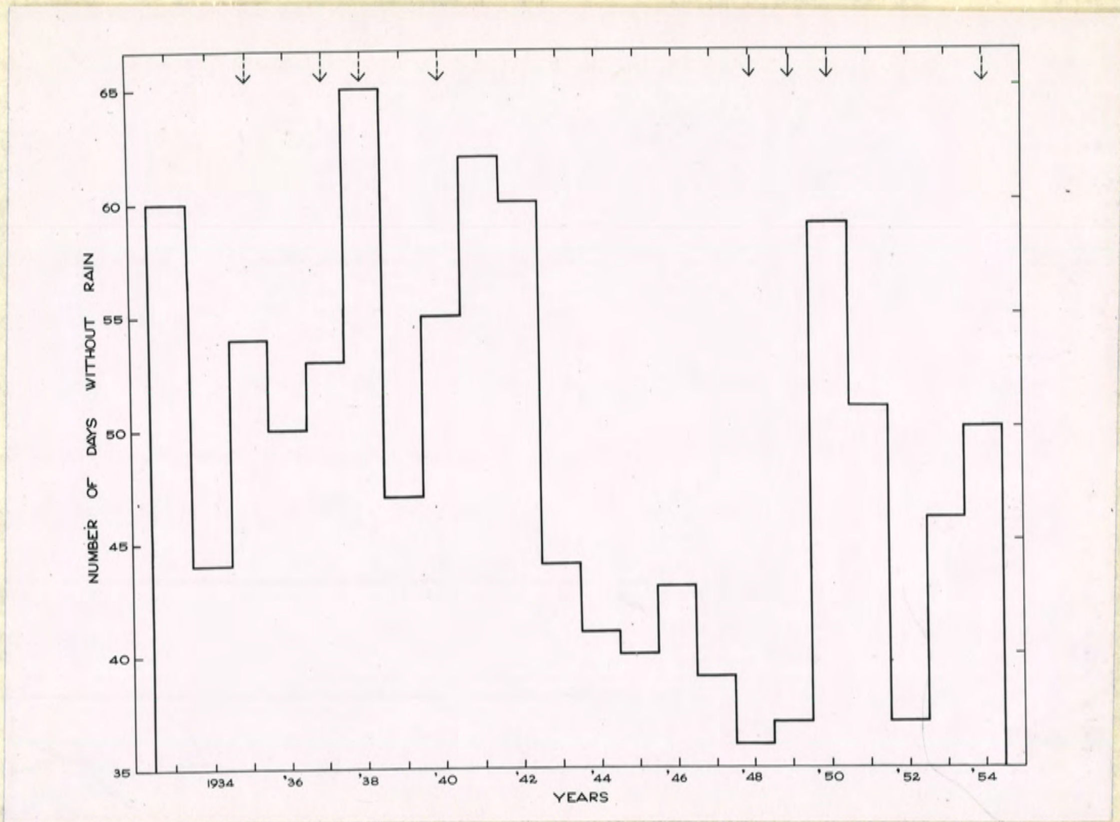

Fig. 18. Histogram showing fluctuations in the number of unfavourable (dry) days at Mt. Gambier during the late egg - early larval stages (October-December). Arrows indicate the relative abundance of O. fasciculata; small numbers are shown by broken shaft and large numbers by solid shaft. For further explanation see text.

It appears that the large numbers reported in 1935 resulted from the favourable weather during the previous spring. Reports indicated that O. fasciculata was abundant in 1937, 1938, 1940 and 1954; Figure 18 shows that there were relatively few dry days during October-December in 1936, 1937, 1939, 1952, and 1953. Similarly, the great outbreak of O. fasciculata which lasted from 1948 to 1950 followed a sequence of years from 1943-49 which was characterized by above-average rainfall and an unusually large number of wet days during the late spring. The evidence suggests that an increase in the numbers of O. fasciculata in any one year may be expected when there are fewer than about fifty dry days during the previous October-December, and economic loss to pastures might be expected when there is a succession of such years.

Examples of waterlogging on poorly-drained soils were seen during 1950-52 and the spread and amount of rain at Kalangadoo (typical of the poorly-drained soils) during July-September of these years were used to estimate the number of days when flooding probably occurred in other years. Fluctuations in the number of "wet" days during July-September at Kalangadoo for the years 1941-54 are shown in Figure 19. It seems reasonable to suggest that the almost complete absence of waterlogging during 1948-49, in addition to favourable weather during the late spring of these years (see Figure 18) allowed a higher survival-rate and was the cause of the outbreak of O. fasciculata which resulted in severe damage to pastures in the Kalangadoo district in 1950.

It would seem that, in this sort of country, O. fasciculata is likely to increase in numbers whenever a favourable (i.e., moist) late spring is followed the next year by a winter in which the rainfall is not severe enough to cause more than about two or three days of flooding during late winter or early spring.

The probable explanation of changes in the distribution and abundance of O. fasciculata during 1948-54 is as follows: Weather

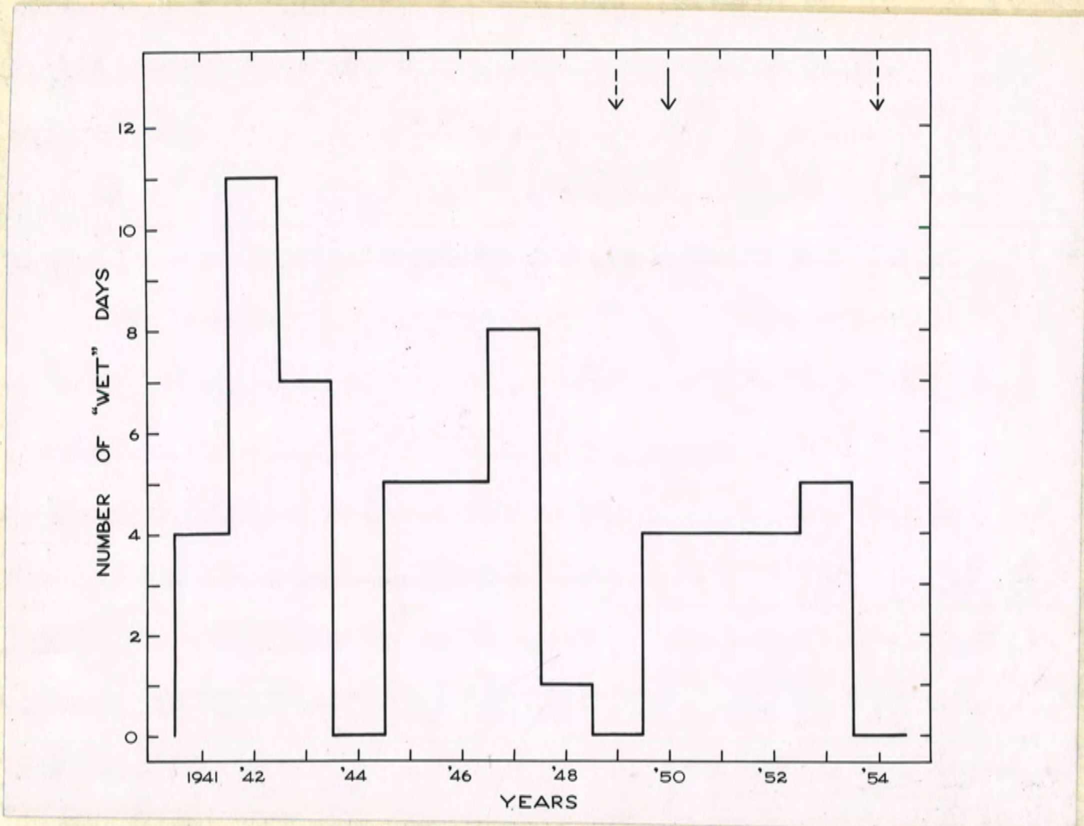

Fig. 19. Histogram showing the number of unfavourable "wet" days at Kalangadoo during the mature larval-pupal stages (July-September). A day was considered as "wet" if flooding was likely to occur. Arrows as in Figure 18. For further explanation see text.

during the late springs of 1943-47 was very favourable and there would have been a corresponding increase in the numbers of the species during those years on the well-drained soils. The use of superphosphate and the absence of livestock on land being developed for soldier settlement would have provided ideal conditions on this land. The late winter of 1947 was very wet and so in 1947 the insect would have been abundant on the well-drained soils but restricted to the higher, drier portions of the poorly-drained soils. Weather during the late winter and late spring of 1948 was very favourable, resulting in a further increase in numbers on the well-drained soils and a high survival-rate on the poorly-drained soils. Weather again was favourable during the late winter and late spring of 1949, so there would have been a high survival-rate on both the well-drained and poorly-drained soils. The late winter and late spring of 1950 were unfavourable and there would have been a very low survival-rate on both types of soil. In 1950, most of the land under soldier settlement was carrying sheep and dairy cows and feeding by these livestock would have resulted in a still less favourable environment for O. fasciculata.

Weather was slightly kinder during the late spring of 1951 but only the higher portions of the poorly-drained land would have been favourable for the development of the insect because of the wet winter. The late spring of 1952 was very favourable and there would have been a high survival-rate on the well-drained soils as well as the higher portions of the poorly-drained soils. Because of the favourable weather during the late spring of 1953 the numbers would have increased on the well-drained soils as well as on those portions of the poorly-drained soils which were not waterlogged during the wet late winter.

The moderately favourable late spring and favourable late winter of 1954 probably would have resulted in a maintenance or slight increase in numbers of the species on both the well-drained and poorly-drained soils.

(b) Places Where O. fasciculata May be Found

(i) Pastures

It would seem that O. fasciculata requires a particular sort of place in which to live. Because of the special behaviour of the moths, eggs are not likely to be laid except in places where the type of cover attracts moths during the mating flight. Places which appear to be ideal for the development of O. fasciculata have not been colonized simply because gravid females were not attracted there to lay eggs. Most farms in County Grey have lawns near the houses and these lawns are watered during the dry summer months, as are lawns in the towns, yet few such lawns were found to be infested with O. fasciculata larvae. Larvae are not usually found in large numbers in any one place for two years in succession, even when weather is favourable. This is because adults are not attracted to areas which have been eaten bare by larvae, and few or no eggs would be laid. Also, the feeding by larvaeusually results in weeds unsuitable as food for larvae replacing the grasses and clovers.

The sort of place where a larva is living may also influence its chance to survive the hazards associated with excessive dryness or excessive wetness. For example, some situations may contain suitable breeding sites and abundant food for larvae but the type of pasture growth does not provide sufficient protection against unfavourable weather and few individuals survive. It would appear that this interaction of place in which to live with weather helps to explain why the species is found only in small numbers on natural grasslands even during years when the weather is favourable, and why it is able to increase so greatly in numbers on improved pastures during favourable years.

Soil type does not restrict the establishment of the insect, for it is found on soils ranging from a heavy black clay to an aeolian sand. However, topography is of great importance and there are critical periods on both the well-drained and the poorly-drained soils. On the well-drained soils the most hazardous period for O. *fasciculata* appears to be during the late egg stage and the early larval stage (October-December), when exposure to extreme dryness may cause a high death-rate. Because of the nature of growth of natural grasslands and unimproved pastures, eggs and larvae in these situations may succumb even in a year when weather during the late spring and early summer was favourable enough to allow a high survival-rate in other places. On improved pastures, however, and especially those which had not been heavily grazed by livestock, growth would be dense and would provide shelter against unfavourable weather. Twenty-two square-foot samples were taken in a paddock in April, 1954, to compare the numbers of larvae in dense herbage and in sparse herbage. Eleven samples were taken at random from each of the two types of cover; the mean value for the dense herbage was 6.8 larvae per square foot and was 1.6 larvae per square foot for sparse herbage.

The development of pastures on land being prepared for soldier settlers should be mentioned because it appears that this development helped to provide an ideal environment for O. *fasciculata*.

(The following information was obtained from F.B. Pearson, District Agricultural Advisor for the lower South-East of South Australia). Most of the land for closer settlement was obtained from large properties south of Mt. Schank, south-east of Tantanoola, north-east of Mt. Gambier and around Kalangadoo. Pastures on this land were of poor quality because before World War II it was not a common practice to use superphosphate except in particular paddocks (lambing paddocks, etc.), and this fertilizer was very scarce during the war. It is very likely that most of the land taken over for soldier settlement received its first liberal application of superphosphate in 1947. This treatment in 1947 would have resulted in about a fifty per cent. increase in the bulk growth of the pasture plants, for the fertilizer would have stimulated the growth of subterranean clover, and a large amount of seed would have been produced. There were no soldier settlers or livestock on the blocks that year. The blocks received a second application of superphosphate in 1948, which would have resulted in about a two hundred per cent. increase in growth of pasture plants; there would have been more clover and, because of the greater amount of nitrogen available, an increased growth of grasses. Some settlers moved onto their blocks late in 1948 (houses were not built and they lived in sheds) and the only stock were a few dairy cows; it was not until 1950 that blocks reached the stage where sheep could be introduced. The result of this development was that during 1947-49 there was a very great increase in the amount of herbage on soldier settlement blocks, and this cover, plus the favourable late springs of these years, would have favoured the multiplication of the species.

When the October-December period is extremely unfavourable, most individuals would die except those in the wettest portions of the improved pastures. A few places were found where it appeared that O. fasciculata would not be exposed to extreme dryness even during a very dry period in late spring-early summer. Two of these "outbreak centres" were at Mil Lel, one was near Mt. Schank and one at Yahl; all were in depressions in paddocks of improved pastures. These places would provide shelter against extreme dryness and, because of the nature of the soil, O. fasciculata would not be exposed to drowning.

On the low-lying, poorly-drained soils, the environment during the late spring and early summer is not as dry as on the well-drained situations. The most hazardous period is during the late winter and early spring, when the poorly-drained soils may become waterlogged. Whether or not a particular situation becomes waterlogged depends not only on the total amount of rain but also on when it falls. A "wet" winter may not be unfavourable (except in the lowest situations) if the rain is spread evenly, while a "dry" winter may be unfavourable if there are heavy falls of rain toward the end of the season. Even when there is extensive flooding some individuals are not exposed to the wet conditions because they are living on the higher, drier banks of land. The sort of pasture growth is also important because a larva might escape the wetness if it could crawl upward into some tussocky growth.

Although O. fasciculata usually is found as a rare species on the heavy black soils, pastures have been damaged in some years when these places have not become too wet during the winter and early spring. The black field cricket, Acheta commodus, is restricted mainly to these heavy soils because few eggs (present in the winter and early spring) will survive if exposed to dryness, and the black soils have a high water-holding capacity (Browning, 1954). In these places, then, a wet winter would be favourable for A. commodus because the eggs would not be exposed to desiccation, but would be unfavourable for O. fasciculata because larvae, prepupae and pupae would be exposed to extreme wetness.

The abundance of O. fasciculata in any one year depends to a large extent on the number and distribution of favourable situations. Before County Grey was settled and developed there would have been few places providing shelter for the insect during the critical October-December period and which were not too wet in the winter and early spring. It seems that O. fasciculata would have been restricted to the lower, wetter portions of the well-drained soils, and the higher land on the poorly-drained soils. Even on the wetter portions of the well-drained land, there would have been a high death-rate in most years because the sparse growth of native grasses would not have provided suitable protection against dryness. Numbers on the poorly-drained soils may have been restricted mainly to places where the native grasses were of a tussocky nature, enabling larvae to escape when the area became waterlogged.

As the native grasses were replaced by introduced clovers and grasses, more situations, especially in areas of high, well-drained soil, became favourable for O. fasciculata because this growth provided a better protection against dryness and heat. Also, the artificial drainage of the poorly-drained soils meant that less of this land would be flooded, and so the insect would be able to survive over a wider area.

Because of the present system of "permanent" pasturing in County Grey, a large proportion of land is favourable for O. fasciculata for it contains good stands of grasses and clovers which are seldom disturbed by being ploughed and sown to crops. Even though this sort of place may be favourable, in that the soil is suitable for the tunnelling larva and good quality food is available, O. fasciculata is unable to increase greatly in numbers unless the weather is favourable. With a succession of favourable years, the insect could be expected to increase to plague numbers.

Although larvae may be able to survive in natural sclerophyll woodland where there are native grasses, only one larva was found in such a situation during this study. This larva was found in a small clearing in a thicket of red gum trees and saplings north-west of Kalangadoo; the tunnel was at the base of a clump of thatching grass (Cladium filum). A careful search was made of the clearing but only the one larva was found. Natural woodlands must be very unfavourable for the establishment of O. fasciculata because there would not be a suitable food supply and there would be little or no protection against dry conditions during October-December; Figure 20 shows a typical view of natural sclerophyll woodland on a well-drained soil.

Fig. 20. A dry sclerophyll forest on well-drained sand. The tree is E. baxteri and undergrowth is composed of Banksia marginata, Pteridium aquilinum and Xanthorrhoea spp.

Larvae were not found in pine plantations. Bracken fern is associated with young plantings but as the trees grow the fern disappears and only a mat of pine needles is found under them. One would not expect to find O. fasciculata here because it is not the sort of place where mating flights or egg-laying would occur, and it is doubtful whether larvae would survive on a diet of pine needles.

Fig. 21. Native grasses on the poorly-drained soils usually have a tussocky habit; here is shown white tussock grass (Poa australis) on a heavy, black soil.

Undeveloped, poorly-drained soils would be unfavourable places for O. fasciculata because of the poor-quality food and wet conditions during the winter and spring. Grasses in these places are tussocky in nature, as can be seen in Figure 21, which shows white tussock grass (Poa australis) on a rendzina soil. When these soils have been developed and are carrying introduced grasses and clovers, conditions still remain unfavourable because the insect may be exposed

Fig. 22. Flooding of a heavy, black soil which carries a well-developed pasture. O. fasciculata has little chance to escape drowning in this sort of place.

to drowning. Figure 22 shows sheet flooding which occurred on a rendzina soil near Millicent in July, 1951. This was taken after the weather had become clear enough for photography; the flooding had been much more extensive the two previous days. A sclerophyllous heath vegetation usually is found on the poorly-drained sandy soils (Figure 23) and it is doubtful whether O. fasciculata ever occurred on this country before it was cleared; the limiting factors being the wet conditions and the absence of a suitable food.

Fig. 23. Typical heath country on a poorly-drained, sandy soil. In the foreground are Banksia sp., Xanthorrhoea sp. and other vegetation associated with these wet soils. In the background, on slightly higher land, are E. baxteri and associated vegetation.

(c) Food

Both the quantity and quality of food are important factors in limiting the development of natural populations of O. fasciculata because the larva must not only obtain enough food to stay alive but must build up reserves to carry it through the prepupal, pupal and adult stages and also to produce eggs or sperm, for the adults do not feed. Larvae have been found so numerous that all of the green herbage has been eaten and then they fed on the old dead stubble remaining from the previous year, or bracken or certain weeds. In such cases it might be expected that the poorer quality food might cause a reduction in the fecundity of the adults which emerge (see Andrewartha and Birch op. cit., Chapter 11). A low rate of increase might also be expected when the food is composed of native grasses, for these are very fibrous and are low in protein. It would seem that before the introduction into the district of clovers and better grasses, the numbers of O. fasciculata may have been restricted by the poor quality of the native grasses. For about the last twenty-five years, the quality of pastures has been improved by the use of superphosphate, trace elements and improved grasses (including perennials) and clovers, and this pasture development must have had an important influence on the fecundity of the insect.

Food usually is abundant but in most places during most years O. fasciculata is rare, compared with the food available. Because of the patchy distribution of the larvae it sometimes happens that local situations are eaten bare. In 1950 many places north of Kalangadoo were severely damaged and because of the very dry conditions there was little regrowth of perennials or germination of annuals (feeding by larvae could be expected to reduce the rate of growth of perennials). What growth there was following slight rains was quickly eaten. Similar conditions were seen at Kaladbro, in Western Victoria. Here, however, there was even less rain and starvation must have killed many larvae. In contrast, there was abundant rain in 1951 and although there were a few places where larvae were numerous, there was a surplus of food and the larvae did not eat all of the herbage.

Larvae which have become established in tunnels apparently do not leave them when the food supply is exhausted, and will remain until food again becomes available or they die. This has been seen many times - areas in a paddock eaten bare, with larvae still in their tunnels, although abundant food may be no more than a few feet away. It is quite certain that the larvae do not crawl across to the nearby pasture, feed, and then return to their tunnels, for there is no evidence of webbing or any other means by which a larva could find its way back to the tunnel. Also, there is little sign of activity around the entrances to the tunnels and most of the silken caps covering the entrances are collapsed.

(d) Other Animals

(i) Animals of the Same Kind

In the field, _O. fasciculata_ is distributed patchily, and even in places where the insect is scarce larvae are more likely to be found in groups than as isolated individuals. This sort of distribution may be explained by the behaviour of the gravid female. After mating, which usually takes place on upright stems or leaves in the paddock, the female crawls down into the herbage and comes to rest under surface debris, where most of the eggs (_ca._ 1,000) are laid. For this reason the largest numbers of _O. fasciculata_ would be expected where pasture growth was upright, and in these places the distribution of the population would be determined largely by where the females came to rest.

This behaviour of the female may have been of great importance to the species in the circumstances in which it originally lived in this area before the development of improved pastures, because it would result in eggs being laid in the tussocky growth of native grasses. Here the eggs and larvae would be less exposed to dryness, larvae would emerge with food nearby and the tussocks would provide a retreat for the larvae when the soil became waterlogged. Also, the communal webbing spun by many larvae may provide better protection than a solitary larva can provide for itself.

Today, with the widespread development of improved pastures, most larvae of O. fasciculata live in places which provide just as much protection for a solitary larva as for a group (see VI (a)). As solitary larvae would also be less likely to experience a shortage of food than members of a dense group, it is difficult to imagine any advantage from having eggs laid in groups. The disadvantage may be all the greater if, as seems likely, the fecundity has increased with the appearance of a better quality food, and so more eggs might be expected to be laid now by a female than when there were only native grasses. It seems best to consider that this behaviour of the female in laying all, or most, of her eggs in a dense group is an adaptation to an environment which has virtually disappeared since the land in this area has been intensively developed for agriculture. It follows that, if during the course of time, O. fasciculata evolves in the direction of scattering its eggs instead of laying them in groups, the species may become even more abundant and a worse pest than it is at present.

(ii) Animals of Different Kinds

Sheep, rabbits and the pasture cockchafer (*Aphodius howitti*) are potentially important components of the environment of *O. fasciculata* because they eat the same sort of food. Sheep usually are of minor importance because as food becomes scarce the owner removes his sheep and there still is abundant food for the insect. With its subterranean habit, the older larva is in little danger of being crushed by sheep or larger animals. However, sheep feeding on herbage during October-November might kill eggs and young larvae directly by crushing them and indirectly by exposing them to unfavourable weather; this would happen only when there were enough sheep to keep the pasture short during the late egg and early larval stages.

The area around rabbit warrens usually is unfavourable for *O. fasciculata* because the rabbits keep the herbage closely-grazed and there is a large proportion of bare ground. Further from the warrens the feeding is less concentrated and the amount of damage to pasture, and the influence of this animal on *O. fasciculata*, depends largely upon seasonal rains.

Larvae of *A. howitti* live in vertical tunnels in the soil and emerge to feed on surface growth. The behaviour of these larvae differs from that of *O. fasciculata* larvae in that the former migrate from places which have been eaten bare and so produce bare patches which increase in size during the feeding period. These two insects have been found living close together when the total numbers were few, but when one species was abundant the other was scarce. Females of *A. howitti* seem to prefer open areas in a pasture for egg-laying (Andrewartha, 1945) while most *O. fasciculata* eggs are laid where pasture is thick. This means that where the one insect is abundant the other would not be expected to be found in large numbers because few eggs would be laid. The mating flights of *A. howitti* take place about February, before *O. fasciculata* larvae have bared any pasture, and so eggs are more likely to be laid where either insect had caused damage the previous year. When the two insects are living close together it would seem that larvae of *O. fasciculata* would have an advantage because they would be about half-way through their development before *A. howitti* larvae appear (*ca.* March). Predators and parasites are considered to have very little influence on the numbers and distribution of *O. fasciculata*. No parasites were found and the most important predators (birds) were effective mainly when unfavourable weather had forced larvae, prepupae and pupae from their tunnels.

XII CHANGES IN THE ENVIRONMENT OF O. FASCICULATA ASSOCIATED WITH THE DEVELOPMENT OF THE LOWER SOUTH-EAST FOR AGRICULTURE

(a) Natural Vegetation and Physiography

Before it was modified by white settlers, County Grey would have been composed mainly of sandy ridges covered with a dry sclerophyll forest, and flats and plains under water for at least part of the year and carrying rushes, sedges and other coarse, reedy growth. Only a small proportion of thetotal area would have been suitable for grasses and so the distribution and abundance of O. *fasciculata* would have been limited by the food supply, as well as the wet conditions on the flats and plains.

The region may be divided roughly into three main groups: (1) low-lying land which may be continuously under water (swamps and lagoons) or exposed to seasonal flooding; (2) well-drained land supporting trees and shrubs and little or no grass; (3) well-drained land supporting trees and shrubs with an undergrowth of grass.

(i) Poorly-drained Land

Swamps are plentiful in County Grey even today; they were much more extensive before artificial drainage was started. The natural vegetation associated with swamps varies considerably, for the swamps themselves vary in salinity as well as in soil type. The main plants are Tea-tree (*Leptospermum* spp., *Melaleuca* spp.), thatching grass (*Cladium* spp.) and cutting grass (*Gahnia* spp.). (Eardley, 1943).

Two types of soil are associated with low-lying land - the heavy rendzinas and the sandy soils.

Trees are almost completely absent on the rendzina plains. Some honeysuckle (Banksia marginata) is present but the dominant plant species are white tussock (Poa australis), cutting grass and thatching grass. Honeysuckle apparently was common before artificial drainage, and Woods (1862) described honeysuckle country as "...extensive flats or plains growing little else but coarse rank grass and Banksia, covered with water in winter". An idea of the natural appearance of the rendzina plains may be obtained from Woods' description of German Flat (south-east of Tantanoola) and the flat at the foot of Mt. Graham in the Mt. Burr range. East of the dune along the eastern side of Lake Bonney was "....a long swamp which runs parallel with the range for the whole length of the lake. It is twenty-five miles long and three wide. Here and there, places may be found where it is passable, but, in general, it is an immense quagmire, thickly covered over with dense reeds". He described the flat at the foot of Mt. Graham as "...a large morass of very deep, black mud. This trends away along the east side of a range of hills [West Avenue Dune] in a north-westerly direction, until it becomes, in a mile or so, a perfect channel, about half a mile wide, containing little or no water, but very boggy, and covered with reeds". These black flats, therefore, would have been very unfavourable for O. fasciculata. Some small, isolated situations may have been dry enough for the insect to complete its development but the food supply available would have had little nutritive value, being mainly of a coarse, reedy nature.

On the more fertile sandy soils (meadow-podsols), the natural vegetation is of a characteristic sclerophyll woodland type. The dominant tree is the red gum (E. camaldulensis); undergrowth is composed of red gum saplings, Banksia spp., Acacia spp. and bracken fern (Pteridium aquilinum). Grasses are found on the higher banks, and sedges and rushes on the wetter land. Native grasses on the higher land are mainly species of wallaby grass (Danthonia spp.); some of the other common native perennial grasses are spear grass (Stipa setacea), kangaroo grass (Themeda australis) and weeping rice grass (Microlaena stipoides).

A description of the appearance of this type of country before settlement by white man is given by Molineux (1882). He described the district near Penola as "...quite a swampy country in wet weather, with good grass wherever the land is slightly elevated. There is a deal of coarse vegetation all over it, consisting of rough grass, rushes, and sedges principally, with plenty of gums".

Before artificial drainage, most of this meadow podsol country was under water for at least part of the winter-spring period. Some of the higher land would have been dry enough for O. fasciculata but, as with the black flats district, only a poor quality food supply would have been available.

A sclerophyllous heath vegetation grows on the less fertile low-lying sands (podsolized sands). This country is characterized by a low, stunted vegetation made up mainly of Banksia spp., yacca (Xanthorrhoea spp.), kidney bush (Hakea spp.), oak bushes (Casuarina spp.)

and tea-tree (Leptospermum scoparium). Yacca and honeysuckle are dominant on the higher sandy banks. Woods' (op. cit.) description of these sandy plains was "...heavy and dusty in summer and boggy in winter, supporting no grass nor any trees but those of a stunted and worthless character, run through, here and there, with belts of short and crooked 'stringy bark' and in all other places covered with tangled brushwood, about two feet high". It is doubtful whether O. fasciculata ever occurred on this country before it was cleared; the limiting factors being the wet conditions and lack of suitable food.

(ii) Well-drained Land with Little or No Herbage

The natural vegetation of the stranded dunes is a dry sclerophyll forest with stringybark (Eucalyptus baxteri and/or E. obliqua) the dominant tree. Beneath the tall trees are a few tall shrubs or small trees, the main ones being Acacia spp., Banksia spp., and native box (Bursaria spp.). Undergrowth consists of tea-tree, yacca, Acacia spp. and bracken fern. Much or this dune country still remains under natural forest, although fires have changed the composition of the undergrowth; bracken fern recovers quickly after fires and becomes much more abundant. In the higher rainfall areas the dunes have been cleared and planted with pines.

Woods (op. cit.) said that the sandy dunes "...are nearly destitute of grass, but are very shrubby, rarely supporting any other tree but a stunted and irregular growth of Eucalyptus Fabrorum, or stringy bark...". He described the hilly land between Mt. Gambier and Mt. Schank (Burleigh Dune) as being "...broken and very hilly. The soil, too, is less rich, as evidenced by the quantity of stringybark and grass tree. The ferns and underwood also become thick and intricate".

Another sort of sandy country, that in the Hundred of Caroline, was described by Ward (1869) as "...lightly timbered, chiefly with honeysuckle or sheoak and covered with ferns".

When surface limestone is abundant, sheoak, native box, honeysuckle and Acacia spp. are the prominent species. Bracken fern dominates the undergrowth and grasses are found occasionally.

Sand-dunes near the coast have been stablized by a dense scrubby vegetation consisting mainly of tea-tree, sheoak, sandalwood (Myoporum insulare), Acacia spp., native box, sandhill daisy (Olearia spp.) and others (Tiver and Crocker, 1951); there is little or no grass.

The almost complete absence of a suitable food supply, as well as the dry summer conditions, would have been the main factors limiting the establishment of O. fasciculata on this country.

(iii) Well-drained Land with Herbage

The original natural vegetation of this land is difficult to determine because it contains the richest soil in the lower South-East and was the first to be cleared for agricultural purposes. The vegetation probably was characterized by an association dominated by stringybark, with honeysuckle, Acacia spp. and bracken fern also prominent (Tiver and Crocker, op. cit.). There would have been a ground cover of grass. Although there are no trees on Mt. Schank today, Grant (1803) described both Mt. Gambier and Mt. Schank as being covered with large trees "...as also was the surrounding land, which was low and flat". Woods (op. cit.)

described the uncleared country around the two mountains as being "...well and almost thickly wooded".

Although O. fasciculata would not have been exposed to drowning on this land, and food would have been available, the well-drained nature of the soil would have meant that the insect would have been exposed to dry conditions during the summer droughts. Early settlers found it difficult to grow crops on the volcanic soils because the soil became so dry in the summer.

Ward (op. cit.) said that the soil around Mt. Gambier was of the "richest character" but that it had one drawback: "...the subsoil is exceedingly porous, and however much rain may fall, it is so quickly absorbed that the crops, especially those which require moisture late in the summer, frequently suffer materially in consequence". However, where clay underlies the top soil, moisture is not lost so quickly; this occurs in the Yahl Paddock area, four miles south-east of Mt. Gambier. The fertile soil overlying the clay makes this district one of the richest in the State; here, also, conditions would have been most suitable for the survival and development of O. fasciculata. It is interesting to note that the first collections of O. fasciculata were made at Yahl Paddock in 1896.

Grasses would have grown on this well-drained country, and in other parts of the County, but they would have been of very poor quality compared with the improved pastures found there today. The original grasslands were high in fibre and low in proteins, for there were no natural medics or clovers (Tiver and Crocker, op. cit.).

(b) Settlement by Europeans

The history of the south-east began in 1800 when Lt. James Grant, R.N., in H.M.S. "Lady Nelson" sighted the southern coast. He discovered two peaks and named them Mt. Gambier and Mt. Schank. The first white men entered the district from a cattle station in western Victoria in 1839. They were droving a herd of cattle to Adelaide; the route previously taken followed the northern side of the River Murray. The group passed through the Mt. Gambier district and followed the coast to Lake Albert at the Murray mouth. The river was crossed further inland and the party then travelled through the Mt. Lofty ranges to Adelaide. This discovery of a shorter route from western Victoria to Adelaide was of great importance as the time taken was one-quarter that taken along the old route.

When Mr. C. Bonney, leader of the group, returned to Victoria he told of the grazing possibilities of the area around Mt. Gambier, and S.G. Henty and two others explored the district the same year (1839).

The first occupation licences for land in the South-East were issued from Adelaide in 1841. Interest in the district grew and in 1844 Governor Grey organized an expedition to examine the area; Lt. Governor Robe later explored the coastal district.

County Grey was proclaimed in 1846, ten years after the Province of South Australia had been founded. In July, 1851, the first pastoral leases (about eighty) were issued. An idea of the agricultural usefulness of the County may be got from the dates when the Hundreds were proclaimed. (see Figure 1 for distribution of Hundreds - a

Hundred is a local government subdivision of about 100 square miles in area). The Hundreds of Blanche, Gambier, Grey, Hindmarsh, MacDonnell and Young were proclaimed in April 1858, following the resumption of a number of pastoral leases which were subdivided and allotted in smaller areas. In this area are the fertile volcanic soils around Mt. Gambier and Glencoe, the meadow podsols around Kalangadoo and the terra rossa soils between Mt. Gambier and Port MacDonnell. The Hundreds of Monbulla and Penola were proclaimed in 1861, followed by Benara, Kongorong and Caroline in 1862. The soil west of the township of Penola is a terra rossa and suitable for various forms of agriculture but most of the remaining land in the Hundreds of Monbulla and Penola is low-lying podzolized sand or sand-dune ranges and both are poor soils. The Hundreds of Benara, Kongorong and Caroline have some terra rossa soils but much of this region is composed of poorer land. Other Hundreds in the County were not proclaimed until later. Although there are some very valuable soils in parts of these Hundreds, little settlement could be started until the land was drained.

Cultivated crops appeared soon after the pastoral settlement of County Grey. Woods (op. cit.) mentioned the green patches of cereal crops around Mt. Gambier in 1862. Whitworth (1866) said that Allendale (between Mt. Schank and Port MacDonnell) "...is an agricultural district growing wheat, oats, hay and potatoes...". He described Kalangadoo as having "...some fine agricultural land, growing wheat, oats and potatoes". The first cultivated crops, then, were grown in the districts with the more fertile soils. By 1865 good crops of flax were grown at Yahl Paddock and "artificial" (introduced) grasses were planted, some of which were cocksfoot (Dactylis glomerata), Yorkshire fog (Holcus lanatus) and perennial rye-grass (Lolium perenne). The area under cultivation increased during the latter part of the nineteenth century; cereals were the most important crop but the acreage under potatoes increased and flax and hops were grown.

By 1880 the Mt. Gambier district produced large crops of "artificial" grasses. These introduced grasses did well on the more fertile soils but the practice of sowing improved pastures (and the subsequent reduction of the area under cultivation) did not become widespread until the 1920's, following the discovery that superphosphate had to be applied to the poorer soils before introduced clovers and grasses would grow well.

(c) Development of Improved Pastures

South Australia has an area of 380,070 square miles; however, 85 per cent. of this land is arid and receives, on the average, less than ten inches of rain annually. Only five per cent. of the land receives more than eighteen inches of rain each year and, for the most part, the soils receiving this rain are low in fertility. Native grasses in the higher rainfall areas have developed under three important environmental conditions: (1) soils low in readily-available phosphate; (2) climate characterized by summer drought; (3) mild influence of light-grazing marsupials.

As mentioned earlier, legumes and grasses were introduced into County Grey soon after settlement began but did not do well except in certain areas. The turning point in pastoral history was about 1923, when superphosphate was first used for manuring grasslands. Soon afterwards it was found that subterranean clover (Trifolium subterraneum) was very valuable on some soils. This plant appeared accidentally but it soon became of great importance when graziers realized how productive it was and how easily it could become established when adequate superphosphate was applied. Subterranean clover has several unique features; seed is set beneath the surface of the soil and so is safe against grazing animals, it does well on the acid soils of the higher rainfall areas, is high-yielding and a good summer feed. It appeared in the Adelaide hills about 1880 and the collecting and selling of seed began in 1906 (Hill, 1936).

When superphosphate is added annually to cleared woodland, subterranean clover may appear, as well as other introduced legumes. Following the increased clover growth, various grasses increase in density because the clovers make available more nitrogen. Continued top-dressing with superphosphate leads to a greater development of subterranean clover, and native grasses are replaced by volunteer annual grasses, as silver grass (Vulpia myuros), barley grass (Hordeum murinum) and great brome (Bromus rigidus); the perennial grass Yorkshire fog also appears.

The next stage in the development of grazing land in County Grey, which began in the 1930's, was the sowing of perennial grasses into subterranean clover pastures and the discovery of legumes for soils where subterranean clover did not grow well. The usual practice now is to sow subterranean clover and one or more of Wimmera rye-grass (Lolium rigidum), perennial rye-grass, Yorkshire fog, Phalaris (Phalaris tuberosa) and cocksfoot. On the heavier or more alkaline soils, subterranean clover is replaced by strawberry clover (Trifolium fragiferum), which is adapted to wet winter conditions and will survive several weeks of flooding. Other legumes planted on the wet soils are black medic (Medicago lupulina), red clover (Trifolium pratense), white clover (T. repens) and King Island Melilot (Melilotus indica).

An idea of the increased carrying capacity of sown pastures which are top-dressed annually with superphosphate can be obtained from the statement that uncleared woodland with sparse native pasture will carry about one sheep to three to five acres while the improved pastures will carry three to six and more sheep per acre (Stephens, et. al., 1941).

A later stage in pasture improvement was the discovery that most soils in County Grey are deficient in one or more of the trace elements copper, zinc, cobalt and manganese (Marston, et al., 1938). For instance, there was an improvement in pasture growth on volcanic soils when manganese was added, improved growth on terra rossa soils when copper was added, improved growth on podzolized sands when copper and zinc were added and improved growth on peaty soils when copper, zinc and manganese were added (Tiver and Crocker, op. cit.).

Each stage in the development of improved pastures in County Grey has resulted in a more favourable environment for O. fasciculata. The increased growth of clovers following the liberal applications of superphosphate would have provided eggs and larvae with a more favourable shelter against dryness and heat while still more favourable conditions would have appeared as a result of the growth of grasses being stimulated by the greater amount of nitrogen available. However, these annual pasture plants die when insufficient rain falls; perennial species, on the other hand, are able to use underground sources of water, and so the development of "permanent" pastures (growth composed of clovers and perennial grasses) has resulted in a greater quantity of herbage being present during more of the year. The incorporation of trace elements with dressings of superphosphate has improved the quality and quantity of pasture species and so also has improved both the amount of shelter and the quality and amount of food available to O. fasciculata.

(d) South-East Drainage Scheme

The first mention of the need for drainage to improve land in the lower South-East was made in 1863 by the Surveyor-General (G.W. Goyder) who was the first to realize that draining of the swamps would make a large area of land available for agriculture and would provide better road facilities (Parliamentary Paper 41/1863). Goyder recommended making cuttings through the narrow ridges (Woakwine Dune) separating the swamps in the Millicent-Tantanoola district from Lake Frome, and a complete survey of the whole of the swamps and dunes.

The first cutting, made in 1863, was four feet deep twelve feet wide and 528 feet long. This was a relatively minor undertaking, costing £81.12.10, and yet it made some very rich peaty soil available for farming. The immediate effect of the first cutting was to let off an immense body of water which had covered the Rendelsham-Millicent district or had moved slowly to the north-west. Ward (op. cit.) said that "Some of the slight rises on the flats that used to be covered as the waters moved down from the south, were 'reclaimed' and finer grasses appeared as the result... and the wet country was improved by the fact of the water being reduced and consequently disappearing so much earlier in the year". It was estimated (Parliamentary Paper 181/1864) that about 50,000 acres of fine agricultural land in the Millicent district would be available almost immediately.

Another job was to remove the surplus water from swamp land in the Hundreds of Riddoch, Grey, Kennion and Short. This involved cutting drains to connect with Reedy Creek, and clearing the creek of obstructions as far north as the Coorong. In 1878 Goyder estimated that 312,320 acres of good land (for cultivated crops) could be reclaimed from this district and 421,120 acres improved for pastures. This work began in 1882 and by the latter part of 1884 a hundred miles of channel had been cleared. Molineux (op. cit.) said that "...already a very large area of swamps is drained, and where at that time last year (1881) there were miles upon miles square covered with water, upon which all kinds of waterfowl were swimming, there is now a springy mass of dry turf, which rocks almost beneath the tread".

Three cuttings were made at Port MacDonnell during 1863-4 to drain that district, and a main channel (now called Eight Mile Creek) was dug about 1878. It was estimated that about 4,500 acres of rich land could be drained but this work was not finished until the World War II period.

Other drains dug during the 1880-1920 period helped to drain the country around Furner and Penola in County Grey and much of the land in the adjoining County of Robe. The drainage of the northern portion of County Grey was improved when a drain was dug from near Furner to the sea near Robe, in County Robe; this provided a much more direct approach to the sea.

Drains still are being dug and present plans are to complete the drainage program by 1956. Recent investigations included the problem of draining swamps to the north-west of Port MacDonnell, German Flat, south of Tantanoola, and the drainage of Dismal Swamp into the Glenelg River in Victoria. Dismal Swamp covers most of the Hundred of Mingbool and the eastern portion of the Hundred of Young, and its drainage was not attempted earlier because it was considered to be, to a great extent, on a sandy bed and comparatively worthless. With the present methods of improving pastures, this land could grow good pasture if drained; the fact that the water so drained would have to flow into another State has defeated this project.

The removal of surplus water from the flats and plains of County Grey has made a large proportion of the area favourable for the establishment of _O. fasciculata_. Some of the drained land, (especially the rendzina soils) is still too wet for the insect to survive, and in years of above average rainfall there is a high death-rate over most of the flats and plains. Even so, _O. fasciculata_ has been able to persist on this land which before artificial drainage would have been almost entirely unsuitable.

(e) State Softwood Industry

The softwood industry in South Australia started in 1870, when attention was drawn to the fact that the State had few suitable native timbers; these were restricted to a comparatively small area of stringybark, red and blue gum (Thomas, 1946). This area has since been reduced considerably, as these trees were growing on some of the best grazing and agricultural land in the State. The planting of pines began in 1876, the most important species being *Pinus radiata*; *P. pinaster*, *P. muricata*, *P. halipensis* and *P. caribaea* also were planted. By 1923 it was found that hardwoods would not make a satisfactory economic forest except under extremely favourable conditions and no hardwoods have been planted since then.

The planting of softwoods has continued progressively since 1876 and a large acreage was planted from 1926-36. By 1946 there were 161,138 acres of forest reserve, of which 81,072 acres were planted to pines (90 per cent. of the plantings were *P. radiata*) and the remainder was under natural sclerophyll forest.

Pine plantations are confined largely to the poorer soils of the dunes and Figure 24, when compared with the stranded dune system in Figure 2, shows the close relationship between land under forest reserve and the area of stranded dunes. Although *P. radiata* is grown successfully on these soils, dieback has been a serious disorder in some areas; spraying young trees with zinc sulphate eliminates this problem.

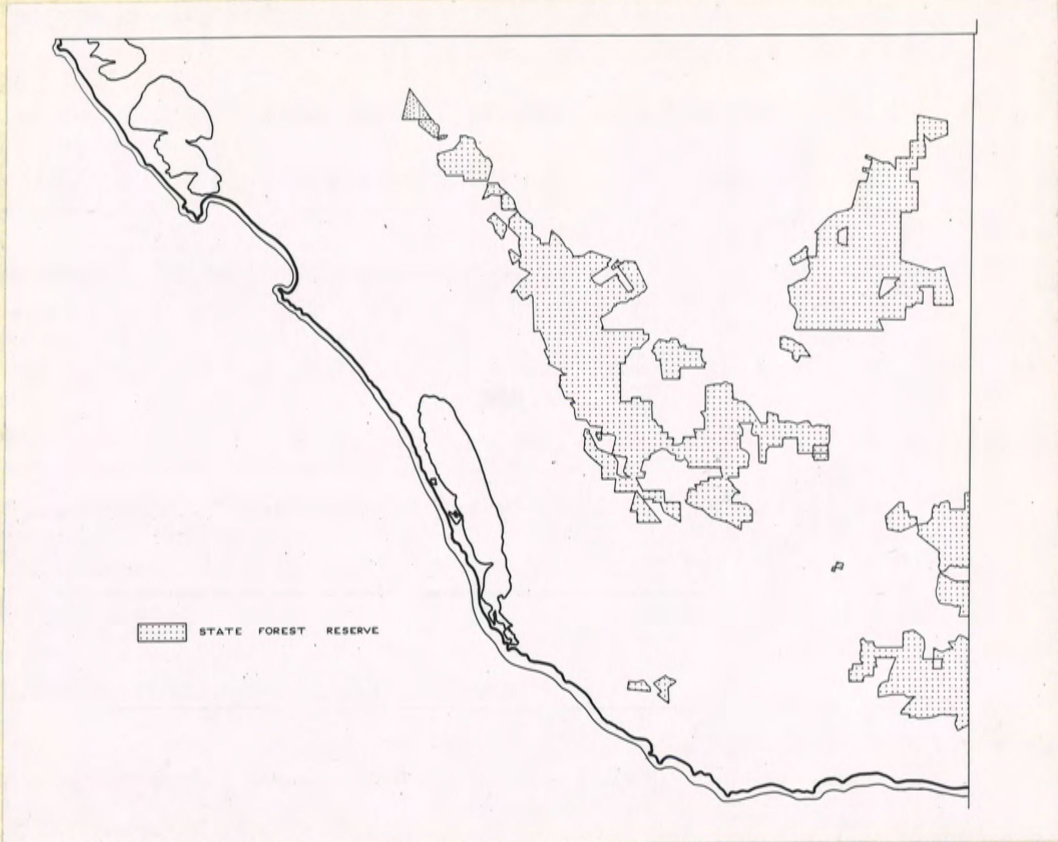

Fig. 24. Distribution of State forest reserves in County Grey. When this Figure is compared with Figure 2 it can be seen that reserve land is closely associated with the poorer soils of the stranded dunes. (Area under reserves obtained from Woods and Forests Department, Adelaide).

As artificial drainage has made more land available for agriculture, there has been a tendency to plant pines on these better soils, resulting in competition between the forest and pastoral interests for some of this land. Pines planted on the more fertile soils do better than those on the sandy dunes and there is less trouble with dieback and other disorders. However, there is a decrease in the quality of timber, for limbs are larger (large knots), annual rings are larger and trunks are more tapered (Stephens, *et al.*, *op. cit.*). It seems, then, that pines should be restricted to the poorer soils, and the more fertile land on the flats reserved for pasture development. It should be noted that there are some pines planted on soils which, before the advent of superphosphate and improved grasses and legumes, were considered unsuitable for growing good pastures.

Land included in the forest reserves is very unfavourable for the survival and multiplication of *O. fasciculata*. No living vegetation is found under the pines, and bracken fern is the dominant species on the firebreaks; vegetation associated with the sclerophyll forests was described earlier.

XIII CONCLUSIONS

The environment of O. fasciculata has changed greatly since the arrival of Europeans. Before settlers arrived, O. fasciculata must have been a rare species because there would have been very little suitable food, and individuals would have been confined to the lower, wetter portions of the well-drained soils and the higher, drier banks of the low-lying land. The total area suitable for the species would have been small and only in these places would it have been able to escape unfavourable weather during the late winter and late spring. Human activities, in the form of extensive destruction of trees, clearing of scrub country, draining of low-lying areas and the development of improved pastures, have resulted in a great increase in the area favourable for the development of the species, and its numbers have increased as a result.

Although O. fasciculata has become more abundant during the past century because man has provided a more favourable environment, the relative numbers and the distribution of the species are determined mainly by weather. The distribution is limited to the southernmost portion of the State where rainfall is reliable and comparatively abundant. Northward from this region O. fasciculata becomes increasingly rare until the area is reached where individuals are never found. This distribution is closely associated with an environment which becomes drier, and thus less favourable for the species, as one travels northward from County Grey.

In the more favourable southern region, O. *fasciculata* is restricted to situations where there is a suitable food supply of natural grasses or introduced herbage plants. The largest numbers of the species are found where pastures are composed of introduced clovers and perennial grasses; these plants provide the greatest amount of shelter against unfavourable weather in the late spring. In these favourable situations the numbers of O. *fasciculata* may increase tremendously when there is a succession of years with weather favourable for the species. A year would be favourable if the population were not exposed to extreme dryness during late spring (October-December) or waterlogging during the late winter (July-September). Even though a series of years of favourable weather resulted in a serious outbreak during 1948-50, O. *fasciculata* was scarce in many favourable situations. Unfavourable weather in 1950-51 (unusually dry late springs) caused a dramatic reduction in the numbers of the species before all of the favourable situations were occupied.

This study has shown that O. *fasciculata* has become of economic importance because the agricultural development of County Grey has provided a more favourable environment, enabling the species to increase in numbers. One way to reduce these numbers to a non-economic level would be by modifying the practice of "permanent" pasturing and thus provide a less favourable place in which O. *fasciculata* could live. By "permanent" pasturing is meant the development of pastures composed of clovers and perennial grasses, and the absence of a systematic rotation programme in which paddocks are ploughed and sown to cultivated crops. A rotation programme would reduce the area favourable for the species by eliminating both the amount of suitable food and the area of shelter.

Another way of making the environment of O. fasciculata less favourable would be to have as little herbage as possible in the paddocks during the flight period and the egg and early larval stages (September-November). This could be done by concentrating livestock on some paddocks while others are cut for hay in October or November and the cuttings removed as soon as possible. Few moths would be attracted to fields where herbage was low and so few or no eggs would be laid, and the absence of a dense cover of herbage would mean that these fields might be unfavourable situations during the late spring.

Even with these changes in farming practice, the relative abundance of O. fasciculata in any one year would be decided mainly by weather during the previous late winter and late spring.

XIV ACKNOWLEDGMENTS

A portion of this investigation was supported by funds from a grant by the Australian Wool Research Trust Fund.

The author is grateful to Dr. H.G. Andrewartha, Department of Zoology, University of Adelaide, for his stimulating guidance and suggestions while supervising these studies. It is a pleasure to acknowledge the encouragement offered by Mr. D.C. Swan, Head of the Department of Entomology, Waite Agricultural Research Institute. Dr. T.O. Browning, Department of Zoology, University of Adelaide, gave advice in the preparation of the manuscript, and the author also is grateful to him for helpful discussions.

The author wishes to thank many colleagues at the Waite Agricultural Research Institute for assistance; to Mrs. I. Mathison, for assistance with statistical problems; to Mr. K.P. Phillips, who prepared the photographs; and to Miss C.M. Hill, who drew the figures.

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APPENDICES

TABLE I

DURATION OF INCUBATION PERIOD AT CONSTANT TEMPERATURES. COMPARISON OF YEARS AND LOCALITIES

	1950 (Mil Lel)		1952 (Kal.)		1952 (Mil Lel)		1953 (Mil Lel)		
	Temperature (°C)	Duration $\log(\bar{y}_t - 10)$	Temperature (°C)	Duration $\log(\bar{y}_t - 10)$	Temperature (°C)	Duration $\log(\bar{y}_t - 10)$	Temperature (°C)	Duration $\log(\bar{y}_t - 10)$	
	9.8(±0.3)	1.67	8.0(±0.1)	1.86	8.0(±0.1)	1.86	10.0(±0.2)	1.64	
	12.8(±0.1)	1.39	9.7(±0.2)	1.64	9.7(±0.2)	1.65	13.4(±0.6)	1.23	
	16.9(±0.3)	0.98	13.0(±0.2)	1.36	13.0(±0.2)	1.36	16.9(±0.3)	0.93	
	20.8(±0.2)	0.52	14.7(±0.3)	1.18	14.7(±0.3)	1.17	21.2(±0.2)	0.52	
	25.2(±0.2)	0.00	16.8(±0.4)	0.99	16.8(±0.4)	0.98	26.7(±0.3)	-0.10	
			20.1(±0.4)	0.60	20.1(±0.4)	0.58			
			24.5(±0.2)	-0.22	24.5(±0.2)	-0.22			
	$\Sigma(x)$=85.5	$\Sigma(y)$=4.56	$\Sigma(x)$=106.8	$\Sigma(y)$=7.41	$\Sigma(x)$=106.8	$\Sigma(y)$=7.38	$\Sigma(x)$=88.2	$\Sigma(y)$=4.22	Total
	$\bar{x}$=17.1	$\bar{y}$=0.91	$\bar{x}$= 15.3	$\bar{y}$=1.06	$\bar{x}$= 15.3	$\bar{y}$=1.05	$\bar{x}$=17.6	$\bar{y}$=0.84	
$\Sigma(x-\bar{x})^2$	151.12		200.22		200.22		171.65		723.21
$\Sigma(y-\bar{y})^2$	1.7931		2.9357		2.9652		1.7861		9.4801
$\Sigma[y(x-\bar{x})]$	- 16.440		- 23.939		- 24.101		- 17.488		- 81.968
$\frac{\Sigma[y(x-\bar{x})]^2}{\Sigma(x-\bar{x})^2}$	1.7885		2.8622		2.9011		1.7817		9.3335
$\Sigma(y-\bar{y})^2 - \frac{\Sigma[y(x-\bar{x})]^2}{\Sigma(x-\bar{x})^2}$	0.0046		0.0735		0.0641		0.0044		0.1466
b	-0.1088		-0.1196		-0.1204		-0.1019		
Vy	0.00153		0.01470		0.01282		0.00147		
Vb	0.0000101464		0.0000734192		0.0000640296		0.0000085639		
Sb	0.00319		0.00857		0.00800		0.00293		
Linear Regression Equation	Y=2.77-0.1088x		Y=2.89-0.1196x		Y=2.89-0.1204x		Y=2.63-0.1019x		

TABLE II

ANALYSIS OF VARIANCE OF DATA FROM FIELD EXPERIMENT ON EGGS, 1951

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Blocks	2	23.10	11.55	-	NS
Egg Levels (L)	1	178.64	178.64	3.66	NS
Error (a)	2	97.56	48.78		
Method of Application (M)	1	162.88	162.88	17.95	5%
Egg Levels x Method (LM)	1	23.66	23.66	2.61	NS
Error (b)	4	36.29	9.07		
Type of Pasture (P)	3	573.26	191.09	16.42	0.1%
Mowing	1	388.97	388.97	33.42	0.1%
Thinning	1	162.29	162.29	13.94	1%
Mowing x Thinning	1	22.00	22.00	1.89	NS
Egg Level x Pasture (LP)	3	17.28	5.76	-	NS
Method x Pasture (MP)	3	17.67	5.89	-	NS
Egg Level x Method x Pasture (LMP)	3	5.32	1.77	-	NS
Error (c)	24	379.32	11.64		
Total	47	1514.98			

TABLE III

ANALYSIS OF VARIANCE OF LABORATORY EXPERIMENT ON EGGS, 1952

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Temperature (T)	1	116.57	116.57	4.45	NS
Levels of Evaporation (L)	5	136.08	27.22	1.04	NS
Egg Stage (S)	2	1986.24	993.12	37.95	0.1%
T x L	5	55.75	11.15	-	NS
T x S	2	289.17	144.59	5.53	5%
L x S	10	515.69	51.57	1.97	NS
T x L x S (error)	10	261.73	26.17		
Total	35	3361.23			

TABLE IV (a)

ORIGINAL WEIGHTS OF EGGS IN LABORATORY EXPERIMENT ON THE INFLUENCE OF WATER-LOSS ON SURVIVAL-RATE

		Levels of Evaporation						
Temp.	Group	0	1	2	3	4	5	6
13.4°C	1	2.44	2.52	2.24	2.24	2.38	2 36	2.38
	2	2.46	2.30	2.16	2.26	2.44	2.46	2.44
	3	2.31	2.48	2.22	2.29	2.46	2.50	2.58
	4	2.16	2.38	2.18	2.28	2.34	2.40	2.58
17.0°C	1	2.54	2.48	2.14	2.33	2.34	2.36	2.28
	2	2.46	2.50	2.14	2.34	2.24	2.32	2.56
	3	2.46	2.30	2.42	2.35	2.52	2.50	2.41
	4	2.37	2.18	2.32	2.46	2.46	2.42	2.32

TABLE OF TREATMENT TOTALS

	Levels of Evaporation								
Temp.	0	1	2	3	4	5	6	Σ	$\bar{x}$
13.4°C	9.37	9.68	8.80	9.07	9.62	9.72	9.98	66.24	2.36
17.0°C	9.83	9.46	9.02	9.48	9.56	9.60	9.57	66.52	2.38
Σ	19.20	19.14	17.82	18.55	19.18	19.32	19.55	132.76	
$\bar{x}$	2.400	2.392	2.228	2.319	2.400	2.415	2.444		2.371

Least significant difference between means of levels of evaporation :

5% level = 0.099
1% level = 0.133
0.1% level = 0.175

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Treatments	13	0.3433	0.026408	2.71	1%
Temp.	1	0.0014	0.0014	0.14	NS
Evap.	6	0.2604	0.043400	4.46	1%
T x E	6	0.0815	0.013583	1.40	NS
Residual	42	0.4089	0.009736		
Total	55	0.7522			

TABLE IV (b)

LOSS OF WEIGHT OF EGGS IN LABORATORY EXPERIMENT ON THE INFLUENCE OF WATER-LOSS ON SURVIVAL-RATE

		Levels of Evaporation						
Temp.	Group	0	1	2	3	4	5	6
13.4°C	1	0.04	0.21	0.10	0.26	0.61	0.49	0.57
	2	0.05	0.20	0.17	0.40	0.49	0.59	0.77
	3	0.11	0.33	0.20	0.31	0.55	0.55	0.60
	4	0.15	0.54	0.13	0.27	0.53	0.58	0.67
17.0°C	1	0.09	0.14	0.11	0.41	0.51	0.48	0.82
	2	0.08	0.28	0.12	0.30	0.58	0.50	0.70
	3	0.18	0.28	0.44	0.26	0.58	0.60	0.75
	4	0.07	0.17	0.34	0.52	0.62	0.67	0.72

TABLE OF TREATMENT TOTALS

	Levels of Evaporation								
Temp.	0	1	2	3	4	5	6	Σ	$\bar{x}$
13.4°C	0.35	1.28	0.60	1.24	2.18	2.21	2.61	10.47	0.374
17.0°C	0.42	0.87	1.01	1.49	2.29	2.25	2.99	11.32	0.404
Σ	0.77	2.15	1.61	2.73	4.47	4.46	5.60	21.79	
$\bar{x}$	0.096	0.269	0.201	0.341	0.559	0.558	0.700		0.389

MEANS WITHIN TABLE

	Levels of Evaporation						
Temp.	0	1	2	3	4	5	6
13.4°C	0.088	0.320	0.150	0.310	0.545	0.552	0.653
17.0°C	0.105	0.218	0.252	0.372	0.572	0.562	0.748

TABLE IV (b)
(Continued)

Min. diff. for signif. between means of levels of evaporation :

5% level = 0.090
1% level = 0.120
0.1% level = 0.158

Min. diff. for signif. within Table of means :

5% level = 0.127
1% level = 0.170
0.1% level = 0.223

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Treatment	13	2.4032	0.184862	23.54	0.1%
Temp.	1	0.0129	0.012902	1.64	NS
Evap.	6	2.3330	0.388833	49.50	0.1%
T x E	6	0.0573	0.009550	1.22	NS
Error	41	0.3221	0.007856		
Total	54	2.7253			

TABLE IV (c)

PERCENTAGE EMERGENCE OF LARVAE IN LABORATORY EXPERIMENT ON INFLUENCE OF WATER-LOSS ON SURVIVAL-RATE

		Levels of Evaporation						
Temp.	Group	0	1	2	3	4	5	6
13.4°C	1	96.00	76.00	81.48	88.00	65.22	29.17	36.00
	2	87.50	96.00	78.26	86.96	68.00	62.50	41.67
	3	84.00	76.00	91.67	88.00	62.96	52.00	20.00
	4	84.00	86.36	96.00	82.61	56.00	48.00	14.82
17.0°C	1	95.65	88.00	92.00	84.00	79.17	64.00	45.45
	2	86.96	92.00	91.67	88.00	82.61	58.33	15.38
	3	100.00	95.65	100.00	96.00	76.00	86.36	27.22
	4	92.00	100.00	75.00	80.00	75.00	62.50	20.83

TRANSFORMATION OF PERCENTAGES TO DEGREES

		Levels of Evaporation						
Temp.	Group	0	1	2	3	4	5	6
13.4°C	1	78.5	60.7	64.5	69.7	53.8	32.7	36.9
	2	69.3	78.5	62.2	68.8	55.6	52.2	40.2
	3	66.4	60.7	73.2	69.7	52.4	46.1	26.6
	4	66.4	68.3	78.5	65.3	48.4	43.9	22.6
17.0°C	1	78.0	69.7	73.6	66.4	62.8	53.1	42.4
	2	68.8	73.6	73.2	69.7	65.3	49.8	23.1
	3	90.0	78.0	90.0	78.5	60.7	68.3	31.4
	4	73.6	90.0	60.0	63.4	60.0	52.2	27.2

TABLE IV (c)

(Continued)

TABLE OF TREATMENT TOTALS

	Levels of Evaporation								
Temp.	0	1	2	3	4	5	6	Σ	$\bar{\bar{x}}$
13.4°C	280.6	268.2	278.4	273.5	210.2	174.9	126.3	1612.1	57.575
17.0°C	310.4	311.3	296.8	278.0	248.8	223.4	124.1	1792.8	64.028
Σ	591.0	579.5	575.2	551.5	459.0	398.3	250.4	3404.9	
$\bar{\bar{x}}$	73.875	72.438	71.900	68.938	57.375	49.788	41.733		60.80

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Treatments	13	12861.51	989.35	16.70	0.1%
Temp.	1	583.08	583.08	9.84	1%
Evap.	6	11992.50	1999.88	33.75	0.1%
T x E	6	285.93	47.66	-	NS
Residual	41	2429.68	59.26		
Total	54	15291.19			

Min. diff. for signif. between temperature means : 1% level = 5.563
0.1% level = 7.305

Min. diff. for signif. bet. means of levels of evap. : 5% level = 7.777
1% level = 10.405
0.1% level = 13.664

EMERGENCE OF LARVAE

	Levels of Evaporation						
Temp.	0	1	2	3	4	5	6
13.4°C	70.15	67.05	69.60	68.38	52.55	43.72	31.58
17.0°C	77.60	77.82	74.20	69.50	62.20	55.85	31.02

Min. diff. for signif. : 5% level = 11.00
1% level = 14.72
0.1% level = 19.33

TABLE V

PERCENTAGE EMERGENCE OF LARVAE IN LABORATORY EXPERIMENT 3, 1953

	Levels of Evaporation							
Group	0	1	2	3	4	5	6	7
1	96	88	67	50	40	42	12	12
2	95	84	61	55	56	48	12	17
3	94	80	70	60	38	48	12	20
4	94	76	65	58	36	47	16	32

TRANSFORMATION OF PERCENTAGE TO DEGREES

	Levels of Evaporation									
Group	0	1	2	3	4	5	6	7	Σ.	$\bar{x}$
1	78.5	69.7	54.9	45.0	39.2	40.4	20.3	20.3	368.3	46.0
2	77.1	66.4	51.4	47.9	48.4	43.9	20.3	24.4	379.8	47.5
3	75.8	63.4	56.8	50.8	38.1	43.9	20.3	26.6	375.7	47.0
4	75.8	60.7	53.7	49.6	36.9	43.3	23.6	34.4	378.0	47.3
Σ	307.2	260.2	216.8	193.3	162.6	171.5	84.5	105.7	1501.8	
$\bar{x}$	76.8	65.1	54.2	48.3	40.7	42.9	21.1	26.4		

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	P.
Levels of Evap.	7	9670.34	1381.48	0.1%
Error	24	288.95	12.04	
Total	31	9959.29		

TABLE VI

ANALYSIS OF DATA FROM FIELD EXPERIMENT WITH LARVAE, 1951

Zero counts replaced by ¼ and figures transformed to degrees

Pasture	Block	50	100	250	500	1000	Total
Unmown	I	25.10	20.27	16.43	13.69	13.18	88.67
	II	14.18	25.10	19.91	12.92	10.63	82.74
	III	30.66	14.18	16.85	11.54	12.39	85.62
	IV	16.43	16.43	13.69	17.26	11.83	75.64
	Σ	86.37	75.98	66.88	55.41	48.03	332.67
Mown	I	26.56	21.13	20.96	15.34	13.69	97.68
	II	4.05	9.98	13.18	9.28	8.33	44.82
	III	16.43	15.34	13.69	15.79	13.81	75.06
	IV	4.05	9.98	8.91	14.18	4.80	41.92
	Σ	51.09	56.43	56.74	54.59	40.63	259.48
Total		137.46	132.41	123.62	110.00	88.66	592.15
	$\bar{\bar{x}}$	17.18	16.55	15.45	13.75	11.08	

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Blocks	3	297.5886	99.1962	2.10	NS
Pasture	1	133.9194	133.9194	2.80	NS
Error (a)	3	142.8465	47.6155		
Total (a)	7	574.3545			
Egg level	4	192.7294	48.1823	2.59	$<7\%, >6\%$
Interaction	4	89.2223	22.3056	1.20	NS
Error (b)	24	445.3065	18.5544		
Total (b)	39	1301.6127			

Block Totals :

I 186.35
II 127.56
III 160.68
IV 117.56

TABLE VII

ANALYSIS OF DATA FROM FIELD EXPERIMENT WITH LARVAE, 1952

Zero counts replaced by ¼ and figures transformed to degrees

		Egg Levels				
Pasture untouched	Block	150	300	450	600	Total
	1	2.29	4.66	1.28	2.36	10.59
	2	2.29	3.29	6.55	6.29	18.42
	3	2.29	4.66	2.69	1.15	10.79
	4	6.55	7.27	6.02	8.53	28.37
	5	8.13	5.74	3.80	6.55	24.22
	6	8.13	1.62	6.02	2.36	18.13
	7	6.55	10.47	4.69	4.69	26.40
	Σ	36.23	37.71	31.05	31.93	136.92
Pasture modified	1	2.29	1.62	1.28	1.15	6.34
	2	2.29	1.62	4.69	1.15	9.75
	3	6.55	1.62	6.02	5.74	19.93
	4	2.29	3.29	5.38	3.29	14.25
	5	2.29	1.62	8.13	1.15	13.19
	6	2.29	6.55	6.02	4.05	18.91
	7	2.29	3.29	1.28	4.69	11.55
	Σ	20.29	19.61	32.80	21.22	93.92
	Total	56.52	57.32	63.85	53.15	230.84

Block Totals:

1	16.93
2	28.17
3	30.72
4	42.62
5	37.41
6	37.04
7	37.95

TABLE VII
(Continued)

2-WAY TABLE

Egg Level	Pasture: Untouched	Pasture: Modified	Σ	Blocks: 1	2	3	4	5	6	7	Σ
150	36.23	20.29	56.52	4.58	4.58	8.84	8.84	10.42	10.42	8.84	56.52
300	37.71	19.61	57.32	6.28	4.91	6.28	10.56	7.36	8.17	13.76	57.32
450	31.05	32.80	63.85	2.56	11.24	8.71	11.40	11.93	12.04	5.97	63.85
600	31.93	21.22	53.15	3.51	7.44	6.89	11.82	7.70	6.41	9.38	53.15
Σ	136.92	93.92	230.84	16.93	28.17	30.72	42.62	37.41	37.04	37.95	230.84

Pasture	Block: 1	2	3	4	5	6	7	Σ	$\bar{x}$
Untouched	10.59	18.42	10.79	28.37	24.22	18.13	26.40	136.92	19.56
Modified	6.34	9.75	19.93	14.25	13.19	18.91	11.55	93.92	13.42
Σ	16.93	28.17	30.72	42.62	37.41	37.04	37.95	230.84	

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Blocks	6	54.949	9.158	1.885	NS
Treatment – Pasture	1	33.018	33.018	6.798	<2%, >1%
Treatment – Egg level	3	4.290	1.430	-	NS
Treatment – P x E	3	16.944	5.648	1.163	NS
Error	42	204.003	4.857		
Total	55	313.204			

TABLE VIII

LENGTH OF LIFE OF NEWLY-EMERGED LARVAE AT CONSTANT TEMPERATURES AND 100% RELATIVE HUMIDITY

(with soil)

Temperature (°C)	Length of Life (hours)	Mean Length of Life
25.2	384	38.4
20.8	432	43.2
16.9	528	52.8
12.8	736	73.6

Min. diff. for signif. : 5% level 10.7
1% level 14.5
0.1% level 19.2

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Temperature	3	7296.0	2432.00	8.77	0.1%
Error	36	9984.0	277.33		
Total	39	17280.0			

TABLE IX

LENGTH OF LIFE OF NEWLY-EMERGED LARVAE AT CONSTANT TEMPERATURES AND 100% RELATIVE HUMIDITY

(without soil)

Temperature (°C)	Length of Life (hours)	Mean Length of Life
25.2	2900	23.2
20.8	4884	38.7
16.9	6220	49.8
12.8	8492	67.9
9.8	9708	77.7

Min. diff. for signif. : 5% level 9.0
1% level 11.9
0.1% level 16.6

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Temperature	4	239133.0	59783.0	45.0	0.1%
Error	620	823447.0	1328.0		
Total	624	1062580.0			

TABLE X

MEAN SURVIVAL PERIOD OF FIRST-INSTAR, UNFED LARVAE IN

LABORATORY EXPERIMENT 3, 1950

(Survival period in logs)

Temperature

Temperature and S.D. / Group	N	25.2°C				20.8°C			
		0.51	1.78	2.79	3.56	0.51	1.78	2.79	3.5[illegible]
1	25	1.3258	1.3059	1.2939	1.1783	1.3199	1.5685	1.3527	1.3[illegible]
2	40	1.1154	1.3610	1.0677	1.2182	1.0080	1.2519	1.0405	1.0[illegible]
3	20	1.0096	1.0833	0.9877	1.0999	1.3296	1.0427	1.0687	1.0[illegible]
4	20	1.0942	1.0465	1.0666	0.8462	1.1733	1.3016	1.3186	1.1[illegible]

2-WAY TABLES

S.D.	Temperature 25.2°	20.8°	12.8°C	ε	Group 1	2	3	4
0.51	4.5450	4.8308	6.0468	15.4226	4.3839	3.4568	3.8091	3.77[illegible]
1.78	4.7967	5.1647	5.6435	15.6049	4.4690	3.9160	3.5638	3.65[illegible]
2.79	4.4159	4.7805	5.5870	14.7834	4.1917	3.3895	3.3571	3.84[illegible]
3.56	4.3426	4.6511	5.5473	14.5410	4.0237	3.7002	3.4613	3.35[illegible]
ε	18.1002	19.4271	22.8246	60.3519	17.0683	14.4625	14.1913	14.62[illegible]

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.	P.
Temperature (T)	2	0.7422	0.3711	53.01	0.1%
Saturation Deficit (SD)	3	0.0643	0.0214	3.06	<6%,>5%
Group (G)	3	0.4439	0.1479	21.13	0.1%
T x SD	6	0.0413	0.0069	-	NS
T x G	6	0.1275	0.0213	3.04	<4%,>3%
SD x G	9	0.1174	0.0130	1.86	NS
Error	18	0.1264	0.0070		
Total	47	1.6630			

Saturation Deficit x Group

12.8°C			
0.51	1.78	2.79	3.56
1.7382	1.5946	1.5451	1.5233
1.3334	1.3031	1.2813	1.3849
1.4699	1.4378	1.3007	1.3162
1.5053	1.3080	1.4599	1.3229

		Temperature			
Σ	Group	25.2°	20.8°	12.8°C	Σ
15.4226	1	5.1039	5.5632	6.4012	17.0683
15.6049	2	4.7623	4.3975	5.3027	14.4625
14.7834	3	4.1805	4.4862	5.5246	14.1913
14.5410	4	4.0535	4.9802	5.5961	14.6298
60.3519	Σ	18.1002	19.4271	22.8246	60.3519

SUBDIVISION OF T x G INTERACTION

		Degrees of Freedom	S.S.	M.S.	V.R.	P.
(1)	Temp. x (Group 2 vs. Others)	2	0.0997	0.0498	7.11	1%
	Remainder	4	0.0278	0.0069	-	NS
			0.1275			
(2)	Temp. x (Group 4 vs. Others)	2	0.0599	0.0299	4.27	5%
	Remainder	4	0.0676	0.0169	2.41	NS
			0.1275			
(3)	Temp. x (Group 1 vs. Others)	2	0.0034	0.0017	-	NS
	Remainder	4	0.1241	0.0310	4.43	2%
			0.1275			